Plant Parasitic Nematodes in Subtropical and Tropical Agriculture

M. LUC, R.A. SIKORA & J. BRIDGE

C · A · B INTERNATIONAL
Institute of Parasitology

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This book is a comprehensive account of the important plant parasitic nematodes of crops in subtropical and tropical agriculture. It is an authoritative resource book for agriculturists, researchers, teachers and students, particularly those working in tropical regions where sustainable agriculture is the goal. It covers the major food and cash crops (rice and other cereals, root and tubers, food legumes, vegetables, peanut, citrus and other fruit trees, coconut and other palms, coffee, tea, cocoa, bananas, sugarcane, tobacco, pineapple, cotton and other fibres, and spices) in sixteen chapters. Information is given on the distribution, symptoms of damage, biology, disease complexes, economic importance, damage threshold levels, control and methods of diagnosis for the different nematodes. The book also includes other chapters on the biology and morpho-anatomy of the main nematode genera, the extraction and processing of nematodes, crop loss assessment methods and host-parasite relationships.

The extensive information provided in the book by experienced nematologists is supported by abundant illustrations, including sixteen pages of colour plates, making this an invaluable, practical manual of subtropical and tropical nematology.

THE EDITORS

Michel Luc Michel Luc has spent all his career at ORSTOM; firstly in 1951 as plant pathologist in ORSTOM Centre of Adiopodoumé (Ivory Coast). He then turned to nematology and established, at the same place, the first nematology laboratory in West Africa. He did large nematode surveys in Ivory Coast and surrounding areas, Madagascar, etc., where little or no information was available on nematodes. His eighteen-year career in Ivory Coast ended with six years as Director of the Centre, the most important of ORSTOM. Then he established a nematology laboratory in Dakar (Senegal), devoted to subsahelian areas, where he worked for a five-year period. In both these laboratories, he developed teams of researchers and technicians, promoted research programmes, etc. Since 1975 he has been based in the Paris Muséum working on taxonomy of plant parasitic nematodes. He was the founder and inspiration of the *Revue de Nématologie*, and has directed and guided it to its premier position amongst plant nematology journals. He is Doctor *honoris causa* of University of Neuchâtel (Swiss) and Chevalier dans l'Ordre National du Mérite.

Richard A. Sikora Richard Sikora has headed nematology in the Institut für Pflanzenkrankheiten of the University of Bonn, Germany since 1971. He received his BS and MS degrees in zoology and botany at Eastern Illinois University where he specialized in helminth physiology. In 1967 he began research on complex disease interrelationships at the University of Illinois in Urbana, completing his PhD in 1970. He has worked in Africa, the Middle East, South and South East Asia and the Pacific, tropical and subtropical countries, mainly for the German Gesellschaft für Technische Zusammenarbeit (GTZ), but also for USAID, and a number of international centres. Most of his experience deals with problems associated with food legumes and vegetable crops, where his research interests include complex disease interrelationships, integrated pest management and biological control.

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He graduated in Botany from the University of Hull in 1965, took an MSc in Plant Pathology at McGill University in 1966, and completed his PhD in nematology at Imperial College in 1970. He has worked continually on tropical nematology since that date.

His work on the tropical nematodes of a wide range of crops has taken him to many countries in Africa, South and Central America, the Middle East, South and South East Asia and the Pacific.

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C·A·B International
Institute of Parasitology

Published on behalf of:
C A B International Institute of Parasitology

by

C·A·B International
Wallingford
Oxon OX10 8DE
UK

Tel: Wallingford (0491) 32111
Telex: 847764 (COMAGG G)
Telecom Gold/Dialcom: 84: CAU001
Fax: (0491) 33508

British Library Cataloguing in Publication Data
Plant parasitic nematodes in subtropical and tropical agriculture
1. Tropical regions. Crops. Pests. Roundworms
I. Luc, M (Michel), II. Sikora, R. A. (Richard A.)
III. Bridge J. (John)
632'.65182

ISBN 0–85198–630–7

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Phototypeset by Input Typesetting Ltd, London
Printed in the UK by Cambrian Printers Ltd, Aberystwyth

TO

MARIETTE, INGRID AND MONICA

Editorial Note

"Plant Parasitic Nematodes of Subtropical and Tropical Agriculture" was conceived as a truly practical book for use by agriculturists, researchers, teachers, students and extension workers. The book covers the major economically important crops of the subtropics and tropics and their main nematode parasites. The aim was not simply to produce an encyclopaedia of nematode associations with the crops but to concentrate on those nematode species which have been shown to cause yield loss.

It is hoped that readers will find that the relevant information necessary for work on plant nematode parasites is readily available in these chapters, which were designed specifically to meet these requirements. The authors were selected for their practical expertise. In the crop chapters, authors from different parts of the world, and with experiences in different types of agriculture, were invited to present as wide a span of knowledge as possible. We are extremely grateful for the full cooperation given by the authors and for the overall high standard of the chapter contributions. We regret that we have had to restrict the size of contributions, in many cases omitting very interesting passages, in order to ensure that the book was produced as a single volume.

Contents

Preface

The science of plant nematology developed dramatically from 1950 to the present day. Progress was founded, in part, on the availability of excellent texts on plant parasitic nematodes. This text, focusing on those nematodes affecting crop plants grown in tropical and subtropical regions of the world, is the first volume addressing tropical nematology to be published in more than 20 years.

Drs. Richard A. Sikora, Michel Luc and John Bridge conceived the idea for this book at the 1986 ESN meeting in Antibes, France, and the proposal gained further momentum when Peter Gooch of C.A.B. International offered his support for publication. At the first editorial meeting in Bonn, Germany, January 12–14, 1987, the overall goals, chapter outlines and general style of the book were formulated. Additional editorial meetings were held in Paris and St. Albans and a workshop for authors of the chapters was conducted in August, 1988, at the German Physic Centre in Bad Honnef.

A unique feature of this treatise is the collaboration of two or more authors in the writing of each chapter. The authors, deliberately chosen from different geographic areas, were selected on the basis of their having worked, often for many years, on particular crop/nematode combinations, for their hands-on experience, and for their understanding of the interactions among hosts, parasites, and the environment. This approach brings diversity, experience and knowledge to the discussions of each major crop and its associated nematode pests.

A noteworthy aspect of this volume is that the authors have taken into account the various ecological differences between the tropical and temperate regions of the world and have shown how and why different approaches to nematode management are necessary. Although losses due to nematodes can be great in almost any region of the world, they are especially severe in the tropical and subtropical regions which comprise most of the developing world and where severe shortages of food and fibre are prevalent.

Tropical and subtropical agriculture differs from that of temperate regions and growers must consider the many ecological differences when they decide on approaches to nematode management. Environmental factors affecting nematode development, reproduction, survival and ability to suppress crop production include temperature, rainfall, soil types, patterns of wet and dry seasons, local vegetation and sometimes the absence of distinct seasons in the tropics.

In the tropical and subtropical regions there are more weed hosts for many nematode species. In general, tropical and subtropical soils have lower organic matter and nutrient levels. There usually are more botanical plants per unit area in the tropics than in temperate regions and cultural practices vary greatly. The target nematode genera and species will also vary, although several important genera are common to both tropical and temperate regions.

In this volume, the authors have delineated those nematode problems which have the greatest economic impact on the particular crops grown in the tropical and subtropical regions. With this information, knowledgeable administrators can facilitate allocation of their available resources to the development and employment of management tactics most appropriate for those nematodes which are judged to be most serious.

The opening chapters constitute a theoretical and practical initiation to nematology. These chapters on morphology, methods, and techniques for determining the impact of nematodes on crop growth are augmented by indexes, and a section of high quality colour plates showing symptoms of damage.

Altogether they comprise an invaluable handbook which can be used even by scientists with little practical experience of nematodes.

The editors, authors and publisher are to be commended for producing this valuable and timely volume on nematode problems in the tropics. They are providing an authoritative resource book for agriculturists and all plant nematologists, especially for those working in tropical regions, where sustainable agriculture is the goal. While there are many constraints to economic production of food and fibre crops in most developing countries, this volume will greatly enhance the ability of scientists whose responsibility it is to minimize the damage caused by plant nematodes.

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Acknowledgements

We are pleased to acknowledge the financial support given to us in the preparation of this book by the following organisations:

Technical Centre for Agriculture and Rural Co-operation (CTA), Netherlands. (CTA was established under the Lomé Convention between the EEC and ACP states, and their mandate is the dissemination of information on agriculture and rural development to ACP countries.)

Fonds der Chemischen Industrie (FCI) in cooperation with the Bundesministerium für Forschung und Technologie (BMFT), Fed. Rep. Germany.

Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) Gmbh, Fed. Rep. Germany.

Overseas Development Administration (ODA), UK.

Institut Française de Recherche Scientifique pour Le Développement en Coopération (ORSTOM), France.

In addition to these organisations that have supported the endeavour financially, we would also like to thank the many colleagues and individuals who have helped, advised and encouraged us during its production. We would particularly like to thank Peter Gooch of CAB International who suffered many discomforts and overcame many difficulties on our behalf. We also wish to thank the staff of CABI Institute of Parasitology especially Gill Kaser and Ann Hall who painstakingly typed and re-typed many of the chapters, Berit Pedersen who provided bibliographic information, and Richard Tranfield for photographic work.

Introduction

Reflections on Nematology in Subtropical and Tropical Agriculture

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Nematologist ORSTOM, Muséum national d'Histoire naturelle, Laboratoire des Vers, 61 rue de Buffon, 75005 Paris; C.A.B. International, Institute of Parasitology, 395a Hatfield Road, St Albans AL4 0XU, England; and Institut für Pflanzenkrankheiten der Rhein. Friedrich – Wilhelms – Universität, Nussallee 9, 5300 Bonn 1, German Federal Republic.

If the birth of nematology in temperate areas can be dated to 1743 with the observations by Needham of the wheat seed gall nematode or "ear cockle eelworm", nematology in the tropics was initiated at a much later date.

The first tropical nematodes were described from Oceania during the late 19th and beginning of the 20th century. Cobb (1891) reported finding nearly 30 species in banana soil and plant tissues from Fiji; among them, he described (Cobb, 1893) several new species, such as *Radopholus similis* and *Helicotylenchus multicinctus*, now well known, even though their names have changed from the original descriptions. Species now known as *Meloidogyne javanica* and *Hirschmanniella oryzae* were identified at an early date from Java, Indonesia, by Treub (1885) and by van Breda de Haan (1902), respectively. Few records are available for this period from other parts of the tropics, a notable exception being the description of the genus *Meloidogyne*, and its type species *M. exigua*, on coffee trees in Brazil by Göldi (1889, 1892); following an earlier report from Jobert (1880), he made an extensive study of the nematode problem in coffee plantations.

In the following four or five decades, nearly all descriptions of tropical nematode species were done in laboratories in temperate countries, particularly in the USA by Cobb, Steiner and Thorne, in England by T. Goodey and J.B. Goodey and in the Netherlands by Schuurmans Stekhoven. Observations and experiments based on field work were rare in countries outside the temperate regions until the 1950's. Two other exceptions were firstly, the study of red ring disease of coconuts in the Caribbean by Nowell (1919, 1920) who established that a nematode was the cause of the disease and instigated further work in the area; and secondly, some outstanding field work by Butler (1913, 1919) in East Bengal (Bangladesh) who identified ufra disease of rice and described its causal organism, *Ditylenchus angustus*. One other finding in the early part of this century which was to have a profound effect on nematology was the discovery in 1935 of a serious nematode parasite in the pineapple fields of Hawaii, later to be described by Linford and Oliveira (1940) as *Rotylenchulus reniformis*. This led, in the early 1940's, to the discovery of the first effective nematicidal soil fumigant, D-D (1,2-dichloropropane, 1,3-dichloropropene) from work done at the Pineapple Research Institute, Hawaii. Notwithstanding these and other evident successes, the amount of

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nematological work in the tropics was very meagre in the first half of this century. For example, when the first nematology laboratory was established in West Africa (by ORSTOM in the Ivory Coast) in 1955, there were only nine published references relating to plant parasitic nematodes found in the whole of West Africa and Zaire.

Nematology laboratories have now been established in many, but by no means all, subtropical and tropical countries, especially in Africa, South America and India. Up to 1983, 278 scientists working on nematodes in the tropics were recorded (Thomason *et al.*, 1983) not including those in India or Pakistan, nor in the semi-arid regions. We would estimate that there are now at least 400 scientists working full or part-time on the nematode problems and in the areas to which the present book is devoted. Most editions of all the nematological journals now contain a number of articles dealing with nematodes or nematological problems from outside the temperate regions, and some journals (Nematropica, Indian Journal of Nematology, Pakistan Journal of Nematology) deal almost exclusively with such work.

Nematology laboratories established comparatively recently in the tropical regions have had to look afresh at nematode problems. Often they have needed to determine initially which problems exist by basic survey work, and accurately identify which nematodes are present (determination systematics), followed by establishing which nematodes are harmful or economically important by pathogenicity tests and field trials, and finally deciding on which treatments or methods are appropriate for control of nematodes. It has been, and continues to be, a long and difficult task and, if many problems are now rather well known, few of them have been fully solved. This is not surprising if we consider that over the past century, approximately 100 nematologists have worked in temperate countries on the problems caused by the potato and sugarbeet cyst nematodes, and satisfactory results, with the bias on integrated control, have been obtained only recently. It is therefore, safe to predict that the future for subtropical and tropical nematology will be long and full of complex and economically important problems especially with regards to subsistence agriculture.

We have been referring to nematology in "temperate" compared to "subtropical and tropical" regions. It is appropriate here to raise the obvious questions of whether there are fundamental differences or whether they differ only in degrees because of the different species of nematodes and types of crop present?

We can state with some certainty and without too many dissenting voices that nearly all the major problems that can be directly caused by nematodes have been detected in temperate countries. This is not to say that a problem new to a particular country could not arise through the introduction and subsequent spread of a known nematode parasite from another temperate country. It is, therefore, the case in temperate countries that surveys are designed to determine the distribution of known nematodes causing known damage. In contrast, in the subtropical and tropical areas, new problems are being, and have yet to be, discovered involving new nematodes species and even genera, or species not previously recorded as harmful to a crop. Examples we can cite from comparatively recent publications are the "legume Voltaic chlorosis" of leguminous crops, discovered in Burkina Faso, associated with a new species, *Aphasmatylenchus straturatus*, and a genus not previously known to be a harmful parasite (Germani & Luc, 1982); "mitimiti" disease of taro (*Colocasia esculenta*) in the Pacific caused by a new species, *Hirschmanniella miticausa* (Bridge *et al.*, 1983); and, in the semi-arid areas, the new cyst species *Heterodera ciceri* causing damage to chickpeas and lentils (Greco *et al.*, 1984; Vovlas *et al.*, 1985). Also the lack of trained nematologists in the past has often meant a lack of awareness of the importance of nematology in the development of quarantine guidelines. This has led to the movement of both tropical and temperate plant parasitic species into new uninfested areas. Good examples in the past are the dissemination of the banana burrowing and root lesion nematodes (*Radopholus similis, Pratylenchus* spp.) and of the citrus slow decline nematode (*Tylenchulus semipenetrans*) to nearly all areas where these crops are grown. As a more recent case, we may cite the movement of *Globodera rostochiensis* into the high altitude tropical growing areas of the Philippines (Sikora, 1982).

There is a greater diversity of nematode genera and species in subtropical and tropical countries

than in temperate ones. As many of these nematodes are new taxa, it is evident that there is a great deal of work for nematode taxonomists in the tropics. This indeed is happening but a big disadvantage of concentrating on this aspect is that surveys are designed to collect nematodes and not to determine problems caused by nematodes. This is often the only possible means of establishing new nematology laboratories with limited staff and financial means. The danger is that such laboratories can limit their activities to systematics and so become production lines for new species and genera, to the exclusion of determining the importance of the nematode being described.

Knowing which nematode genera and species occur is the necessary first step, but establishing the pathogenicity of the nematodes involved in subtropical and tropical agriculture has to be made a main priority. Many nematodes are now recognized as serious or potentially serious pests of tropical crops, as detailed in the following chapters, but information on the *actual* yield losses caused by the nematodes in different situations and on different crops is still sadly lacking for a large proportion of these nematodes. This knowledge is essential to provide agricultural scientists, extension officers and administrators with the information needed to recommend practical and economic means of controlling the harmful nematodes in the face of all the other constraints on crop production. The chapters in this book contain pertinent information on nematodes of the most widely grown crops in subtropical and tropical agriculture but there are still gaps in our knowledge. The chapters show the extent of damage that can be caused by nematodes which is recognised by the nematologists concerned but generally not by other agriculturists. This crop damage by nematodes invariably remains hidden by the many other limiting factors operating in subtropical and tropical agriculture. Nematodes have rarely been considered or recognized as major limiting factors until all other constraints on yield increase have been removed (Bridge, 1978).

The practical problems of determining nematode pathogenicity in the tropics can often be far more difficult than in temperate countries. Problems such as maintaining controlled conditions in glasshouses or screenhouses with air-conditioning or cooling tanks because of the excessive heat can be a daunting and expensive task. The stories behind failure of field experiments are legendary in the tropical countries with everything from lizards to elephants and hurricanes to volcanoes doing their utmost to frustrate the attempts of nematologists to obtain accurate and replicated results. Isolated, irrigated field trials during the dry season tend to result in every hungry pest and predator for some distance around descending in droves on the plots with thanks to the irate research worker. It does mean that nematologists in the tropical countries have to be more resourceful and patient than their counterparts in the temperate countries.

There are more intrinsic differences between temperate and tropical areas based mainly on the wide diversity of nematode crops and agricultural systems.

The range and severity of parasitism on all living organisms, humans, animals and plants, is greater in the subtropical and tropical countries. Plant parasitic nematodes generally have shorter life cycles resulting in a more rapid population explosion than in temperate areas. For example, in temperate areas *Heterodera* spp. produce generally one or two generations per year, whereas *H. oryzae,* in West Africa, produces one generation every 25 days (Merny, 1966). More often than not a crop is attacked by a number of damaging nematodes. In temperate areas, there are also "secondary species" but most often there is only one main nematode parasite of a crop which is easily recognizable and upon which control efforts can be focussed. This is not the case for many tropical crops where a number of species of several different genera may be major parasites of a crop. For instance, sugar cane can be damaged by 10–20 different species of genera such as *Meloidogyne, Heterodera, Pratylenchus, Xiphinema* and *Paratrichodorus*. The component species of a nematode population do differ from country to country, making predictions of damage that much more difficult. Such types of multi-species populations have a number of consequences concerning control of the nematodes. Firstly, it can seriously hinder the establishment of an effective crop rotation as the host status of each crop will differ depending on the nematode species present. We have an example of such a phenomenon in Ivory Coast where *Crotalaria* was recommended as an intercrop to control *Meloidogyne* spp. on pineapple. The intercrop produced an effective control of the root-knot

nematodes but increased the populations of *Pratylenchus brachyurus* to levels which were at least as harmful to the crop as *Meloidogyne* spp. A second consequence is that multispecies populations increase the complexity of the search for crop resistance to nematodes; targeting one nematode species for resistance is normally not sufficient. The lesson of breeding for resistance to one species of nematode should have been learned with the emergence of the potato cyst nematode *Globodera pallida* following extensive planting of *G. rostochiensis* resistant cultivars.

The most fundamental facts of subtropical and tropical agriculture that differ from the temperate regions and markedly affect the study and control of plant nematodes are the crops grown, the cultural practices and the farming systems. Commercial, plantation crops are a common feature of subtropical and tropical agriculture but by far the largest proportion of cultivated land in most of the tropical countries is farmed by farmers with small-holdings, using traditional cropping practices. The crops grown cover a very wide range of grain, root and vegetable food crops, also many different cash and utility crops. Monocropping is practised but multiple or intercropping is more common. Much of the traditional agriculture in the tropics is based on the reproduction of crops by vegetative propagation, in contrast to the dependence upon seed-reproduced plants in the temperate countries. This can increase the dissemination of nematodes. The outstanding feature of traditional agriculture, and one that makes life difficult for nematologists, is the complexity of the methods involved (Bridge, 1987). In contrast, modern farming in temperate countries is comparatively simple and the study and control of the nematodes is also, in comparison, relatively straightforward. The many different farming systems operating in the tropics fall into four main categories: 1. shifting cultivation; 2. fallow farming; 3. permanent upland cultivation, and 4. systems with arable irrigation (Ruthenberg, 1983). In some of these farming systems, nematodes are less likely to be causing damage, in others the cultivation practices will greatly increase the risk of nematodes causing serious yield losses (Bridge, 1987).

The nematode control methods that can theoretically be employed in the subtropical and tropical countries differ little from those used in temperate countries but in practice they are more difficult to implement and need to be considerably modified in many circumstances. There will be obvious differences in the methods to control nematodes in developed countries compared to developing countries and in large, modern farms or plantations compared to small rural farms with more traditional cultivation systems.

Chemical soil treatment is recognized as an essential means of controlling nematodes on a number of cash crops in the tropics. In many instances these crops cannot be grown economically without the use of nematicides. The use of nematicides and pesticides to control nematodes is of limited or no importance on most field crops especially at the subsistence level in developing countries. Nematicide usuage in the past has been strongly limited by their high price. The choice and availability of many nematicides is now even more limited with the banning on most of the world markets of the fumigants D-D, EDB and DBCP. Some of the more easily applied granular, non-volatile nematicides are effective and are used extensively on a number of crops. They have disadvantages in being expensive and extremely toxic to man and animals when used improperly. Their availability may be further curtailed because of their recent detection in groundwater. The future of nematicides for the control of nematodes will depend on the formulation of new compounds that are effective and environmentally safe. The development of new application technology, for example, treatment by seedcoating or chemicals applied to irrigation water as well as development of systemic nematicides that move basipetally, is urgently needed (Thomason, 1987).

The modification of existing agricultural practices in order to control nematode populations is one of the most acceptable alternatives to chemical control for both the small and large scale farmers in the tropics. Crop rotation can vary from non-existent, where there is continuous cultivation of a susceptible crop or crops, through what can be termed random rotation, to a relatively sophisticated form of rotation. However, most of the rotation schemes in operation have been designed to prevent disease outbreaks or increase available nutrients, and are not always compatible with nematode control. With an understanding of the nematodes involved and the accepted cropping systems,

modifications can be made to produce effective control by rotation of crops. Many other cultural methods, apart from rotation, can be used and are outlined in the following chapters.

Resistant cultivars can produce the most dramatic increases in the yields of many crops and appear to hold the solution to most nematode problems, particularly with the recent increase in research on gene transfer. Unfortunately, this solution is more apparent than real as it is now clear that such cultivars mainly show resistance to only a limited number of nematode genera. These nematodes tend to belong to the groups of parasites, such as the Heteroderidae, which have a highly developed host-parasite relationship where cell modification occurs and is required for successful reproduction of the nematodes (Luc & Reversat, 1985). Many of the major subtropical and tropical plant parasitic nematodes belong to the group of migratory endoparasites which cause cell destruction without modifying the host tissues. Examples are to be found in the genera *Radopholus, Pratylenchus, Hirschmanniella, Scutellonema, Helicotylenchus* and *Hoplolaimus*. At the present time, no true resistance has been found for this group of nematodes. Even when the possibility does exist, for nematodes such as *Heterodera, Meloidogyne* and *Rotylenchulus*, such research nevertheless remains aleatory and very costly: many years and several millions of US dollars were necessary to obtain a cultivar of soybean resistant to *Heterodera glycines* (Miller, pers. comm.). A major limiting factor affecting the effectiveness of newly introduced resistant cultivars is the selection of pathotypes or races that are able to breakdown the resistance. The existence of resistant breaking pathotypes are major problems in breeding programmes in temperate crops. Similar complications must be expected when resistant cultivars are bred for tropical crops. Another difficulty which applies more to subtropical and tropical countries is in the practical introduction of these resistant cultivars. Where resistant cultivars are available and suited to the conditions prevailing in a country, many other factors have to be taken into account before their successful introduction. There will be again a marked contrast in what can be achieved with the big producer compared to the rural farmer, but consideration has to be given to local needs. A good illustration of this difficulty was when dwarf rice cultivars were introduced to prevent lodging (Mydral, 1974): people in South East Asia were deprived of their normal source of rice straw for animal feed, bedding, and thatching material. Because of economic constraints, research in nematode management in the tropics often focuses on low-input methods involving crop rotations, multicropping, adjustment of planting and harvest dates, use of various soil amendments and mulches, trap and antagonistic crops, fallow, flooding, etc. Emphasis on these forms of control strategies by agricultural scientists working in the tropics and subtropics reflects increased awareness of the need for nematode management systems that rely less on use of nematicides.

We have outlined some of the differences and difficulties facing nematology in the tropics but wish to emphasize that none of the problems are insurmountable with the appropriate effort, expertise and backing. You will see, reading through the chapters, that there is a great deal of accumulated knowledge on the importance of nematodes as plant parasites and, more relevantly, there are successes in their control. However, nematology in the tropics is underfunded and there is a shortage of nematologists to work on the problems. Sasser and Freckman (1987) have estimated that less than 0.2% of the crop value lost to nematodes worldwide is used to fund nematological research to combat these losses which probably exceed $100 billion annually. The percentage funding for nematological research in the tropics is considerably less than it is in most of the temperate countries, which makes the amount infinitesimal. But the need for such research in subtropical and tropical agriculture is greater than in temperate agriculture. Many temperate countries are suffering the embarassment of massive surpluses in food production which are not transferable. In contrast, the majority of countries in the tropics have shortfalls in the production of most crops. An increase is needed in food crops, to improve the nutritional level of the populations, and in export cash crops, to obtain essential foreign currency. Solving nematode problems can play an important part in improving crop yields to the benefit of commercial and subsistence farms, the consumers and governments.

This book details our present knowledge on plant parasitic nematodes associated with the main

crops grown in subtropical and tropical agricultural systems. It also includes nematodes of warm temperate crops growing in semi-arid regions and those of crops growing in high altitude, temperate regions of the tropics. The presentations are by some of the most experienced nematologists from both the developed and developing countries who have worked in full cooperation to present a practical and informative guide to the nematodes found in these areas. The book is by no means aimed solely at nematologists but is designed to provide up-to-date information on the nematodes for all people working in agriculture, whether they be crop protection specialists, agronomists, economists or administrators.

References

Bridge, J. (1978). Agricultural aspects – Comments and discussion I. In: Taylor, A.E. & Muller, R. (Eds). *The Relevance of Parasitology to Human Welfare Today*. Oxford, Blackwell Scientific Publications: 111–117.

Bridge, J. (1987). Control strategies in subsistence agriculture. In: Brown R. & Kerry, B.A. (Eds) *Principles and practice of nematode control in crops*. Melbourne, Australia, Academic Press: 389–420.

Bridge, J., Mortimer, J.J. & Jackson, G.V.H. (1983). *Hirschmanniella miticausa* n. sp. (Nematoda: Pratylenchidae) and its pathogenicity on taro (*Colocasia esculenta*). *Revue de Nématologie*, 6:285–290.

Butler, E.J. (1913). Diseases of rice. *Bulletin of the Agriculture Research Institute, Pusa, India,* 34:40 p.

Butler, E.J. (1919). The rice worm (*Tylenchus angustus*) and its control. *Memoirs of the Department of Agriculture of India,* 10:1–37.

Cobb, N.A. (1891). Diseased banana plants. *Agricultural Gazette of New South Wales*, 2:622–624.

Cobb, N.A. (1893). Nematodes, mostly Australian and Fijian. *McLeay Memorial Volume, Linnean Society of New South Wales*: 252–308.

Germani, G. & Luc, M. (1982). Etudes sur la chlorose voltaïque des légumineuses due au nématode *Aphasmatylenchus straturatus* Germani. 1 & 2. *Revue de Nématologie*, 5:139–146 & 161–168.

Göldi, E.A. (1889). Der Kaffeenematode Brasiliens (*Meloidogyne exigua* G.). *Zoologische Jahrbücher, Abt. Systematik,* 4:261–267.

Göldi, E.A. (1892). Relatório sobre a moléstia do cafeeiro na província do Rio de Janeiro. *Archivos Museo nacional de Rio de Janeiro,* 8 (1887):1–121.

Greco, N., Di Vito, M., Reddy, M.V. & Saxena, M.C. (1984). A preliminary report of survey of plant-parasitic nematodes of leguminous plants in Syria. *Nematologia mediterranea,* 12:87–93.

Jobert, C. (1880). [Maladie du caféier au Brésil.] *Comptes-rendus des Séances de la Société de Biologie,* 6ème série, 5:360–361.

Linford, M.B. & Oliveira, J.M. (1940). *Rotylenchulus reniformis*, nov. gen., nov. sp., a nematode parasite of roots. *Proceedings of the helminthological Society of Washington,* 7:35–42.

Luc, M. & Reversat, G. (1985). Possibilités et limites des solutions génétiques aux affections provoquées par les nématodes sur les cultures tropicales. *Comptes-rendus des Séances de l'Académie d'Agriculture de France,* 71:781–791.

Merny, G. (1966). Biologie d'*Heterodera oryzae* Luc & Berdon, 1961. II. Rôle des massess d'oeufs dans la dynamique des populations et la conservation de l'espèce. *Annales des Epiphyties,* 17:445–449.

Mydral G. (1974). The transfer of technology to underdeveloped countries. *Scientific American,* 231:173–182.

Nowell, W. (1919). The red ring or "root" disease of coconut palms. *West Indies Bulletin,* 17:189–202.

Nowell, W. (1920). The red ring disease of coconut palms. Infection experiments. *West Indies Bulletin*, 18:74–76.

Ruthenberg H. (1983). *Farming Systems in the Tropics* (3rd ed). London, Oxford University Press, XX + 424 p.

Sasser, J.N. & Freckman, D.W. (1987). A world perspective on nematology: The role of the Society. In: Veech, J.A. & Dickson, D.W. (Eds). *Vistas on Nematology*, Hyattsville, U.S.A., Society of Nematologists Inc.: 7–14.

Sikora, R.A. (1982). *Globodera rostochiensis* on potato in the Philippines. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz,* 89:532–533.

Thomason, I.J. (1987). Challenges facing nematology: Environmental risks with nematicides and the need for new approaches. In: Veech, J.A. & Dickson, D.W. (Eds). *Vistas on Nematology*. Hyattsville, U.S.A., Society of Nematologists Inc., 469–476.

Thomason, I.J., Freckman, D.W. & Luc, M. (1983). Perspectives in nematode control. *Revue de Nématologie*, 6:315–323.

Treub, M. (1885). Onderzoekingen over sereh-zieh suikerriet gedaan in's Lands Plantentuin te Buitenzorg. *Mededeelingen's Lands Plantentuin (Buitenzorg)*, 2:1–39.

Van Breda de Haan, J. (1902). Een aaltjes-ziekte der rijst "omo mentek" of "omo-bambang". Voorlooping rapport. *Medeleelingen's Lands Plantentuin (Buitenzorg)*, 53:1–65.

Vovlas, N., Greco, N. & Di Vito, M. (1985). *Heterodera ciceri* sp. n. (Nematoda: Heteroderidae) on *Cicer arietinum* from Northern Syria. *Nematologia mediterranea*, 13:239–252.

Chapter 1

Morphology, Anatomy and Biology of Plant Parasitic Nematodes – a Synopsis

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Nematodes successfully colonize a greater variety of habitats than any other group of multicellular animals. They are found in all oceans; from the polar regions to the equator, from the litoral zone to the abyssal depths; they colonize freshwater lakes, rivers and marshes and all types of soil from the antarctic to the tropics; they parasitize most groups of animals, including other nematodes, and a wide variety of algae, fungi and higher plants. However, despite such ecological diversity they are surprisingly similar in structure.

A very brief, simplified account[1] of the basic morphology, anatomy and bionomics of plant parasitic nematodes forms the first part of this chapter and is followed by illustrated descriptions concentrating on the diagnostic features of the most commonly occurring and/or most important plant parasitic genera referred to in the corpus of the book, together with other pertinent data.

Morpho-Anatomy of the Plant Parasitic Nematodes

Plant parasitic nematodes can be divided into three major groups: the tylenchs (including tylenchids and aphelenchids); the longidorids; and the trichodorids (see: Outline Classification, p. 9). The tylenchs are the most numerous and the most important on a world scale and so will be dealt with in greatest detail.

Tylenchs (Fig. 1 A-J)

Tylenchs are vermiform animals, usually ranging from 0.2 to 1 mm long, but occasionally over 3mm. In some genera the female loses the vermiform shape and becomes obese or even globose.

The head end or **labial region**, when seen *en face* (Fig. 1C), is typically hexaradiate and has a central orifice, the mouth, through which the **stylet** is protruded. Various sensory structures, including

ormation on nematode morpho-anatomy and biology can be found in: Dropkin, V. H. (1980) *Introduction to plant* New York, John Wiley & Sons, XIV + 293 p. Maggenti, A. M. (1981) *General nematology*. New York, Springer + 372 p.

n, excellent illustrated descriptions of various plant and insect parasitic nematodes, together with data on biology, d classification can be found in: Siddiqi, M. R. (1986) *Tylenchida Parasites of Plants and Insects*. Farnham Royal, nwealth Agricultural Bureaux, ix + 645 p.

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

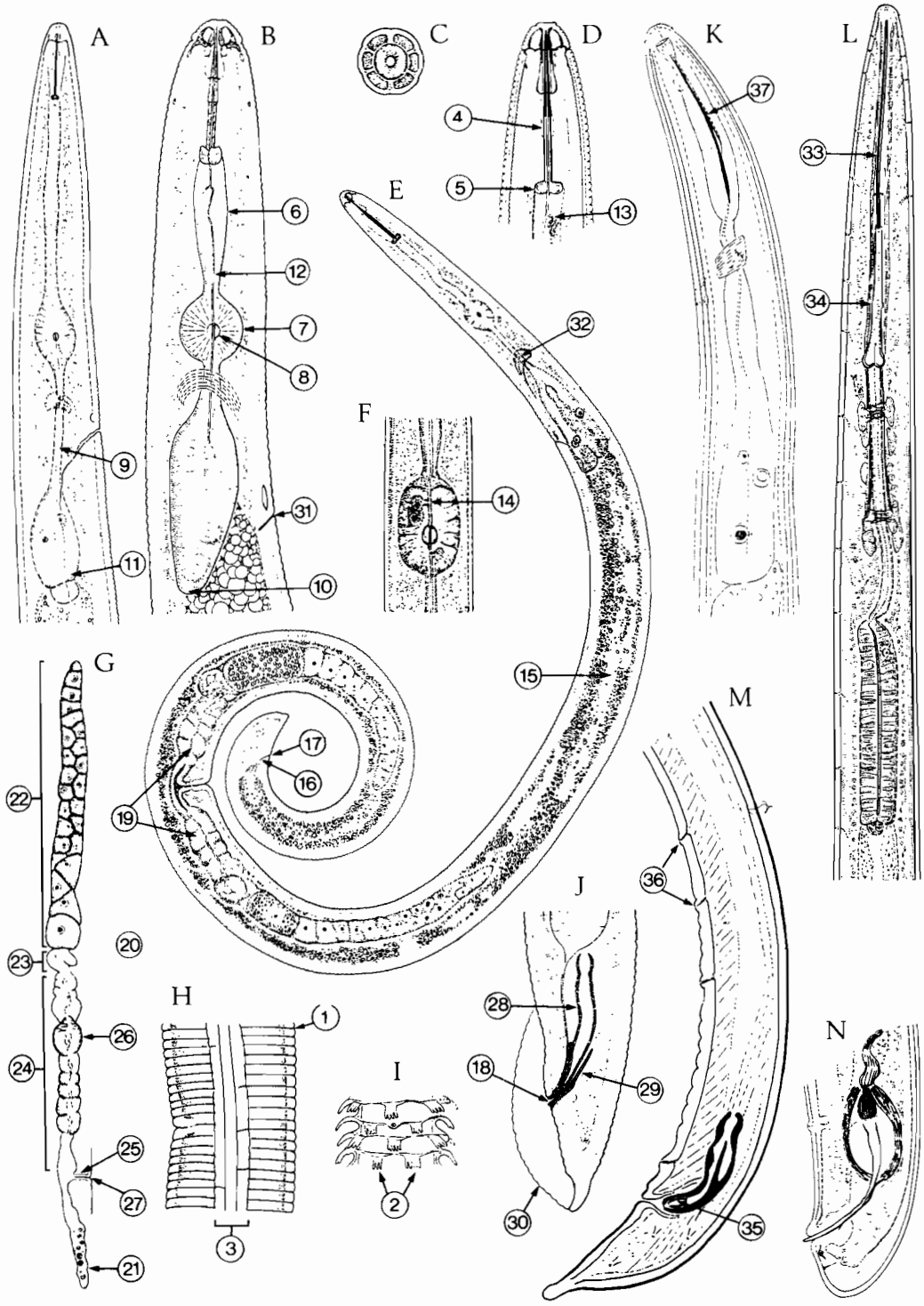


Fig. 1. Major diagnostic features of plant parasitic nematodes.

the **amphids**, occur on the head which is often transversely annulated and usually separated from the body by a constriction. Internally the head contains a sclerotized **framework** (or skeleton) to support the structure and for attachment of the stylet protractor muscles.

The body is enclosed in a **cuticle** which is usually transversely annulated (H1) and may be ornamented with a variety of processes in the criconematid forms (I2). Longitudinal ridges occur in some species. Beneath the cuticle is the **hypodermis** and the **muscles** which are attached to four **chords** – longitudinal thickening of the cuticle and hypodermis. The lateral chords are better developed than the ventral and dorsal ones and correspond externally to the **lateral field** which is marked by a number of **longitudinal lines** (H3) or **incisures**. The central cavity of the nematode, the **pseudocoelom**, contains a viscous fluid which acts as an **hydrostatic skeleton**. Suspended within the fluid are the three major organs – digestive, reproductive and excretory.

The digestive system comprises: **stylet; oesophagus; intestine** and **rectum**. The stylet (D4) is a protrusible cuticular tube, pointed anteriorly and with a subterminal aperture and generally swelling posteriorly to form three **basal knobs** (D5). Protractor muscles run from the knobs to the cephalic (labial) skeleton.

The **oesophagus** (or pharynx) comprises a narrow cylinder or **procorpus** (B6) which expands to form the **median bulb** (B7) a muscular swelling containing refringent **valve plates** (B8) and then narrows to form the **isthmus** (A9) before expanding into the **oesophageal glands** (B10, A11). There are three glands, one dorsal and two subventral, which may form a bulb-like structure (A11) abutting the intestine or be extended into an overlapping lobe (B10). Between the stylet and the oesophago-intestinal junction runs a central tube, the **oesophageal lumen** (B12), through which glandular secretions and food passes. In tylenchids, the dorsal oesophageal gland opens into the oesophageal lumen near the stylet base (D13) and the two subventral glands open within the median bulb. In aphelenchids, all three glands open within the median bulb (F14). The **intestine** (E15) is a largely undifferentiated tube which opens via the **rectum** (E16) at the **anus** (E17) or, in adult males, the **cloaca** (J18). In the males of certain genera the digestive system is degenerate and non-functional.

The reproductive system in both sexes is tubular. The female genital system may be composed of two (E19), usually opposed, branches (**didelphic**) or reduced to one (**monodelphic**). In monodelphy (G20) the posterior branch is reduced to a **post-uterine sac** (G21) or entirely absent. Each branch has four major parts: **ovary**; (G22) **oviduct** (G23); **uterus** (G24) and **vagina** (G25). A specialized uterine structure for storing sperm, the **spermatheca** (G26), may be present. The vagina opens to the exterior via the **vulva** (G27), a ventrally situated transverse slit in the middle or posterior section of the body. The male system is less variable. The single genital tube consists of a **testis, seminal vesicle** and **vas deferens** opening to the exterior via a common pore with the rectum, the **cloaca** (J18). The copulatory organ consists of the paired **spicules** (J28) with a guiding piece, the **gubernaculum** (J29). The protrusible spicules are heavily cuticularized and serve to open the female vulva and channel sperm. The male tail often has cuticular expansions, the caudal alae (J30) or **bursa**, which aid in copulation.

The excretory system consists of a uninucleate **gland cell** connected via an **excretory canal** to the ventrally situated **excretory pore** (B31). This pore is usually in the oesophageal region but may be posteriorly located (e.g. *Tylenchulus*).

The nervous system consists of a circumoesophageal commisure – the **nerve ring** (E32) – and a network of nerves connected to body organs and various sensory structures. These sense organs are mostly on the head (**sensillae** and **amphids**), in the oesophageal region (**cephalids, deirids, hemizonid** and **hemizonion**) and on the tail (**phasmids**).

Longidorids (Fig. 1 L, M)

Compared with tylenchs these are much longer and range from 0.9–12mm in size. The cuticle is smooth and lateral fields are absent. The stylet is more properly called an **odontostylet** and is up to 300 μm long. It consists of needle-like **odontostyle** (L33) attached posteriorly to a cuticular extension – the **odontophore** (L34). The oesophagus consists of a narrow anterior section and a posterior bulb

which is both muscular and glandular. The female reproductive system is didelphic or monodelphic, the anterior branch regressing in the latter case. The male spicules are well-developed and have **lateral guiding pieces** (M35). There is no gubernaculum or bursa but a series of sensory **ventral supplements** (M36) run anteriorly from the cloaca. Some morphological features of tylenchs are missing (e.g. excretory pore, phasmids, deirids, cephalids).

Trichodorids (Fig. 1 K, N)

Short (0.5–1.1mm) cigar-shaped nematodes with bluntly rounded head and tail. The cuticle is smooth and may swell with acid fixatives. The stylet or **onchiostyle** (K37) is curved and the oesophagus comprises a narrow cylindrical anterior section and a posterior bulboid expansion. The female genital system is usually didelphic. The male spicules are slightly curved and a weak bursa may be present. Ventral supplements occur.

Bionomics of Plant Parasitic Nematodes

Reproduction and development

Reproduction is either **amphimictic** (separate males and females) or **parthenogenetic** (males absent, non-functional, or very rare). Eggs are either laid singly or stuck together in masses in a **gelatinous matrix** which is secreted by the female. Such egg-masses are associated with species where the females swell and become sedentary, although some obese genera retain all the eggs within the body, the cuticle tanning on the death of the female to form a **cyst**. Egg-sacs and cysts serve to protect the eggs.

Nematodes typically have four juvenile stages between the egg and adult with intervening moults allowing an increase in size. In tylenchs the first stage juvenile, J1, moults to the J2 within the egg, but in longidorids and trichodorids it is the J1 which emerges.

Environmental conditions

Although occupying many different ecological niches, nematodes are essentially aquatic animals. Plant parasitic nematodes require at least a film of water to enable locomotion and, as all species spend a greater or lesser proportion of their life within soil, the soil water content is a primary ecological factor. Many species die in dry soils whilst others may survive in an anhydrobiotic state. Conversely, too much soil water results in an oxygen deficit and many nematodes succumb – although certain genera, such as *Hirschmanniella*, thrive in such conditions.

Soil temperature is not a particularly important factor as it tends to remain reasonably stable. Most tropical nematodes do not survive prolonged periods below 10°C and some are able to survive soil temperatures of 50°C if they have sufficient time to enter anhydrobiosis.

Soil structure has an important effect on nematodes as the pore size affects the ease with which they can move through the soil. In general, sandy soils provide the best environment – soils with a high clay content or those with an excessively open texture inhibit movement. However, saturated clay soils can be colonized successfully by certain specialised nematodes, including *Hirschmanniella* and some *Paralongidorus*. Soil pH may influence nematodes, but few data are available for tropical and subtropical species.

The maxim that 'where a plant is able to live, a nematode is able to attack it' is a good one. Nematodes are even able to attack the aerial parts of plants provided that the humidity is high enough to facilitate movement. Such conditions are provided in flooded rice fields where foliar species such as *Aphelenchoides besseyi* and *Ditylenchus angustus* can be very damaging.

Hatching, host location and penetration

The eggs of many plant parasitic nematodes are deposited singly, either in the soil or within the plant tissues, and hatch irrespective of the presence of a host plant, provided that other factors are favourable.

In the more advanced parasites, however, the eggs may be embedded in a gelatinous matrix to form an egg-mass (e.g. *Meloidogyne*) or retained within the swollen female body, the cuticle of which tans to form a protective cyst (e.g. *Heterodera, Globodera*). The eggs of cyst nematodes require the presence of root exudates from the host to promote hatching and this is associated with a restricted host range.

Nematodes are attracted to plant roots by a variety of factors which have yet to be fully elucidated. Such attractive factors can operate over considerable distances – up to one metre in *Meloidogyne*. Having found a host there are three main types of parasitism (Fig. 2):

1. **ectoparasitic** – the nematode does not enter the plant tissues, but feeds by using the stylet to puncture plant cells – the longer the stylet the deeper it can feed.

2. **semi-endoparasitic** – only the anterior section of the nematode penetrates the root, the posterior section remaining in the soil.

3. **endoparasitic** – the entire nematode penetrates the root. Migrating endoparasites retain their mobility and move through the tissues feeding as they go. Sedentary endoparasites, on the other hand, have a fixed feeding site (nurse cells), lose their mobility and become obese.

The above categories are not mutually exclusive as some genera may be semi-endoparasitic or migratory ectoparasitic depending on the host e.g. *Helicotylenchus*, whilst some sedentary parasites have only the anterior section embedded in the root (= sedentary semi-endoparasites) e.g. *Rotylenchulus, Tylenchulus*.

In *Meloidogyne* and *Heterodera/Globodera* the J2 is the infective stage, but in ectoparasites and most migratory endoparasites all stages may feed on or penetrate the root (Fig. 3). Rarely, as in *Rotylenchulus*, the immature female is the infective stage, the juveniles and males remaining in the soil and not feeding.

Host reactions

As ectoparasites do not enter the plant, the damage they cause is usually limited to necrosis of those cells penetrated by the stylet e.g. *Tylenchorhynchus*. However, those species with longer stylets (e.g. *Xiphinema, Hemicycliophora*, etc) penetrate the tissues more deeply thus killing more cells. As such nematodes tend to feed on meristematic tissue near the root tips, galling or hooked roots result and secondary root proliferation may occur if the growing point is destroyed.

Endoparasites not only kill the cells they feed upon but, by burrowing through the root tissues, they cause extensive destruction leading to cavitation and secondary infection. Successive generations of nematodes compound the damage and it is not surprising that some of the most pathogenic nematodes belong to this group (*Pratylenchus, Radopholus, Hirschmanniella*).

Sedentary endoparasites have a sophisticated relationship with the host involving transformation of root cells into a trophic system of nurse or transfer cells. The function of these nurse cells is to act as a nutrient sink so that the sedentary nematode enjoys a continuous supply of nutrients, thus enabling it to enlarge enormously and produce a large number of eggs. In *Meloidogyne* multiplication of the root cells is also stimulated leading to the characteristic galls.

Plants with the root system damaged by nematodes often show above-ground symptoms such as retarded growth, chlorosis and reduced yield. These symptoms are a direct result of the impaired ability of the root system to deliver water and nutrients and thus may be confused with similar symptoms resulting from poor soil conditions and/or nutrient deficiencies.

The exact ways in which nematodes affect plants have yet to be fully elucidated and besides impairing root function by physical damage, toxins may also be involved. An interesting case involves 'Ontario peach-decline' where a very low population of *Pratylenchus* can kill young trees. The nematodes metabolize the sugar part of cyanosides in the plant tissue and thus liberate the CNH radical which is highly toxic to the tree.

In nematology the following terms are used to describe the inter-relationships of host and parasite. Plants can be divided into **hosts** or **non-hosts** depending on whether nematode reproduction occurs. Non-hosts may be **immune** i.e. no nematode penetration or reproduction, or **resistant** i.e. allowing

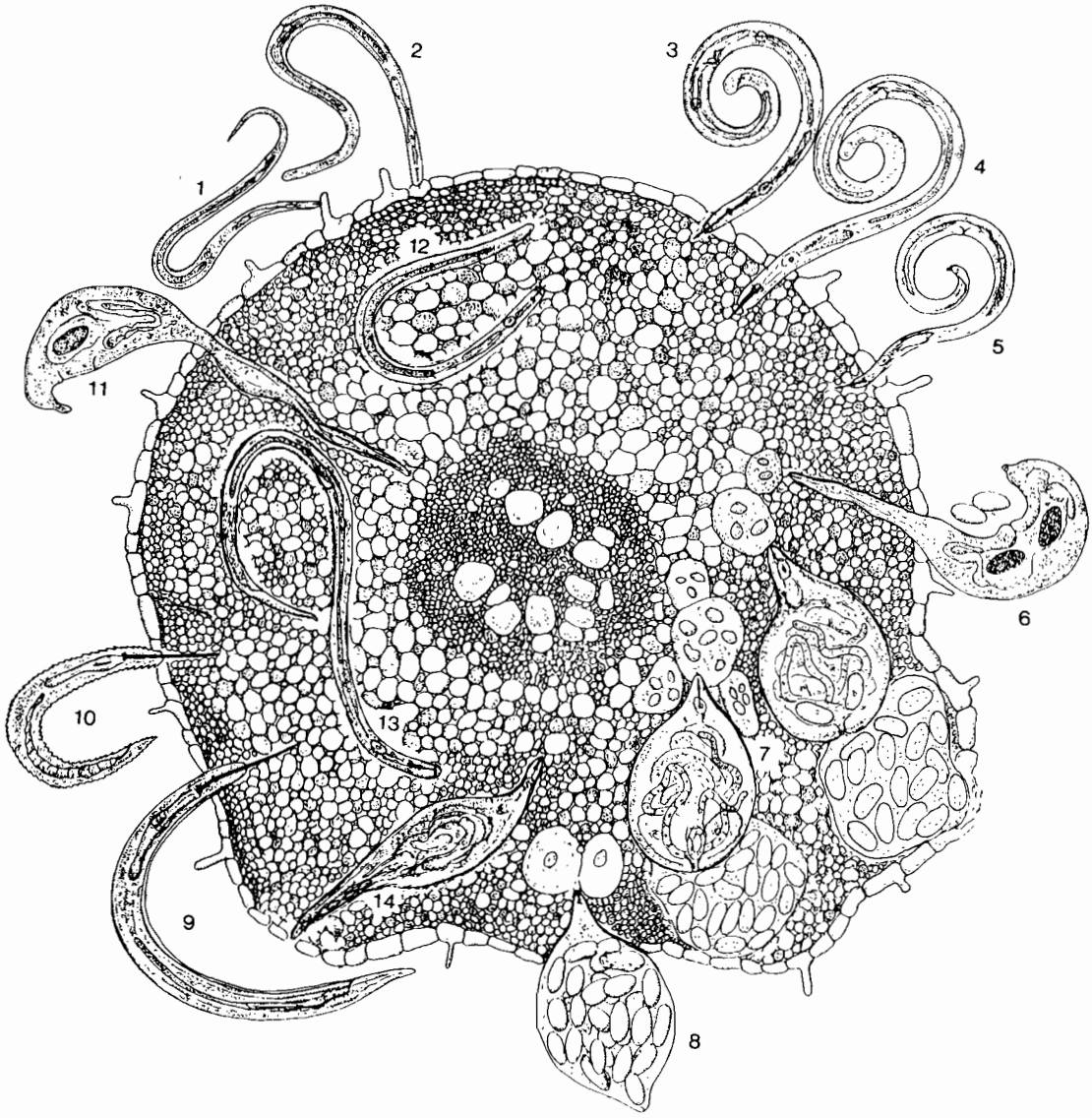


Fig. 2. Diagrammatic presentation of various types of tylenchid feeding on root tissue. 1. *Ditylenchus*. 2. *Tylenchorhynchus*. 3. *Rotylenchus*. 4. *Hoplolaimus*. 5. *Helicotylenchus*. 6. *Rotylenchulus*. 7. *Meloidogyne*. 8. *Heterodera*. 9. *Hemicycliophora*. 10. *Criconemella*. 11. *Tylenchulus*. 12. *Pratylenchus*. 13. *Hirschmanniella*. 14. *Nacobbus*. (Modified after Siddiqi, 1986).

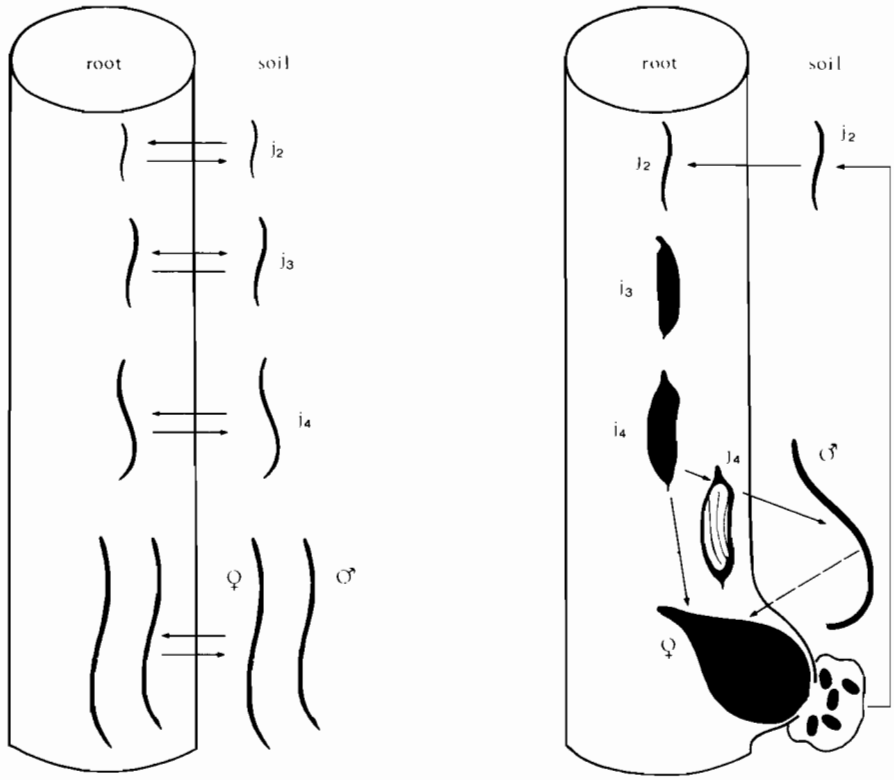


Fig. 3. Diagrammatic comparison of the life-cycle of a migratory endoparasite (left) and a sedentary endoparasite (right). (Modified after Merny, 1972).

nematode penetration/parasitism but not reproduction. Host plants are **non-resistant** or **susceptible** and can be **good hosts** or **poor hosts** depending on whether reproduction is high or low. Susceptible plants which support the lowest levels of reproduction within a dataset have been referred to as partially resistant or even, in some cases, as 'resistant'.

Variations in the ability of nematodes to reproduce on given plant species or cultivars are of great agricultural significance and are of two principal types. Nematode populations, distinguished by their ability or inability to reproduce on designated plant species are known as **host races. Pathotypes** are variants of a host race or species which are distinguished by their ability to reproduce on a designated host plant genotype (e.g. cultivar, line, etc).

Tolerance refers to the amount of damage caused by the nematode to the plant and should not be confused with resistance (q.v.). A **tolerant host** suffers little damage even when heavily infected whilst an **intolerant host** may be severely damaged, even if only lightly infested.

Survival

In the absence of a live host nematodes may survive in the soil or in plant residues. Provided that the environment dries slowly, many nematodes are able to enter a reversible anhydrobiotic state when they are less susceptible to desiccation, temperature and chemicals. In a number of genera

the eggs are the survival stage and are protected in a gelatinous matrix (*Meloidogyne, Tylenchulus, Rotylenchulus*) or within the hardened cyst-like body of the female (*Heterodera, Globodera*). In the later case, infective J2 nematodes may emerge several years after being laid. Anhydrobiosis is probably more common in tropical and subtropical areas than is currently realized and enables the nematode to survive the dry season and also some non-chemical control methods such as dry-fallow. The record for longevity in the anhydrobiotic state is held by seed nematodes, such as *Anguina*, where they have been recorded surviving for 39 years. A practical consequence of anyhydrobiosis is that when extracting dry soil a sufficient period of soaking should be allowed to re-activate the nematodes.

Identification of the Major Genera

This section is intended to serve as a basic guide to the identification of the major parasitic genera of tropical and subtropical agriculture. Each generic diagnosis has the major characters printed in bold and numerically cross-referenced, where appropriate to the illustrations. The descriptions are designed to be multi-level and should be of benefit to both the novice and the more experienced user. The systematic arrangement used is outlined in Table 1 although the descriptions are arranged according to the mode of parasitism – stem or foliar parasites (p. 10), ectoparasites (p. 14), migratory endoparasites (p. 24), sedentary endoparasites (p. 34) – in order to facilitate rapid comparison between genera which are systematically distant, yet share a similar biotope.

TABLE 1 Outline classification.

Order/Sub-order	Family	Genus	Page
TYLENCHIDA			
Tylenchina	Anguinidae	*Anguina*	12
		Ditylenchus	12
	Belonolaimidae	*Tylenchorhynchus*	14
	Pratylenchidae	*Hirschmanniella*	30
		Nacobbus	38
		Pratylenchus	28
		Radopholus	32
	Hoplolaimidae	*Aorolaimus*	26
		Helicotylenchus	24
		Hoplolaimus	26
		Rotylenchulus	40
		Scutellonema	26
	Heteroderidae	*Globodera*	34
		Heterodera	34
		Meloidogyne	36
	Criconematidae	*Criconemella*	16
		Hemicriconemoides	18
		Hemicycliophora	18
	Tylenchulidae	*Tylenchulus*	42
Aphelenchina	Aphelenchoididae	*Aphelenchoides*	10
		Rhadinaphelenchus	10
DORYLAIMIDA			
Dorylaimina	Longidoridae	*Longidorus*	22
		Paralongidorus	22
		Xiphinema	22
Diphtherophorina	Trichodoridae	*Paratrichodorus*	20
		Trichodorus	20

Aphelenchoides Fischer, 1894

Systematic position: Aphelenchina, Aphelenchoididae

Morphology: Small to medium sized (0.4–1.2 mm), slender nematodes. Females die straight or ventrally arcuate on heat relaxation while the **male tail curls ventrally to produce a 'walking-stick' shape** (1). Head region weakly sclerotized; stylet weak, with or without basal swellings. **Oesophageal bulb well-developed, spherical to rounded-rectangular in shape and more or less filling the body width** (2). **Dorsal oesophageal gland duct opening within bulb** (3), just anterior to the valve plates. Oesophageal gland lobe overlapping intestine dorsally. Female: **vulva posterior** (60–75%) (4); **genital tract single**, anteriorly directed. Tail medium conoid, with or without terminal mucron(s). Male: tail medium conoid, **spicules well-developed, thorn shaped** (5). No bursa.

Biology: Ecto-parasitic on leaves, stems and other parts of higher plants. Most species can also be readily cultured on various fungal hyphae. *A. besseyi* can withstand desiccation for several years. The life-cycle is rapid and can be completed in as little as a week.

Major species: *A. arachidis, A. besseyi, A. fragariae, A. ritzemabosi.*

Distribution: *A. arachidis* is only recorded from groundnut in northern Nigeria but the other species are well-distributed with *A. besseyi* being found in most rice-growing areas.

Rhadinaphelenchus J. B. Goodey, 1960

Morphology: Similar in general respects to *Aphelenchoides* but both sexes are **very slender (body length/body width = about 100)**. In addition, the female has a **very long post-vulval sac, a very long, slightly tapering tail with a rounded tip** (6), and **a vulval flap** (7). The **male tail tip bears a small cuticular flap** (8) ('bursa') visible most easily in ventral view. **Dorsal limb of spicule elongate** (9).

Biology: Parasitic in cortical tissues of coconut roots but mainly found in the stem where 10 g of tissue may contain 50,000 nematodes. Infection often causes the development of a red or orange-red ring of tissue within the stem (hence the common name of 'red-ring' for the nematode). The nematode is believed to be vectored by the palm-weevil during oviposition and death of the palm occurs in 2–4 months.

Major species: *R. cocophilus* (no other species described).

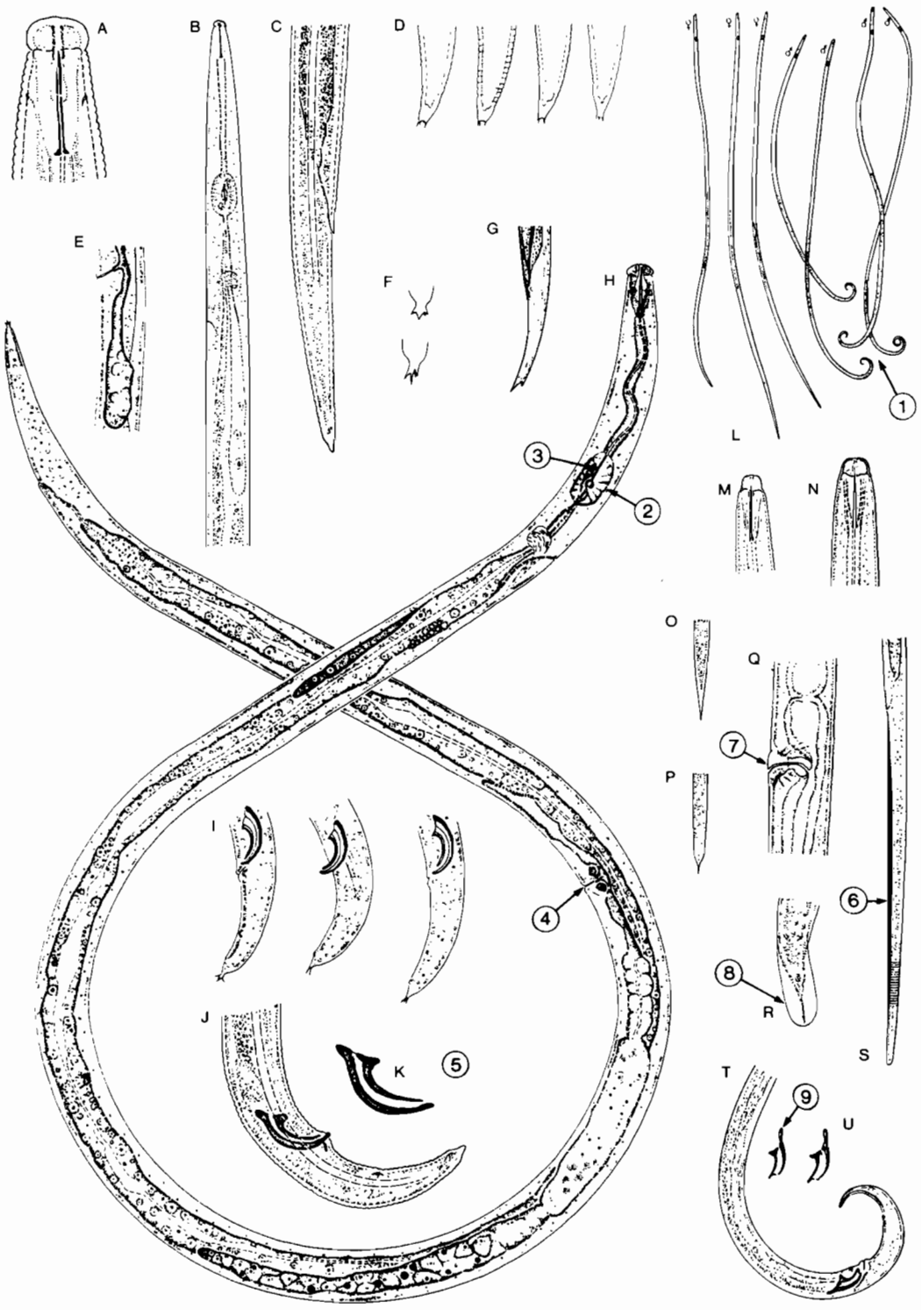
Distribution: Widespread in the Caribbean, Central and South America.

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 4; Set 3, No. 32; Set 5, No. 72; Set 8, No. 116).

Dean, C. G. (1979) Red ring disease of *Cocos nucifera* L. caused by *Rhadinaphelenchus cocophilus* (Cobb, 1919) Goodey 1960. An annotated bibliography and review. *Technical Communication No. 47.* CAB International, Wallingford, UK.

Fig. 4. *Aphelenchoides besseyi.* A: head; E: postvulval sac; F: tail tips; H: entire female; I: male tails. *A. bicaudatus.* G: female tail. *A. fragariae.* C: female tail; J: male tail; K: spicule. *A. ritzemabosi.* B: oesophagus; D: female tail tips. *Rhadinaphelenchus cocophilus.* L: adults; M: male head. N: female head; O,P: juvenile tail tips; Q: vulva; R: male tail tip; S: female tail; T: male tail; U: spicules.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Ditylenchus Filipjev, 1936

Systematic position: Tylenchina, Anguinidae

Morphology: Slender nematodes dying straight or slightly curved ventrally on heat relaxation. **Head skeleton weakly sclerotized** (1), stylet of moderate strength and with small basal knobs. Oesophagus with a muscular median bulb and **isthmus gradually expanding to form the basal bulb** (2) which may extend as a lobe over the intestine. Female: **vulva well posterior** (3). **Genital tract single, anteriorly outstretched. Post-uterine sac present** (4). **Tail elongate, conoid** (5). Male: **bursa adanal** (6), not reaching tail tip. **Tail elongate, conoid** (7).

Biology: Ectoparasites of plant stems and leaves but also found within the tissues. Infected stems and leaves are often stunted and deformed.

Major species: *D. angustus, D. dipsaci.*

Distribution: *D. angustus* is found in rice-growing areas of Bangladesh, Vietnam and other areas of Asia. *D. dipsaci* is restricted to the cooler regions of the tropics and subtropics.

Confusable genus: *Aphelenchoides*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, U.K. (Set 1, No. 14; Set 5, No. 64).

Fortuner, R. (1982). On the genus *Ditylenchus* Filipjev, 1936 (Nematoda: Tylenchida). *Revue de Nématologie, 5*: 17–38.

Anguina Scopoli, 1777

Morphology: Sexually dimorphic. Adult stages found only in plant galls, juveniles found in galls, plant tissue or soil depending on stage of life cycle. General morphology similar to *Ditylenchus*. Female: **obese**, medium to large nematodes (1.5–5mm) **dying spirally coiled** (8) on heat relaxation. **Vulva very posterior with a single, anteriorly directed genital tract** which is **reflexed two or more times** (9). **Numerous oocytes** (10). Male: small to medium sized (1–2.5mm) dying ventrally or dorsally (e.g. as in *A. tritici*) arcuate. **Testis well developed with one or more flexures** (11). **Bursa adanal** (12).

Biology: Forming galls on stems, leaves or flowers of various plants. The J2 stage is found in the soil and feeds ecto-parasitically on the plant tissues. The final moult takes place after gall formation, each female laying one to two thousand eggs. As the gall matures and dries, the J2 infectives slowly desiccate and in this anhydrobiotic state can survive many years.

Major species: *A. agrostis, A. tritici*

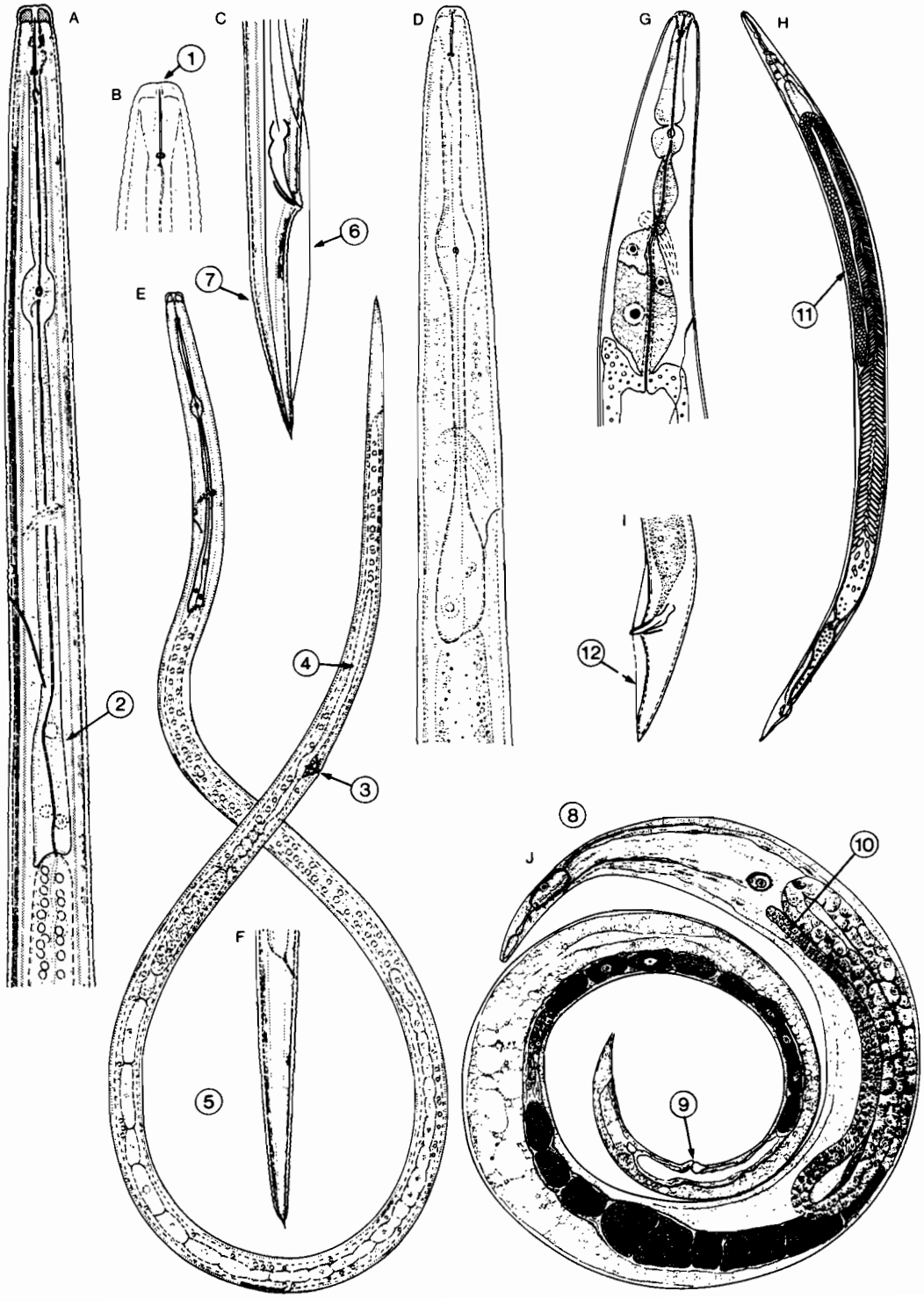
Confusable genus: juveniles in soil very similar to juvenile *Ditylenchus*.

Useful Literature

CIH Descriptions of Plant-Parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK (Set 1, No. 13; Set 2, No. 20).

Brzeski, M. W. (1981). The genera of Anguinidae (Nematoda, Tylenchida). *Revue de Nématologie, 4*: 23–34.

Fig. 5. *Anguina agrostis*. I: male tail. *A. tritici*. G: female oesophagus; H: entire male; J: entire female. *Ditylenchus angustus*. A: female oesophagus; C: male tail; E: entire female; F: female tail. *D. myceliophagus*. B: head region; D: oesophagus.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Tylenchorhynchus Cobb, 1913

Systematic position: Tylenchina, Belonolaimidae

Morphology: Small nematodes (rarely over 1 mm long), dying more or less straight or slightly curved ventrally on application of gentle heat. **No marked sexual dimorphism in form of anterior region**. Head region rounded, continuous with body contour or slightly offset, with thin annules, and **weak sclerotization** (1). **Stylet slender, 15–30 µm long, moderately sclerotized with rounded, backwardly sloping knobs** (2). Lateral field with 2, 3, 4 or 5 lines; cuticle sometimes divided into blocks. Oesophagus equally developed in both sexes; median bulb fusiform, moderately developed; oesophageal glands abutting the intestine (3) or, very rarely, overlapping. Female: **vulva median with two equally developed genital tracts** (4); one directed anteriorly, one posteriorly. Spermatheca rounded. **Tail about three anal body diameters long, conoid to subcylindrical, with rounded tip** (5). Male: tail elongate, conical-pointed, bursa extending to tail tip (6), trilobed in some species. Spicules slightly curved.

Biology: Migratory ecto-, semi-ecto- or endo-parasites. Most species bisexual. Polyphagous. Not considered as being very important parasites. Well distributed in all climatic areas.

Major species: *T. annulatus, T. brassicae, T. mashoodi*

Synonyms: *Telotylenchus, Quinisulcius, Dolichorhynchus, Trilineellus, Divittus, Morasinema, Tessellus, Neodolichorhynchus, Mulkorhynchus.*

Confusable genera: *Trichotylenchus, Merlinius, Amplimerlinius*

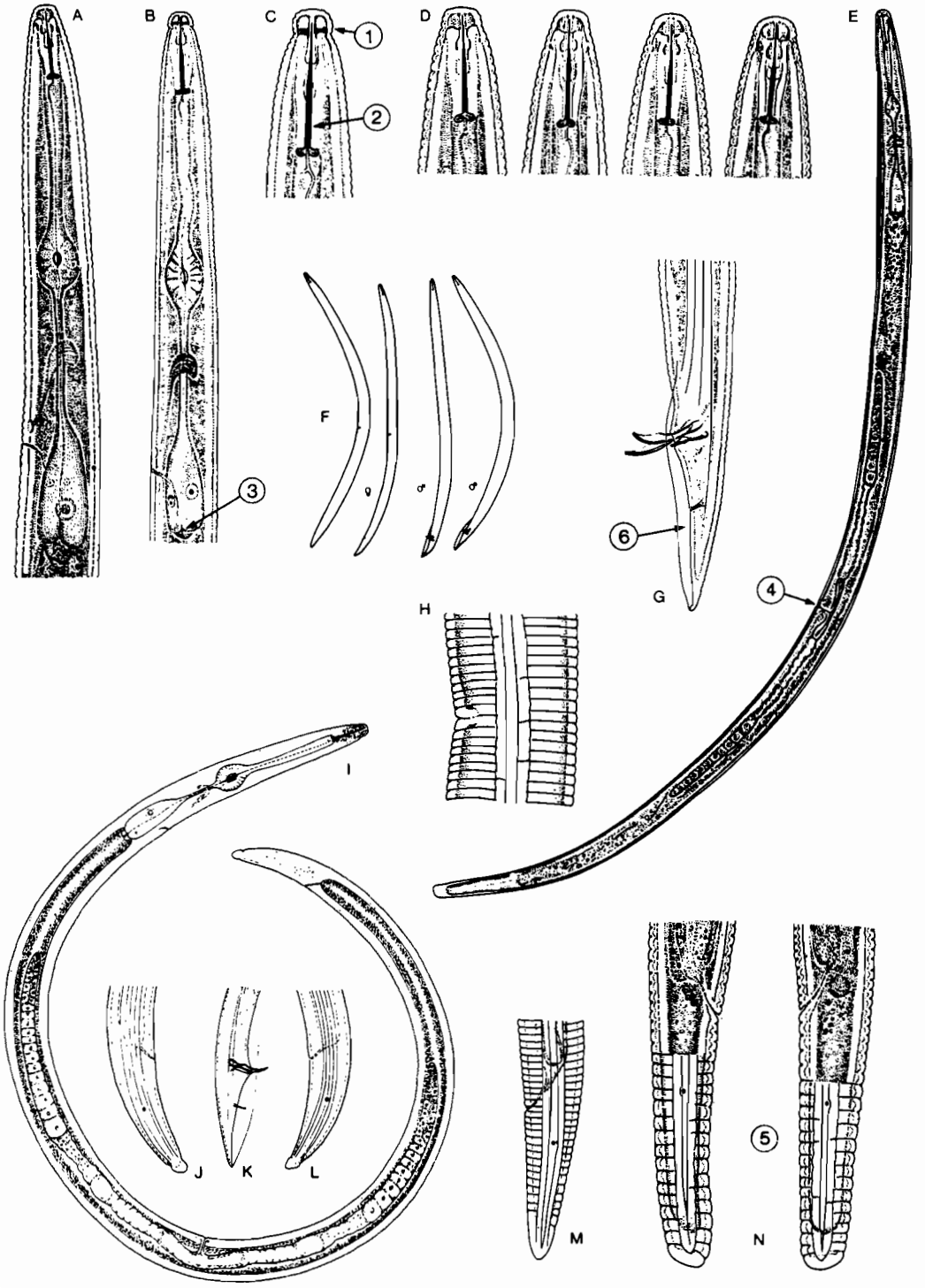
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK (Set 6, No. 85).

Fortuner, R. & Luc, M. (1987). A reappraisal of Tylenchina (Nemata). 6. The family Belonolaimidae Whitehead, 1960. *Revue de Nématologie, 10*: 183–202.

Siddiqi, M. R. (1986). *Tylenchida Parasites of Plants and Insects*. CAB International, Wallingford, UK. 645 pp. [see pp. 172–221].

Fig. 6. *Tylenchorhynchus annulatus*. A: oesophagus; D: head ends; E: entire female; H: lateral field; N: female tails. *T. capitatus*. I: entire female; K: male tail; J,L: female tails. *T. claytoni*. F: adults. *T. cylindricus*. B: oesophagus. C: head; G: male tail; M: female tail.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Criconemella De Grisse & Loof, 1965

Systematic position: Tylenchina, Criconematidae

Morphology: Sexually dimorphic. Female: body 0.20–1mm long, stout, dying straight or slightly curved, with rounded anterior end, and rounded to conical posterior part. **Cuticle provided with 42–200 prominent, retrorse annules** (1), with a **smooth** (2) **or finely crenate posterior margin** (3). Labial area not well separated from rest of body, marked by one or two thinner annules. **Stylet strong, basal knobs with a forwardly directed process** (4) (= anchor shaped). Oesophagus with a strong median bulb which is fused with the procorpus; glands forming a small posterior bulb. Vulva posterior. **One genital tract, extending anteriorly** (5). Spermatheca laterally situated. Male: Body slender and short (6). Anterior end rounded. No stylet; oesophagus degenerate. Spicule short, slightly curved. **Bursa weakly developed**, exceptionally absent. Tail pointed. Juveniles: Resembling female. **Annules smooth to finely crenate** (exceptionally with a row of scales) on posterior margin.

Biology: Migratory ectoparasites on perennial crops, trees and vines. Males non-feeding. Most species are parthenogenetic. Only a few species have been proved to be harmful. Found in all geographic areas.

Major species: *C. axestis, C. onoensis, C. sphaerocephala, C. xenoplax*

Synonyms: *Xenocriconemella, Mesocriconema, Madinema, Seshadriella, Neobakernema, Crossonemoides. Macroposthonia* and *Criconemoides*, two generic names often found in the literature, could also be regarded as synonyms of *Criconemella* but are better considered as *genera dubia*.

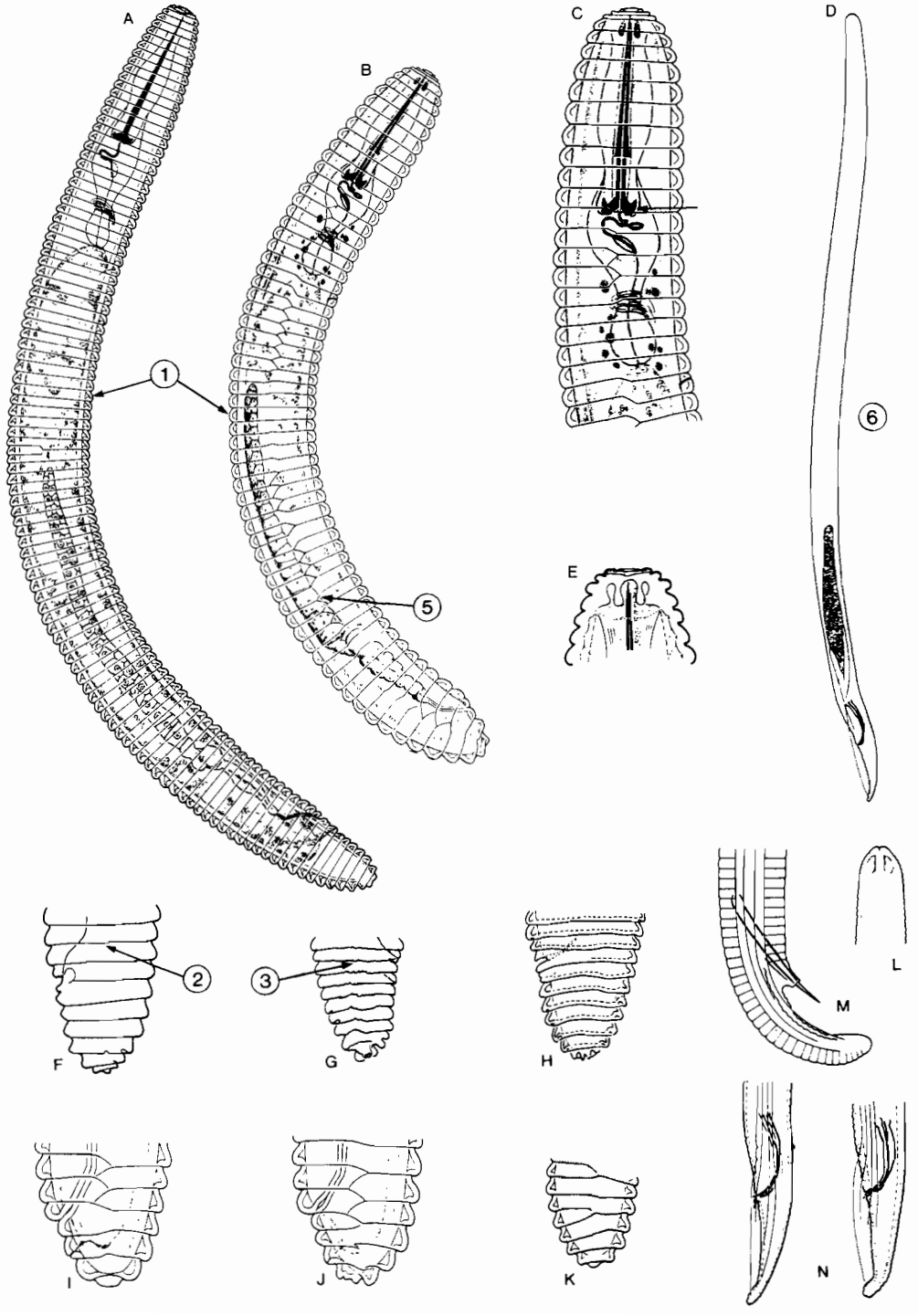
Confusable genera: *Criconema, Discocriconemella, Hemicriconemoides*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 127; Set 2, No. 28).

Raski, D. J. & Luc, M. (1987). A reappraisal of Tylenchina (Nemata). 10. The superfamily Criconematoidea Taylor, 1956. *Revue de Nématologie, 10*: 409–444.

Fig. 7. *Criconemella pseudohercyniensis*. D: entire male; E: head region; G: female tail; N: male tails. *C. onoensis*. H: female tail. *C. sphaerocephala*. B: entire female; C: head region female; I,J: female tails. *C. xenoplax*. A: entire female; F: female tail; K: juvenile tail. L: male head; M: male tail.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Hemicycliophora de Man, 1921

Systematic position: Tylenchina, Criconematidae

Morphology: Sexually dimorphic. Female: Body straight, or slightly ventrally curved, 0.6–1.9 mm long, stout. Anterior end rounded. Posterior end pointed, more rarely rounded. **Cuticle** (1) **with two detached layers** (= 'double' cuticle); external layer marked by **numerous (up to 400) prominent, but not retrorse annules**. No true lateral field, but cuticle may be variously ornamented (longitudinal lines, squares, dots, scratches, etc.). Labial area not separated from body, marked by 2–3 annules. **Stylet strong** (2), long, with **rounded basal knobs** (3). Oesophagus with strong median bulb fused with the procorpus (4); glands forming a small terminal bulb. Vulva posteriorly situated. **One anteriorly directed genital tract**; spermatheca lateral. **Vestigial anus and rectum**. Postvulval part generally conical, with pointed terminus, more rarely cylindrical with rounded extremity. Male: Slender, with simple cuticle. **No stylet**. Oesophagus degenerate. **Spicule strong, semi-circular to hook-shaped** (5). **Bursa adanal, well developed. Tail long** (6), conical, often presenting a ventral angle to the body axis. Juveniles: resembling female.

Biology: As for *Criconemella*

Major species: *H. arenaria, H. parvana, H. typica*

Confusable genus: *Hemicriconemoides*

Synonyms: *Aulosphora, Colbranium, Loofia*

Useful Literature

Brzeski, M. W. (1974). Taxonomy of Hemicycliophorinae (Nematoda, Tylenchida). *Zesz. probl. Postep. Nauk robn. 154*: 237–330.

Hemicriconemoides Chitwood & Birchfield, 1957

Systematic position: Tylenchina, Criconematidae

Morphology: Sexually dimorphic (7). Female: Similar in many ways to *Hemicycliophora*, but shorter (usually around 0.5 mm long) with fewer annules and very **closely adpressed 'double' cuticle** (8). **Stylet knobs with anteriorly directed processes** (9). Tail short, conoid (10).

Biology: Similar to *Criconemella*.

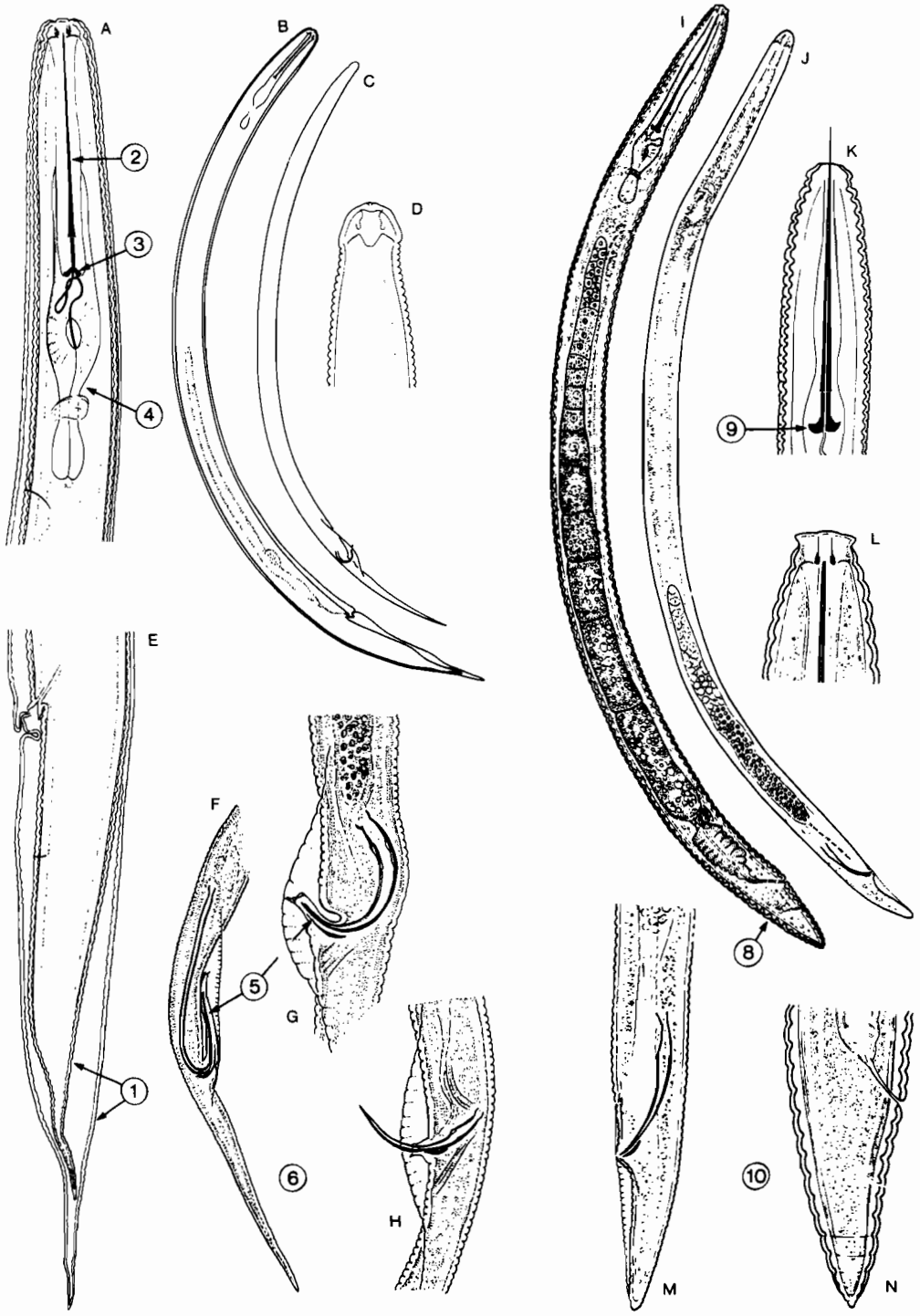
Major species: *H. cocophillus, H. mangiferae*

Confusable genera: *Caloosia, Hemicycliophora*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK (Set 7, No. 99).

Fig. 8. *Hemicycliophora chathami*. A: female oesophagus; B: entire female; C: entire male; D: male head; E: female posterior region; G: male tail. *H. penetrans*. F: male tail. *H. thienemanni*. H: male tail. *Hemicriconemoides mangiferae*. I: entire female; J: entire male; L: female head; M: male tail; N: female tail. *H. chitwoodi*. K: female stylet.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Trichodorus Cobb, 1913

Systematic position: Diphtherophorina, Trichodoridae

Morphology: Body stout, 0.8–1.2 mm long, **cigar shaped** (1). Cuticle smooth. Head continuous with body contour; papillae prominent. **Onchiostyle** (= stylet) **tripartite, curved** (2). **Oesophagus anteriorly slender with a posterior bulboid expansion** (3). Female: vulva median with **strong vaginal sclerotization** (4), **one pair of lateral body pores present within one body width of vulva** (5). Typically two genital tracts present, but very rarely only one is present (= '*Monotrichodorus*'). **Tail rounded, very short** (6) with anus almost terminal (7). Male: spicules arcuate, gubernaculum present. **Protractor muscles conspicuous, of unusual form** (8) and encapsulating the spicule shafts. Ventral supplements present, **bursa** usually **absent or very small** if present.

Synonym: *Monotrichodorus*

Paratrichodorus Siddiqi, 1974

Morphology: Very similar to *Trichodorus* but **cuticle markedly swelling with acid fixation** (9). Female: **vulva with weak vaginal sclerotization** (10). **No lateral body pores within one body width of vulva** (11). Male: **spicule protractor muscles inconspicuous. Bursa present** (12).

Synonyms: *Atlantadorus, Nanidorus*

Biology: Ectoparasitic on the roots of perennial and woody plants. The main area of attack is just behind the root tip, restricting root elongation. The root tip is then attacked as are lateral root initials as they form. The characteristic 'stubby-root' syndrome results. Both genera are more common in light or sandy soils and highest densities tend to occur at depths of 30–40 cm. Some species are known to be virus vectors and it is likely that the other species are potential vectors.

Major species: *T. primitivus, T. similis, T. viruliferus, P. minor, P. pachydermus.*

Distribution: Worldwide. *Trichodorus* tends to be more temperate whilst *Paratrichodorus* is more tropical.

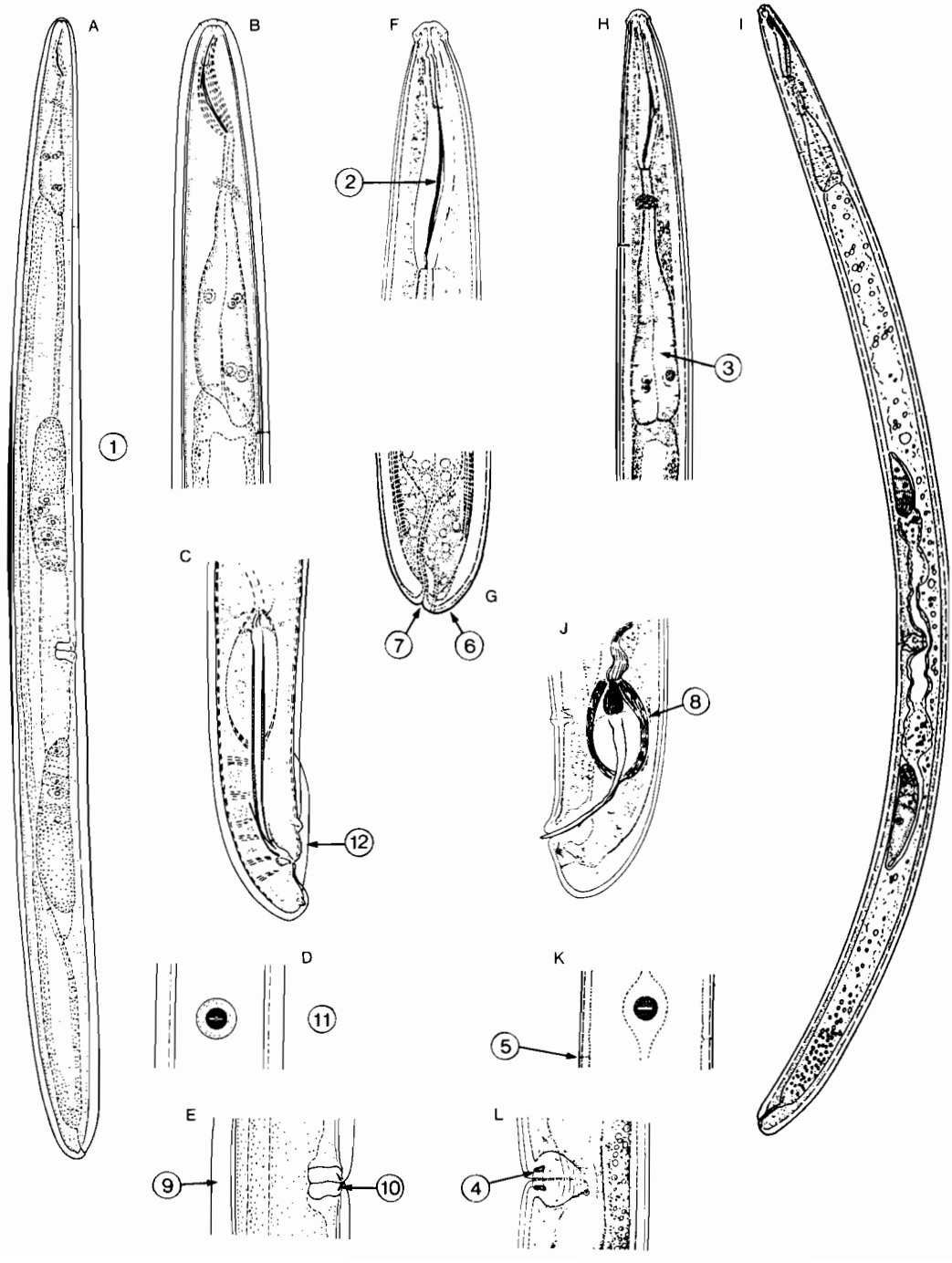
Confusable genera: each other

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 15; Set 4, No. 59; Set 6, No. 86; Set 7, No. 103; Set 8, No. 112

Decraemer, W. (1980) Systematics of the Trichodoridae (Nematoda) with keys to their species. *Revue de Nématologie 3*: 81–99.

Fig. 9. *Paratrichodorus minor*. A: entire female; B: oesophagus; C: male tail; D: vulva, ventral view; E: vulva, lateral view. *Trichodorus primitivus*. F: head region; H: oesophagus; J: male tail; L: vulva lateral view. *T. similis*. G: female tail; K: vulva, ventral view. *T. viruliferus*. I: entire female.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Xiphinema Cobb, 1913

Systematic position: Dorylaimina, Longidoridae

Morphology: Slender nematodes, 1.5–5 mm long. Head region continuous or offset. **Amphidial apertures a broad slit** (1) leading back to a **funnel-shaped pouch** (2). **Stylet very long** (60–250 μm) consisting of an anterior **odontostyle** (3) which is **needle-like** and has a **forked base** (4) and a posterior **odontophore** (5) with **three prominent basal flanges** (6). **Stylet guiding ring located in posterior half of odontostyle** (7). Oesophagus consisting of a long, narrow, procorpus and a short, glandular, bulb. Female: vulva usually at 40–50% but may be more anterior. Usually two genital tracts, but when the vulva is more anterior only the posterior tract remains. Tail very variable from short and rounded to long filiform. Male: spicules very powerful, arcuate. Ventral supplements form a pre-cloacal row.

Longidorus Micoletzky, 1922

Morphology: Similar to *Xiphinema* but body thinner and may be up to 11 mm long. **Amphids pouch-like** (8) and **opening via a minute, inconspicuous pore. Odontostyle/odontophore junction not forked** (9), **odontophore lacks flanges** (10) and both parts are less strongly cuticularized. **Guide ring in anterior half of odontostyle** (11).

Paralongidorus Siddiqi, Hooper & Khan, 1963

Morphology: Similar to *Longidorus*, but amphids and amphidial aperture (12) as for *Xiphinema*.

Synonym: *Siddiqia*

Biology: Long lived migratory ectoparasites attacking a wide variety of hosts. The favoured point of attack is at or near the root tip leading to hooked root-tips and/or terminal galls. Attacked root systems are stunted, lack developed laterals and show necrosis at the feeding sites. *Xiphinema* tends to be more abundant under woody hosts whereas *Longidorus* and *Paralongidorus* are more common under non-woody plants, particularly grasses and cereals. Greatest populations are found below 30 cm. With few exceptions, sandy soils support higher populations than heavier clays. Some species have been shown to be virus vectors. Reproduction is amphimictic or parthenogenetic.

Major species: *X. americanum* sensu lato, *X. index, X. elongatum, L. africanus, L. laevicapitatus, P. australis*

Distribution: *Longidorus* is mainly found in cooler areas whilst *Xiphinema* and *Paralongidorus* are more tropical.

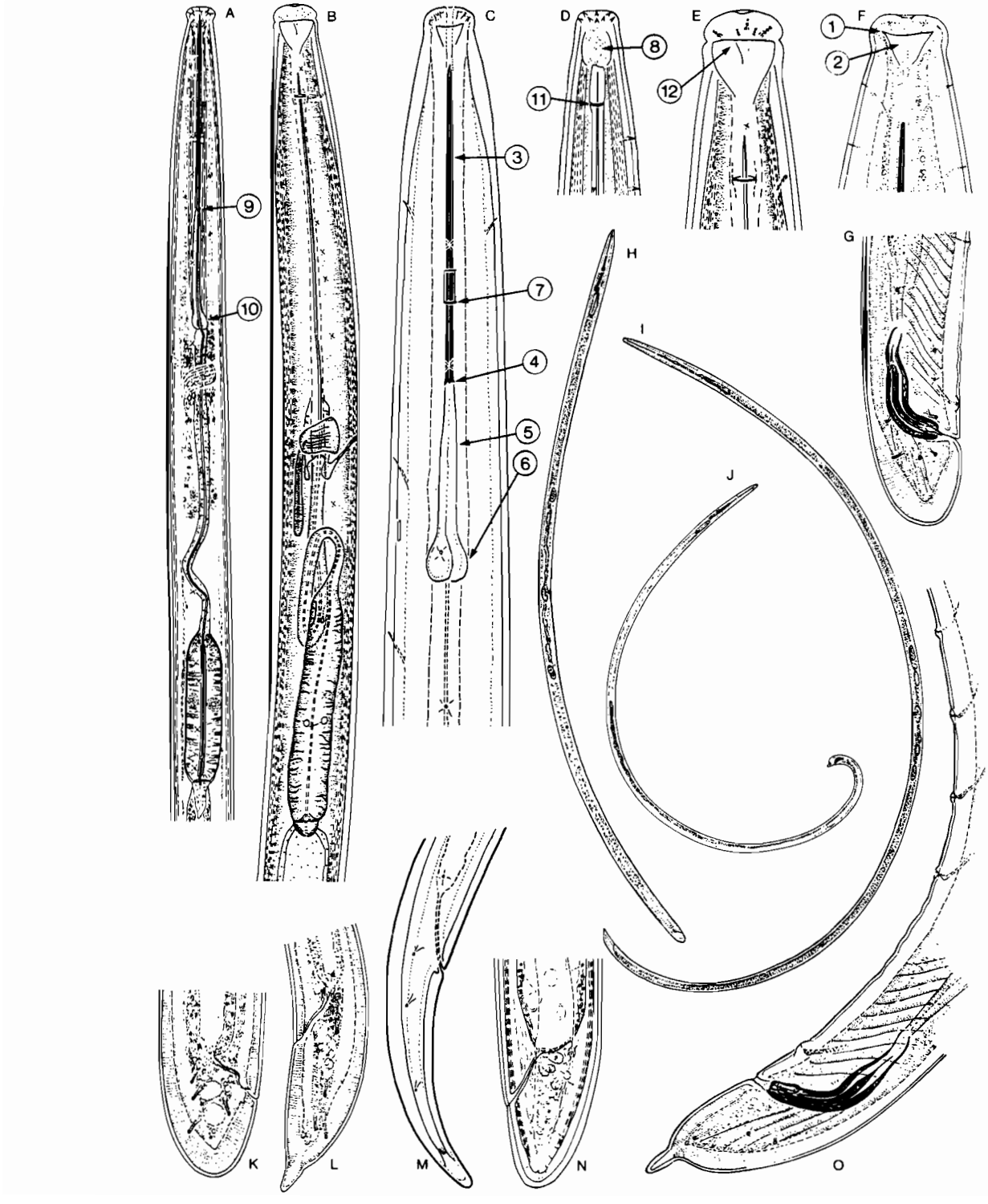
Confusable genera: each other

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK (Set 2, No. 29; Set 3, No. 45; Set 8, No. 117).

Loof, P. A. A. & Luc, M. A revised polytomous key for the identification of species of the genus *Xiphinema*, Cobb, 1913 (Nematoda: Longidoridae) with exclusion of *X. americanum* group. *Systematic Parasitology* (in press).

Fig. 10. *Longidorus fursti*. A: oesophagus; N. female tail. *L. elongatus*. D: head region. *Paralongidorus natalensis*. B: oesophagus; E: head region. *Xiphinema diversicaudatum*. J: entire male *X. heynsi*. G. male tail; H: entire female; K: female tail. *X. mammatum*. O: male tail. *X. neobasiri*. F: head region; I: entire female; L. female tail. *X. savanicola*. C: oesophagus; M: female tail.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Helicotylenchus Steiner, 1945

Systematic position: Tylenchina, Hoplolaimidae.

Morphology: Small to medium-sized nematodes (0.4–1.2 mm) **usually dying in a spiral** (1) (rarely C-shaped) on heat relaxation. Head region conoid-rounded, rarely truncate, sclerotization moderate. **Stylet well-developed, usually 3–4 times the lip width in length** (2) and with rounded or cup shaped knobs. **Opening of dorsal oesophageal gland duct 25–50% of stylet length posterior to knobs** (3). **Oesophageal gland lobe overlapping intestine mainly ventrally** (4). Female: **vulva posterior** (5) (60–70%), **both genital tracts usually fully developed**, posterior branch rarely reduced and non-functional (= "*Rotylenchoides*") . Tail short, usually dorsally convex-conoid or hemispherical. A terminal projection may be present. **Phasmids small, dot-like** (7). Male: Tail short (8), spicules well developed, arcuate. Bursa reaching tail tip.

Biology: Ecto-parasitic, semi-endoparasitic or endoparasitic nematodes of roots. All stages can be found in the root cortex but migration through the tissues has not been reported. Small lesions are formed which become necrotic as secondary invasion proceeds. Polyphagous. Most species are parthenogenetic but one of the commonest and most damaging species, *H. multicinctus*, is bisexual.

Major species: *H. dihystera, H. erythrinae, H. mucronatus, H. multicinctus, H. pseudorobustus.*

Distribution: Throughout the tropical and subtropical areas.

Synonym: *Rotylenchoides*

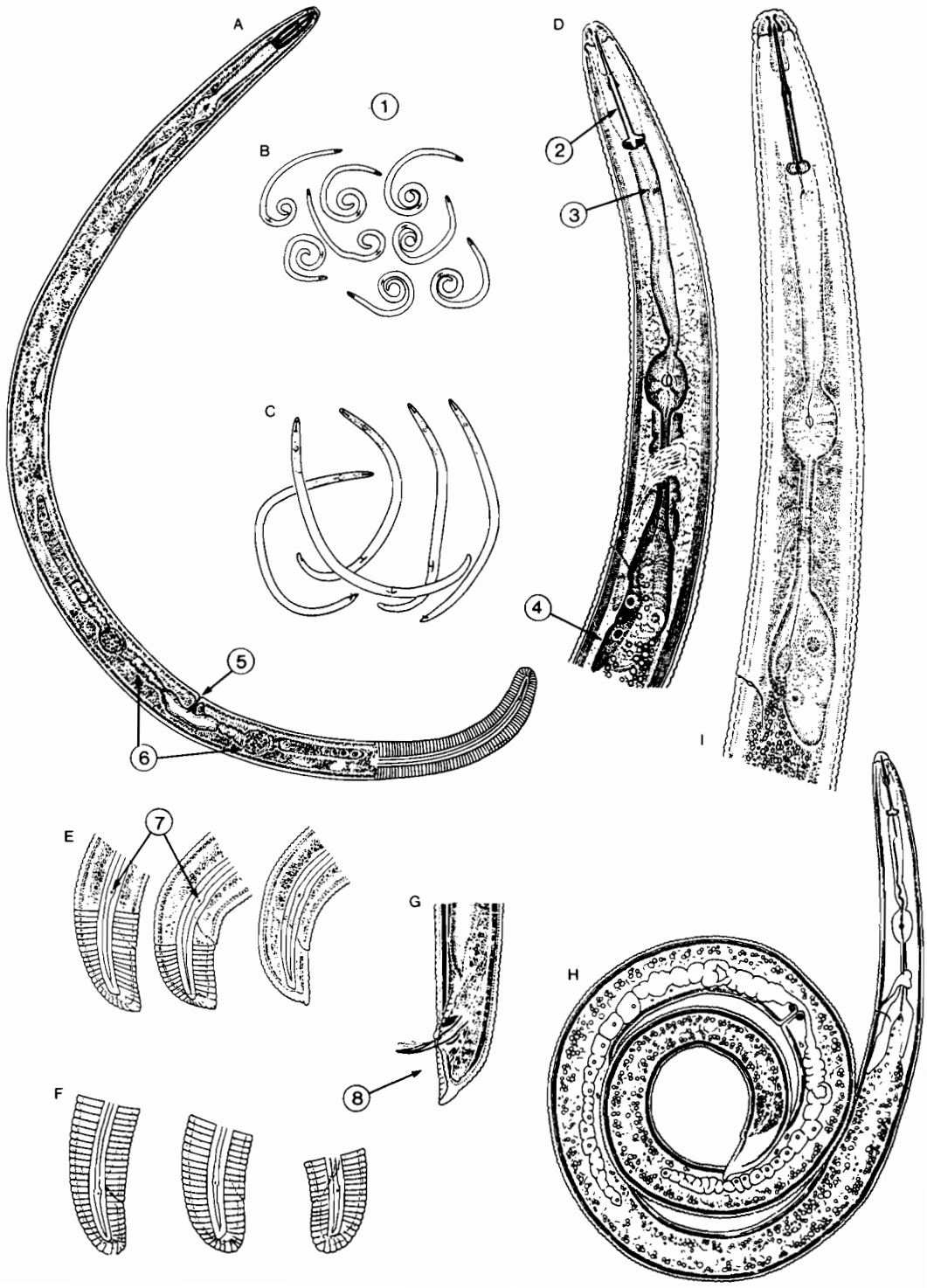
Confusable genus: *Rotylenchus* (has dorsal oesophageal gland duct opening more anterior and dorsal overlap of gland lobe).

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 9; Set 2, No. 23; Set 8, No. 109).

Boag, B. & Jairajpuri, M. S. (1985). *Helicotylenchus scoticus* n.sp. and a conspectus of the genus *Helicotylenchus* Steiner, 1945 (Tylenchida: Nematoda). *Systematic Parasitology* 7: 47–58.

Fig. 11. *Helicotylenchus dihystera*. B: females; E: female tails. *H. multicinctus*. A: entire female; C: males and females. F: female tails; G: male tail. *H. pseudorobustus*. D: oesophagus; H: entire female. *Rotylenchus buxophilus*. I: oesophagus.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Hoplolaimus von Daday, 1905

Systematic position: Tylenchina, Hoplolaimidae

Morphology: Nematodes of medium length (1–2 mm) dying slightly curved ventrally on application of gentle heat. **Head region high, offset, rounded and with massive sclerotization** (1). Basal lip annule may be divided into small squares. **Stylet massive, 40–50 µm long, with well developed basal knobs bearing anterior tooth-like projections** (2). **Oesophagus** well-developed **with a dorsally overlapping gland lobe** (3) containing 3 or 6 nuclei. Female: vulva median, genital system consisting of two opposed tracts. Tail short, bluntly rounded. **Phasmids enlarged to form scutellae, one being between the anus and the vulva** (4) **and the other anterior to the vulva** (5). Male: tail short, spicules well-developed, arcuate. Bursa extending to tail tip. **Scutellae situated at similar relative positions to the female.**

Major species: *H. columbus, H. indicus, H. pararobustus, H. seinhorsti*

Synonyms: *Basirolaimus, Hoplolaimoides*

Scutellonema Andrássy, 1958

Morphology: Small to medium sized nematodes (0.3–1.5 mm) usually dying in a C-shape or open spiral, **Head region with moderate sclerotization** (6). **Stylet of medium development with rounded knobs** (7). **Oesophagus with dorsal overlap**. Female: vulva median with two opposed genital tracts. Tail short, bluntly rounded. Phasmids enlarged to form **scutellae which are opposite one another and either on or very near to the tail** (8). Male: tail short, spicules well-developed, arcuate. Bursa extending to tail tip. **Scutellae opposite one another on tail region.**

Major species: *S. brachyurus, S. bradys, S. cavenessi*

Aorolaimus Sher, 1964

Morphology: Similar to *Scutellonema* in general characters but females differ in having the **scutellae well anterior to the anus (yet posterior to the vulva)** (9) and **not opposite one another**. Males have a similar arrangement of the scutellae and the **bursa is large, often extending beyond the tail tip as two lobes** (10).

Major species: *A. luci*

Synonym: *Peltamigratus* Sher, 1964

Biology: All three genera are migratory endoparasites of roots and/or tubers. Most species are polyphagous. Reproduction can be amphimictic or parthenogenetic. *Scutellonema bradys* causes a serious dry rot of yam tubers.

Distribution: Widespread in tropical and subtropical areas although *Aorolaimus* is more restricted to S. America and parts of Africa.

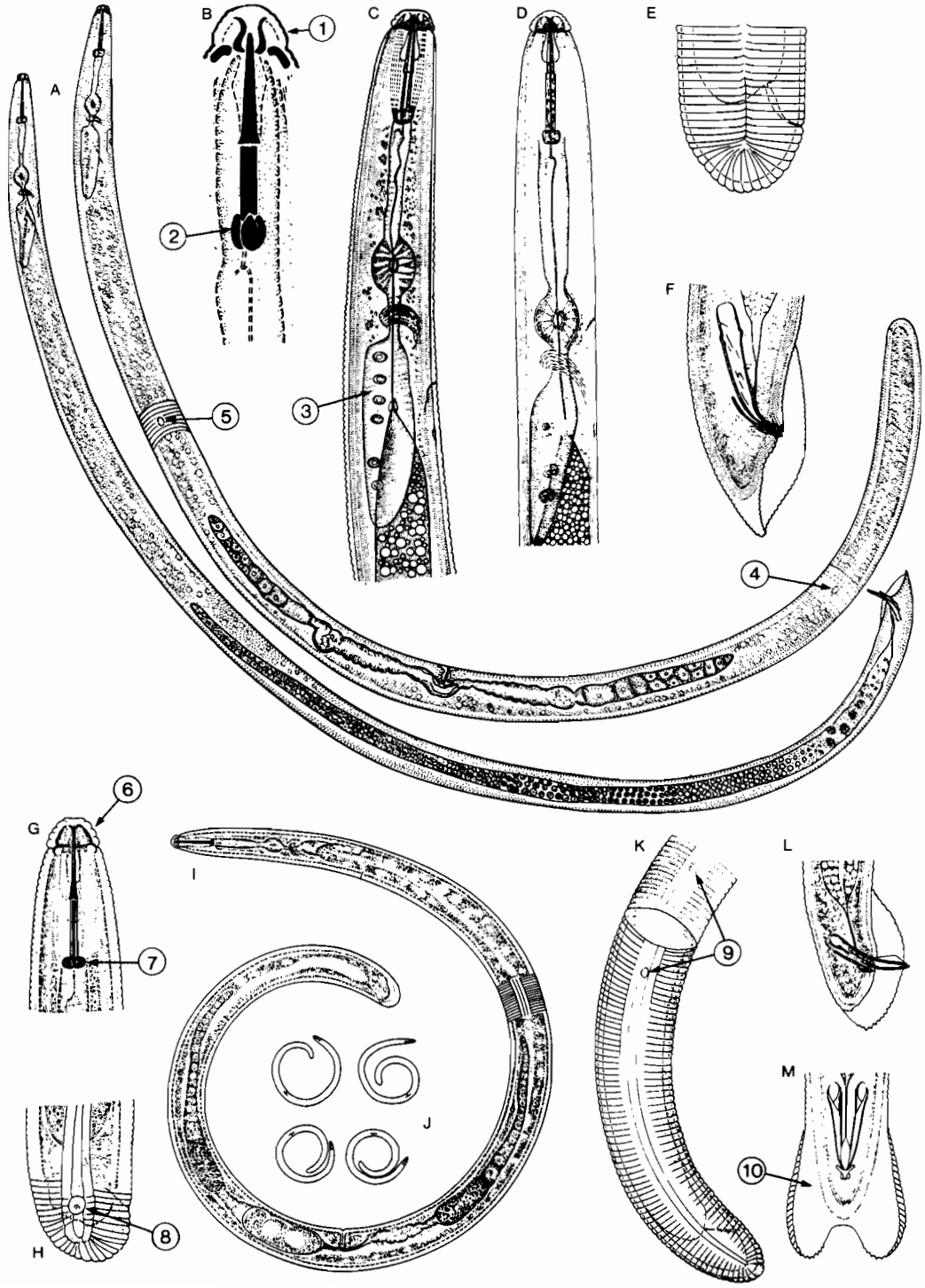
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 10; Set 3, No. 33; Set 4, No. 54; Set 5, No. 66; Set 6, Nos. 76, 81).

Bittencourt, C. & Huang, C. S. (1986) Brazilian *Peltamigratus* Sher, 1964 (Nematoda: Hoplolaimidae), with descriptions of six new species. *Revue de Nématologie 9*: 3–24.

Germani, G., Baldwin, J. G., Bell, A. H. & Wu, X. Y. (1985). Revision of the genus *Scutellonema* Andrássy, 1958 (Nematoda: Tylenchida). *Revue de Nématologie 8*: 289–320.

Fig. 12. *Aorolaimus luci*. K: posterior region; L,M: male tails. *Hoplolaimus indicus*. A: adults; C: oesophagus. *H. pararobustus*. D: oesophagus; E: female tail; F: male tail. *H. seinhorsti*. B: stylet. *Scutellonema brachyurus*. G: head region; H: female tail; I,J: adult females.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Pratylenchus Filipjev, 1936

Systematic position: Tylenchina, Pratylenchidae

Morphology: Small nematodes (less than 1 mm long) dying slightly curved ventrally on application of gentle heat. **No marked sexual dimorphism in form of anterior region** (1). **Head region low, flattened** (2), usually appearing as a flat, black cap under the stereomicroscope. Lip region divided into 2, 3 or 4 annules and continuous with the body contour; strongly sclerotized. Stylet 20 µm or less in length (i.e. about twice the head width) moderately sclerotized and with rounded or anteriorly concave knobs. Oesophagus equally developed in both sexes, median bulb well-developed; **oesophageal gland lobes overlapping the intestine ventrally** (3). Female: **vulva well posterior at 70–80% of body length** (4); genital system with a single anteriorly directed tract and a variable post-vulval section which may show some differentiation but is never functional (5) (**mono-prodelphic**); spermatheca oval or round and usually filled with sperm in bisexual species; **tail sub-cylindrical or more or less conoid with a broad to narrowly rounded** (6) **or truncate terminus** (7) which may be smooth (8) or annulated (9). Male: tail short, dorsally convex-conoid; **bursa extending to tail tip** (10); spicules slender, arcuate.

Biology: Migratory endoparasites with all stages found in the root cortex. Low soil populations can be associated with high root populations. The nematodes feed mainly on cortex cells and form cavities containing 'nests' or colonies of nematodes of all stages. Discolouration of affected tissues is usually pronounced. Above ground symptoms of attack include chlorosis and stunting.
Some species reproduce sexually while others are parthenogenetic. The life-cycle can be completed in three to four weeks and the nematodes can survive in the absence of host plants for several months. Most important species are polyphagous, although *P. goodeyi* may be restricted to banana.

Major species: *P. brachyurus, P. coffeae, P. goodeyi, P. penetrans, P. zeae*

Distribution: *P. brachyurus, P. coffeae* and *P. zeae* are widely distributed in tropical and subtropical areas; *P. penetrans* mainly in cooler regions of the tropics; *P. goodeyi* on banana in Crete and the Canary Islands and in the cooler areas of Ethiopia, Kenya, Tanzania, Uganda and Burundi.

Confusable genus: *Radopholus*

Useful Literature

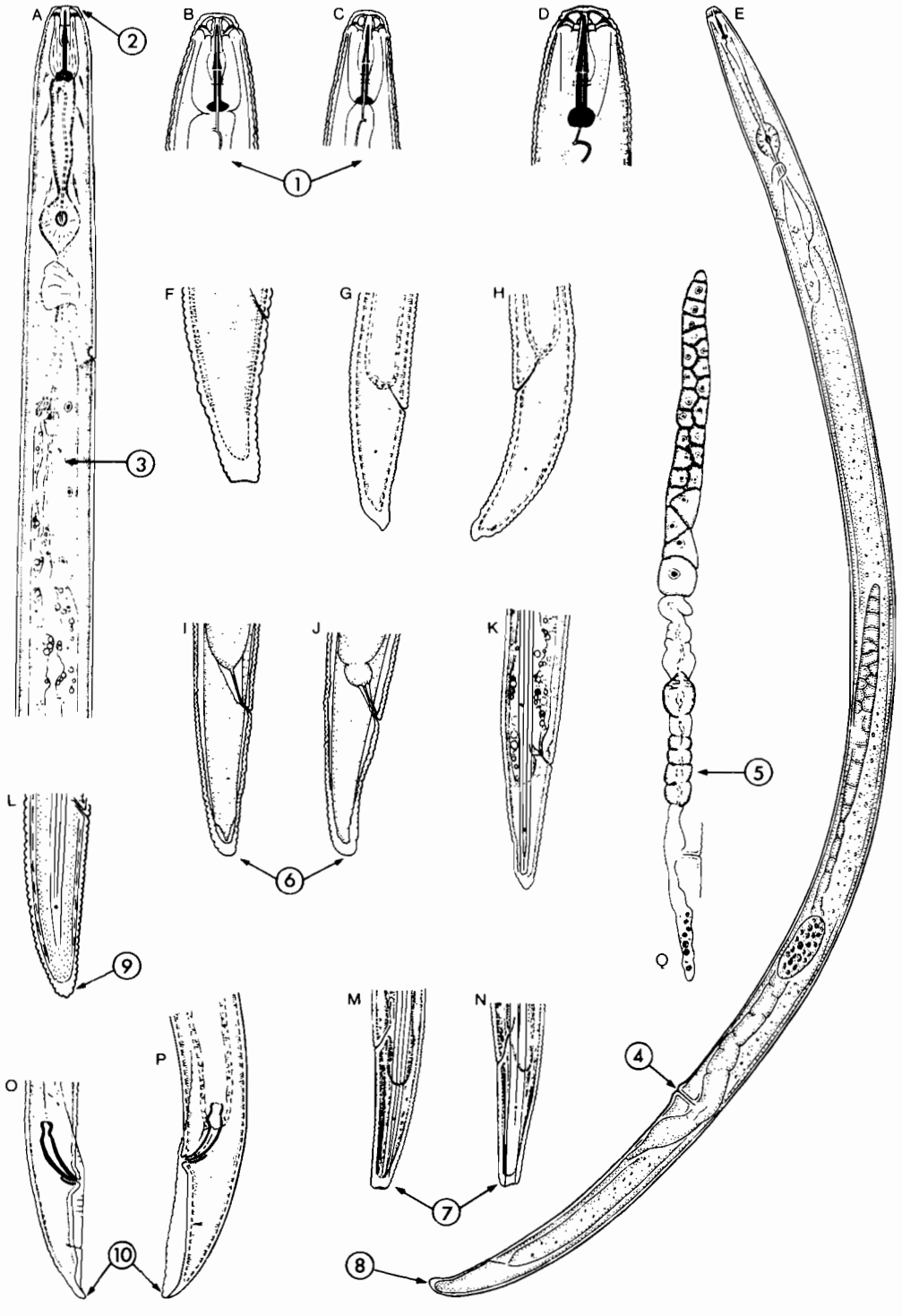
CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 6; Set 2, No. 25; Set 6, Nos. 77, 89; Set 8, No. 120).

Café Filho, A. C. & Huang, C. S. (1989) Description of *Pratylenchus pseudofallax* n.sp. with a key to species of the genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae) *Revue de Nématologie, 12*: 7–15.

Handoo, Z. A. & Golden, A. M. (1989). A key and diagnostic compendium to the species of the genus *Pratylenchus* Filipjev, 1936 (Lesion nematodes). *Journal of Nematology, 21*: 202–218.

Loof, P. A. A. (1978). The genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae): a review of its anatomy, morphology, distribution, systematics and identification. *Vaxskyddsrapporter, Jordbruk 5* Uppsala. Sweden, 50 pp.

Fig. 13. *Pratylenchus zeae*. A: oesophagus; K: female tail; O: male tail; Q: female genital tract. *P. vulnus*. B: female head; C: male head. *P. brachyurus*. D: female head; F: female tail. *P. pratensis*. E: entire female; L: female tail. *P. goodeyi*. G,H: female tail. *P. coffeae*. M,N: female tail. *P. penetrans*. I, J: female tail.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Hirschmanniella Luc & Goodey, 1963

Systematic position: Tylenchina, Pratylenchidae

Morphology: Medium-sized to long, slender nematodes (1–4 mm) dying more or less straight or ventrally arcuate (1) on application of gentle heat. No marked sexual dimorphism in form of anterior region (2). **Head region** continuous with body contour, **hemispherical** (3) **or anteriorly flattened** (4). Stylet strongly developed (15–46 μm) with rounded basal knobs. **Oesophageal glands elongate and overlapping the intestine in a long ventral lobe** (5). Female: **vulva median** (6); **genital system with two functional and equally developed genital tracts** (7), one anteriorly and one posteriorly, directed; **tail elongate, conoid** (8), **terminal mucron often present** (9). **Male tail similar to female** (10); **bursa not reaching to tail tip** (11), spicules slender, arcuate.

Biology: Migratory endo-parasites, mainly of roots, but also corms and rhizomes, where they move freely through the tissues. Eggs are laid within the root and development to the adult takes about 5–6 weeks. The genus is associated with aquatic environments – marsh, freshwater and marine. Most species are bisexual.

Major species: *H. mexicana (= caudacrena), H. imamuri, H. miticausa, H. mucronata, H. oryzae, H. spinicaudata*

Distribution: The genus is distributed worldwide in suitable habitats. *H. oryzae* is the major species and is well-distributed in the rice-growing areas of India, Bangladesh, Malaysia, Indonesia, Philippines, Japan. It is also found in parts of Africa and South America.

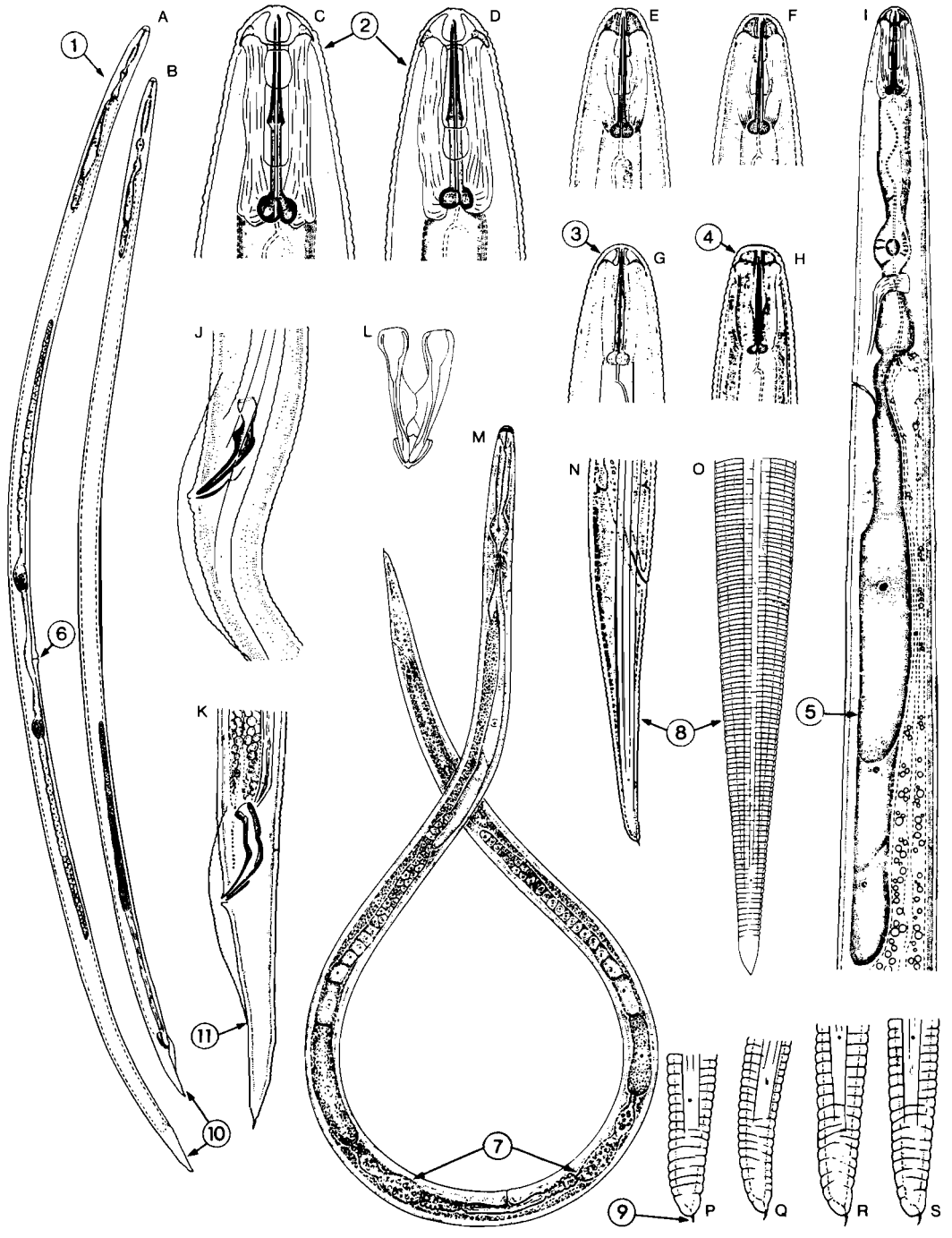
Confusable genus: *Radopholus*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 2, No. 26; Set 5, No. 68).

Ebsary, B. A. & Anderson, R. V. (1982). Two new species of *Hirschmanniella* Luc & Goodey, 1963 (Nematoda: Pratylenchidae) with a key to nominal species. *Canadian Journal of Zoology, 60*: 530–535.

Fig. 14. *Hirschmanniella spinicaudata*. A: entire female; B: entire male; C: female head; D: male head; I: oesophagus; K: male tail; L: spicules. *H. oryzae*. H: female head; N: female tail; P-S; female tail terminus. *H. magna*. E: female head; F: male head; J: male cloacal region. *H. mucronata*: female head. *H. nana*. (= *H. oryzae*). M: entire female. *H. diversa*. O: female tail.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Radopholus Thorne, 1949

Systematic position: Tylenchina, Pratylenchidae

Morphology: Small nematodes (less than 1 mm long) dying more or less straight or slightly curved ventrally on application of gentle heat. **Marked sexual dimorphism in form of anterior region** (1): female head region low, rounded, continuous or slightly offset from body contour; male head region higher, often knob-like and more offset. **Male cephalic sclerotization, stylet and oesophagus reduced** (2); female cephalic sclerotization strong, stylet and oesophagus well-developed (3). Median bulb in female oesophagus well-developed and **oesophageal glands overlapping the intestine mostly dorsally** (4). Female: **vulva median** (5), **usually with two functional and equally developed genital tracts** (6) but posterior tract may be reduced, spermathecae rounded and with sperm in bisexual species; **tail elongate** (7), conoid (about 60 µm long in *R. similis*). Male: **tail elongate** (8), conoid, ventrally arcuate; **bursa not reaching to tail tip** (9) in *R. similis* and most other species; spicules slender, arcuate.

Biology: Migratory endoparasites of root and corm/tuber tissues. In roots the feeding activities are restricted to the cortex causing cavitation, discolouration and severe damage allowing secondary invasion by other micro-organisms. The adult male is non-feeding. The major species is *R. similis* which has two recognised host races or biotypes. *R. similis similis* attacks banana and many other plants, but not citrus, whereas *R. similis citrophilus* (recognised as a separate species by some authorities on differing chromosome count and minor morphological details) attacks both citrus and banana as well as a variety of other plants. However, it is possible that *R. similis similis* includes a range of host races.

Major species: *R. similis similis, R. similis citrophilus*

Distribution: The majority of species have been described from Australasia. However, *R. similis similis* is found worldwide in tropical regions and occurs virtually everywhere that banana is grown. *R. similis citrophilus* is only recorded from Florida at present.

Synonyms: *Neoradopholus, Radopholoides*

Confusable genera: *Achlysiella, Pratylenchus, Hirschmanniella.*

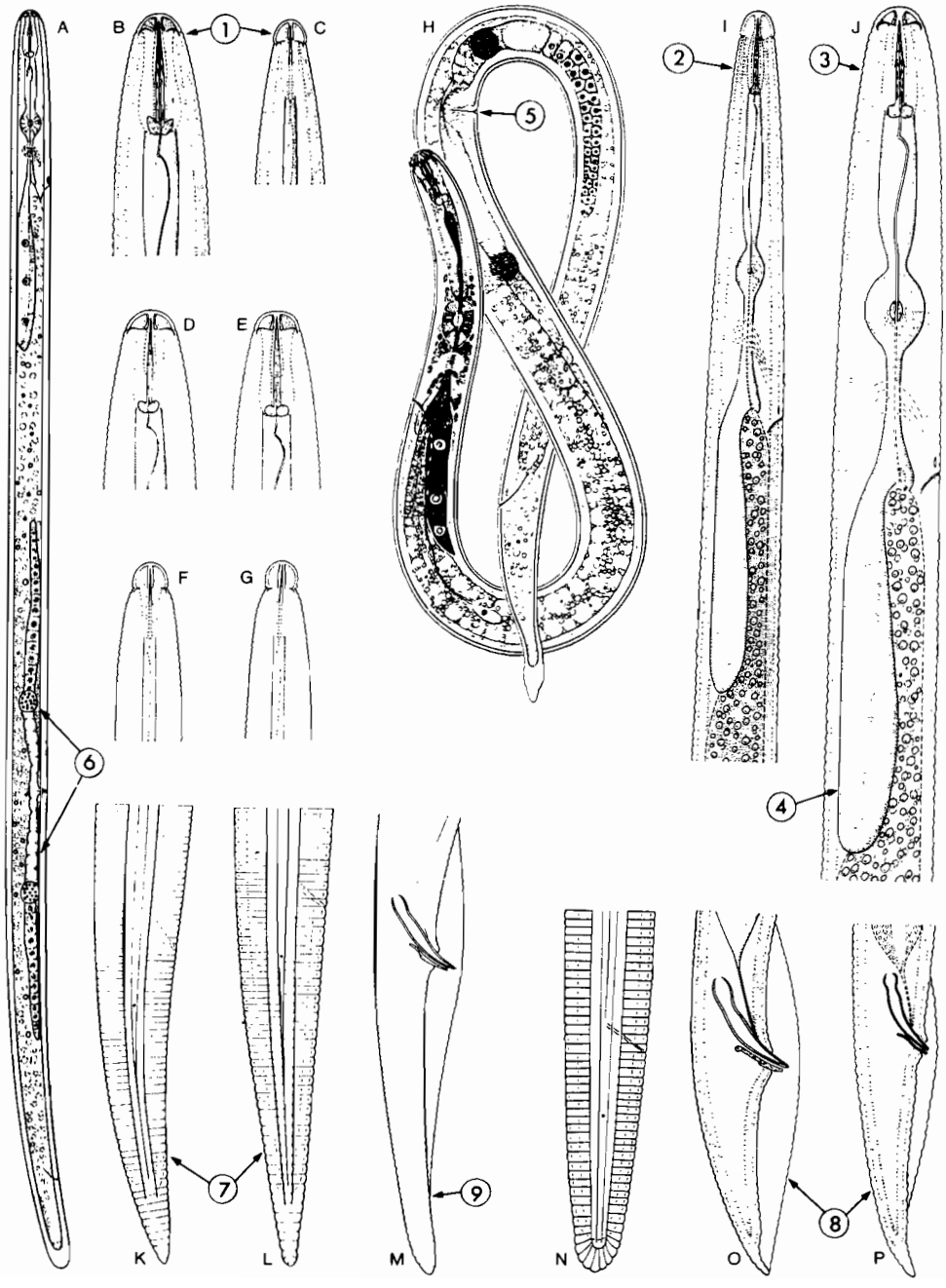
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 2, No. 27).

Colbran, R. C. (1970) Studies of plant and soil nematodes. 15. Eleven new species of *Radopholus* Thorne and a new species of *Radopholoides* de Guiran (Nematoda: Tylenchoidea) from Australia. *Queensland Journal of Agricultural and Animal Sciences, 27*: 437–460.

Sher, S. A. (1968) Revision of the genus *Radopholus* Thorne, 1949 (Nematoda: Tylenchoidea). *Proceedings of the Helminthological Society of Washington, 35*: 219–237.

Fig. 15. *Radopholus similis*. D,E: female head; F,G: male head; H: entire female; K,L: female tails; M: male tail. *R. rotundisemenus*. A: entire female. *R. inaequalis*. B: female head; C: male head; N: female tail; O: male tail. *R. vangundyi*. I: male oesophagus; J: female oesophagus; P: male tail.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Heterodera Schmidt, 1871

Systematic position: Tylenchina, Heteroderidae

Morphology: Sexually dimorphic. Female: obese, **lemon-shaped**, 300–600 µm, in diameter with a distinct neck (1) and either partially enclosed in root tissue or in the soil. **Vulva subterminal, near anus. Cuticle thick**, whitish at first but **tanning** to a **brownish-black colour** as the **cyst matures. Eggs retained within the protective cyst. Vulva and anus located** on a **terminal cone** with **two** translucent areas, the **fenestrae**, on **either side of the vulval slit** (2). Two convoluted genital tracts. In young females the excretory pore can be seen at the level of, or posterior to, the median bulb valve plates (3). **Male: vermiform** with the **body often twisted through 180° on heat relaxation**; found free in soil. Stylet and head skeleton robust. **Tail short**, hemispherical. **Spicules opening subterminally** (4). **No bursa**. Juvenile (J2): vermiform, 450–600 µm long. **Stylet and head skeleton robust** (5), **tail** conical **with hyaline area starting well before tail terminus** (6).

Synonym: *Bidera*.

Globodera Skarbilovich, 1959

Morphology: Similar to *Heterodera* but the **cyst is globose** (7) (i.e. the vulva and anus are not on a terminal cone) and the **vulval slit** is **surrounded by a single, circular, fenestra** (8).

Biology: In most species all the eggs are retained within the mature cyst, although in some a few eggs are also held in an external gelatinous matrix. Eggs often hatch in response to root exudates from a host plant, although other hatching factors can be involved. The J2 emerges from the egg, invades a root and induces a feeding site composed of syncitial nurse cells. Root galling is not induced. The J2 swells and moults three times to form the adult female which enlarges rapidly, the posterior region bursting through the root epidermis. Males are more commonly produced when food is in short supply. They assume a vermiform state within the J4 cuticle before burrowing out of the root into the soil. Females produce several hundred eggs, and after death, the cuticle of the female tans to form a protective cyst.

Major species: *H. avenae, H. cajani, H. ciceri, H. glycines, H. latipons, H. sacchari, G. pallida, G. rostochiensis*

Distribution: Most *Heterodera* species are more tropical or subtropical whereas *Globodera* species tend to be confined to the cooler areas.

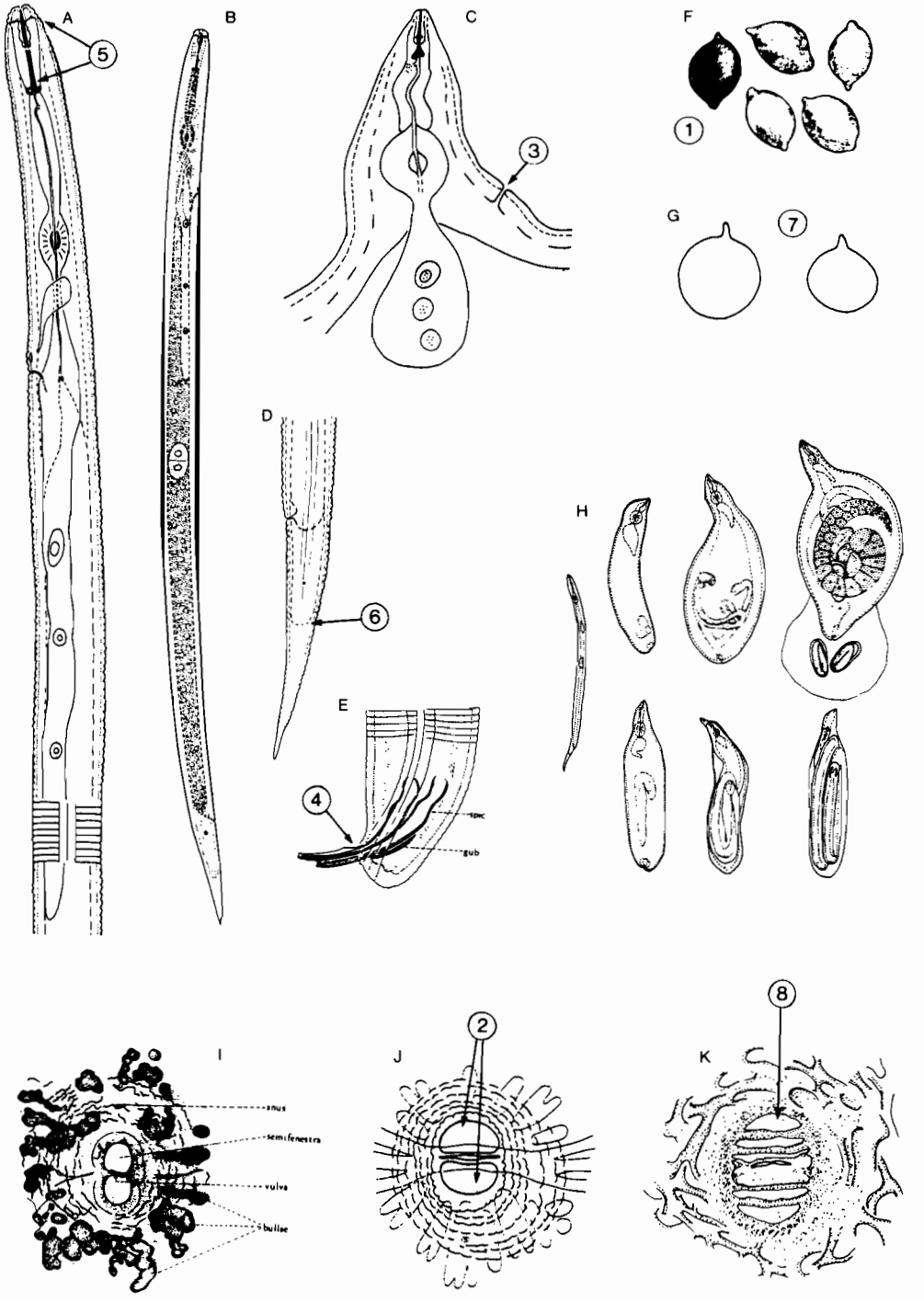
Confusable genera: *Cactodera, Punctodera*. J2 infectives can be confused with those of *Meloidogyne*.

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 2; Set 2, Nos 16, 17; Set 4, No. 48; Set 8, No. 118).

Golden, A. M. (1986). Morphology and identification of cyst nematodes. In: *Cyst Nematodes*. Ed. Lamberti & Taylor, NATO ASI Series, Plenum Press, London, pp. 23–46.

Fig. 16. *Globodera rostochiensis*. C: female anterior region; G: entire cysts; K: perivulval area. *Heterodera avenae*. E: male tail; F: cysts; I: perivulval area. *H. glycines*. J: perivulval area. *H. oryzae*. D: juvenile tail. *H. sacchari*. A: J2 oesophagus; B: juvenile (J2 infective). *H. schachtii*. H: developmental stages.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Meloidogyne Goeldi, 1887

Systematic position: Tylenchina, Heteroderidae

Morphology: Sexually dimorphic. **Female: embedded in root tissue, globose**, 0.5–0.7 mm in diameter **with a slender neck** (1). **Vulva subterminal near anus** (2). Cuticle whitish, thin, annulated. Stylet short, moderately sclerotized. Head skeleton weak. **Excretory pore anterior to median bulb valve plates** (3) and often near stylet base. Two convoluted genital tracts. **Eggs deposited outside the body in a gelatinous matrix. Male: vermiform** (4), free-living in soil, 1–2 mm long. **Body usually twisted through 180° along its length on heat relaxation. Stylet and head skeleton robust. Tail short** (5), hemispherical. Spicules robust. **Bursa absent**. Juveniles (J2): Slender, vermiform (6), about 450 µm long. **Stylet and head skeleton weakly sclerotized. Tail conical with hyaline portion starting near the tail tip** (7).

Biology: In most species the eggs are retained within a gelatinous matrix outside the swollen female body. On hatching the J2 invades a host root and induces a trophic system of giant cells. Cortical cells are also induced to multiply and so form the characteristic gall. The remainder of the life cycle is similar to *Heterodera/Globodera* except that, in most species, the females do not normally burst out of the root as they are surrounded by the gall tissue.

Major species: *M. arenaria, M. exigua, M. graminicola, M. incognita, M. javanica.*

Distribution: Widely distributed throughout the tropical and subtropical regions.

Synonym: *Hypsoperine*

Confusable genera: *Nacobbus, Heterodera/Globodera.* J2 infectives can be confused with those of *Heterodera/Globodera.*

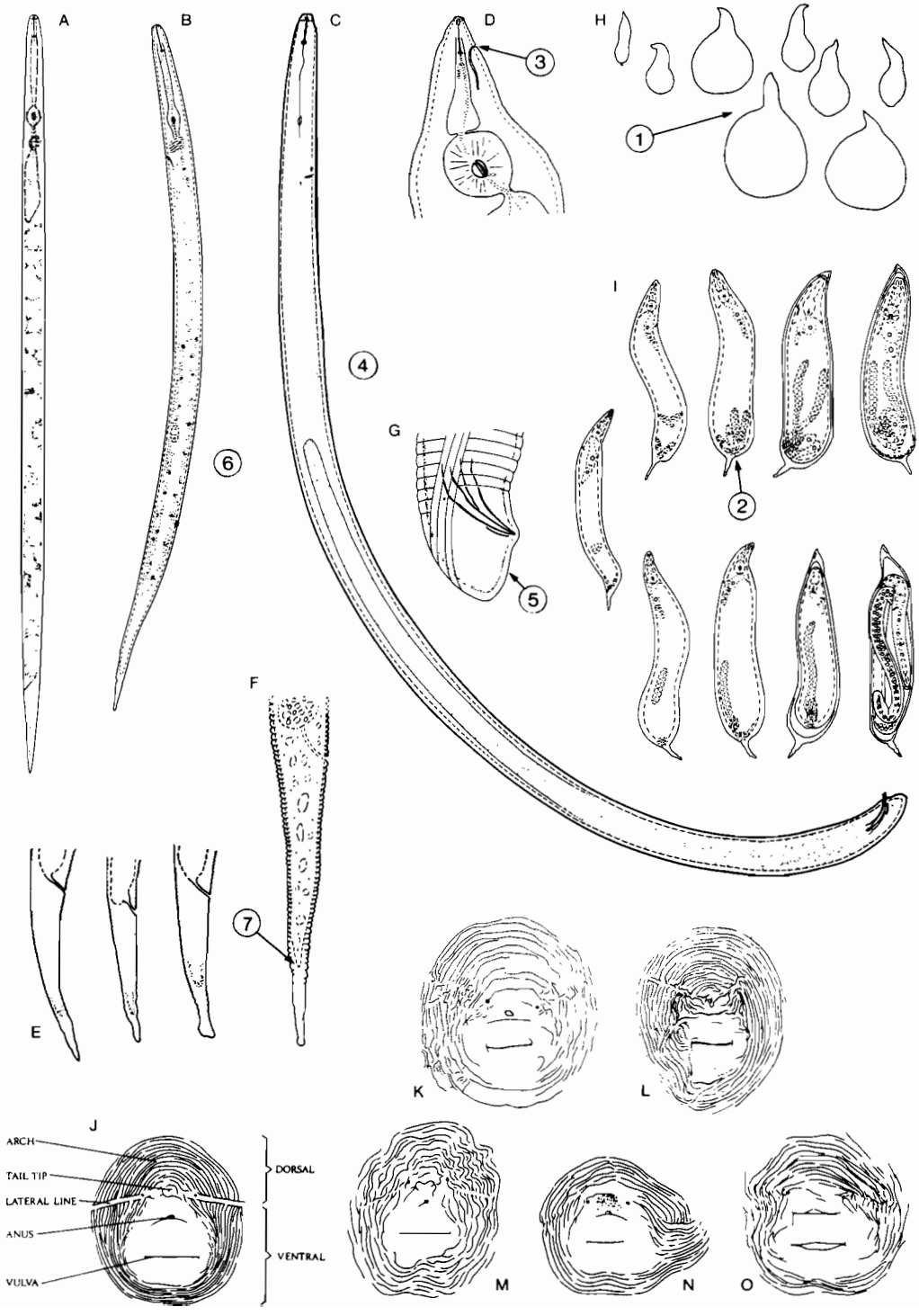
Useful Literature

CIH Descriptions of Plant-parasitic Nematodes. Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 3; Set 2, No. 18; Set 4, No. 49; Set 5, No. 62; Set 6, No. 87).

Jepson, S. B. (1987). *Identification of root-knot nematodes* (Meloidogyne *species*). CAB International, Wallingford, UK. 252pp.

Sasser, J. N. & Carter, C. C. (Editors) (1985). *An advanced treatise on* Meloidogyne. Vols. I & II. North Carolina State University, Raleigh, USA.

Fig. 17. *Meloidogyne arenaria*. O: perineal pattern. *M. chitwoodi*. C: male *M. exigua*. K: perineal pattern. *M. graminicola*. F: juvenile tail; L: perineal pattern. *M. hapla*. E: juvenile tails; N: perineal pattern. *M. incognita*. I: developmental stages of male and female; M: perineal pattern. *M. javanica*. A: J2 infective; H: development of female; J: perineal pattern. *M. naasi*. B: J2 infective; D: female oesophageal region.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Nacobbus Thorne & Allen, 1944

Systematic position: Tylenchina, Pratylenchidae

Morphology: Sexually dimorphic. Immature female (in soil or in roots). Vermiform, slender (1), 0.6–1 mm long. Labial area rounded, continuous with body contour. **Cephalic sclerotization strong** (2); **stylet robust, with rounded basal knobs** (3). Oesophagus with strong median bulb and strong valves; oesophageal glands long, dorsally overlapping the intestine (4). **Vulva posteriorly situated** (5) (V = 90–95%); vulval lips not protruding. **One anterior genital tract**. Tail short, rounded. Mature females: (in roots). **Body saccate; anterior and posterior portions tapering** (6). Genital tract convoluted, spermatheca axial, generally filled with sperm. Tail short. Male: Similar to immature female, except for sexual characters. Spicules curved. Tail short; **bursa reaching tail tip** (7). Juveniles: Resembling immature female.

Biology: The eggs are laid within a gelatinous matrix formed by the female. On hatching, the J2 invades a root, but does not form a fixed feeding site. Instead the juveniles migrate through the tissue and may even leave the root and enter another. The J3 and J4 stages are less mobile. After the final moult the immature female may leave the root and enter another before taking up a position near the vascular tissue and initiating a syncitial trophic system and gall formation. As the female develops, the posterior section extends towards the epidermis and an opening in the gall is formed through which the gelatinous matrix and eggs are extruded.

Major species: *N. aberrans, N. dorsalis*

Distribution: Known only from the Americas.

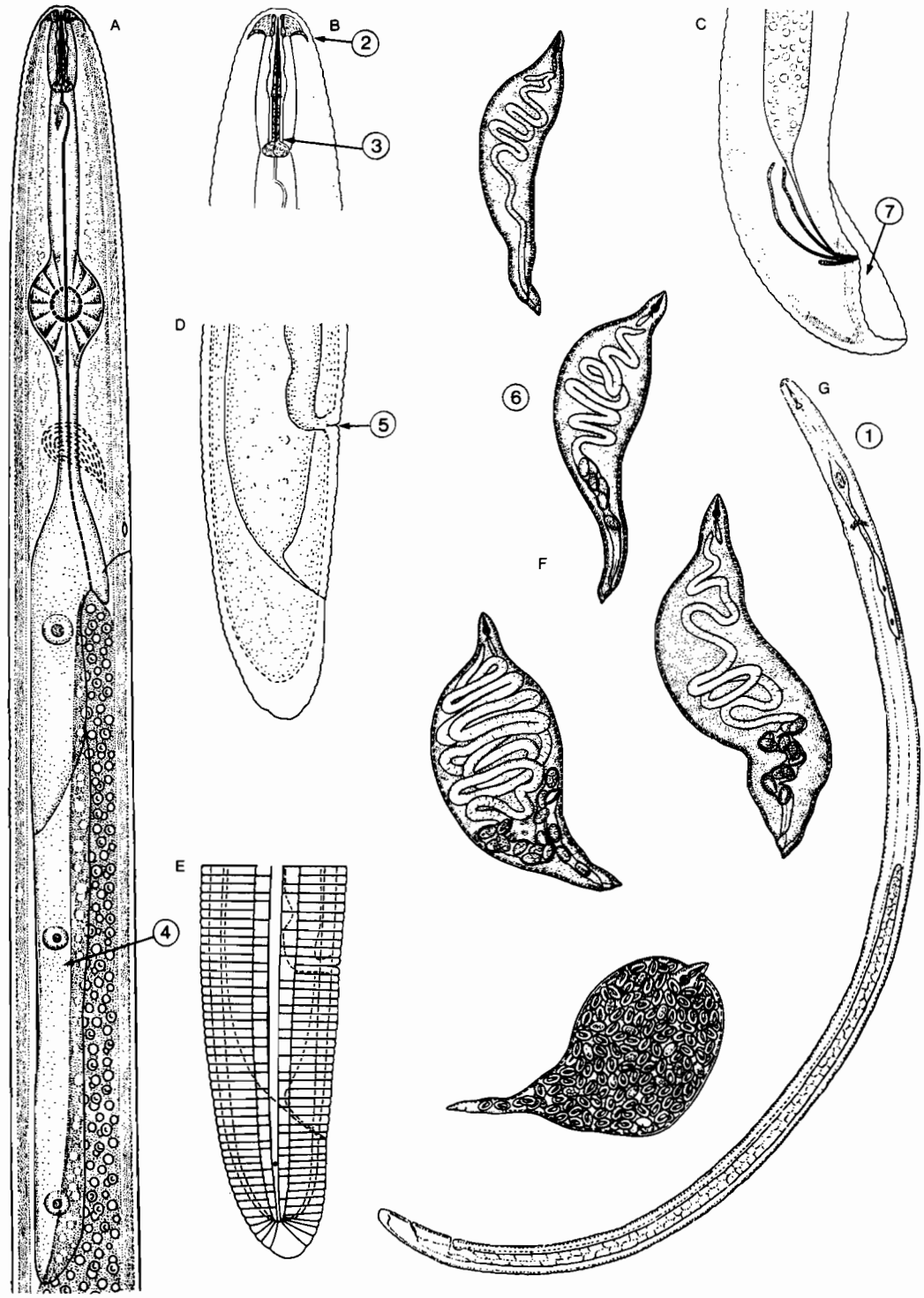
Confusable genus: *Meloidogyne*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 8, No. 119).

Doucet, M. E. (1989). The genus *Nacobbus* Thorne & Allen, 1944 in Argentina. 1. Study of a population of *N. aberrans* (Thorne, 1935) Thorne & Allen, 1944 on *Chenopodium album* L. from Rio Cuarto, Province of Cordoba. *Revue de Nématologie, 12*: 17–26.

Fig. 18. *Nacobbus aberrans*: Immature female. A: oesophagus; B: head; D,E: posterior region; G: entire. Male. C: tail. Mature female. F: developmental stages.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Rotylenchulus Linford & Oliveira, 1940

Systematic position: Tylenchina, Hoplolaimidae

Morphology: Sexually dimorphic. Immature female (free in soil): Body vermiform, small (0.23–0.64 mm), dying ventrally arcuate on application of gentle heat. **Head region** rounded to conoid, **continuous with body contour** (1), striated. Cephalic sclerotization of medium development. Stylet of medium strength, with rounded basal knobs. Oesophagus with well-developed median bulb and valves; dorsal oesophageal gland opening well posterior to stylet base (2) (0.6–1.9 times the stylet length); glands well developed with a long lateral overlap. **Vulva posteriorly situated** (V = 58–72); **vulval lips not protuberant** (3). **Two genital tracts**, each with a double flexure. Tail conoid, with rounded terminus. Mature female (on roots): **Swollen to kidney shaped body** (4). Anterior part irregular. **Vulval lips protruding** (5). Genital tracts convoluted. Male: Vermiform. Cephalic sclerotization, stylet and oesophagus reduced (median oesophageal bulb weak, without valves) but conspicuous. Spicules curved. **Tail pointed. Bursa not reaching tail tip**. Juvenile: Resembling immature female, but shorter, and lacking vulva and genital tracts.

Biology: The eggs are laid in a gelatinous matrix. On hatching the juveniles moult to the immature female or male without feeding. The immature female is the invasive stage, but only the anterior section penetrates the root tissue, the posterior part remaining in the soil and becoming obese (i.e. a sedentary semi-endoparasite). About 50 eggs are deposited in a gelatinous matrix which is secreted by specialized vaginal cells.

Major species: *R. borealis, R. parvus, R. reniformis*

Distribution: *R. reniformis* is almost ubiquitous in tropical and subtropical soils, but the other species are more restricted in their distribution.

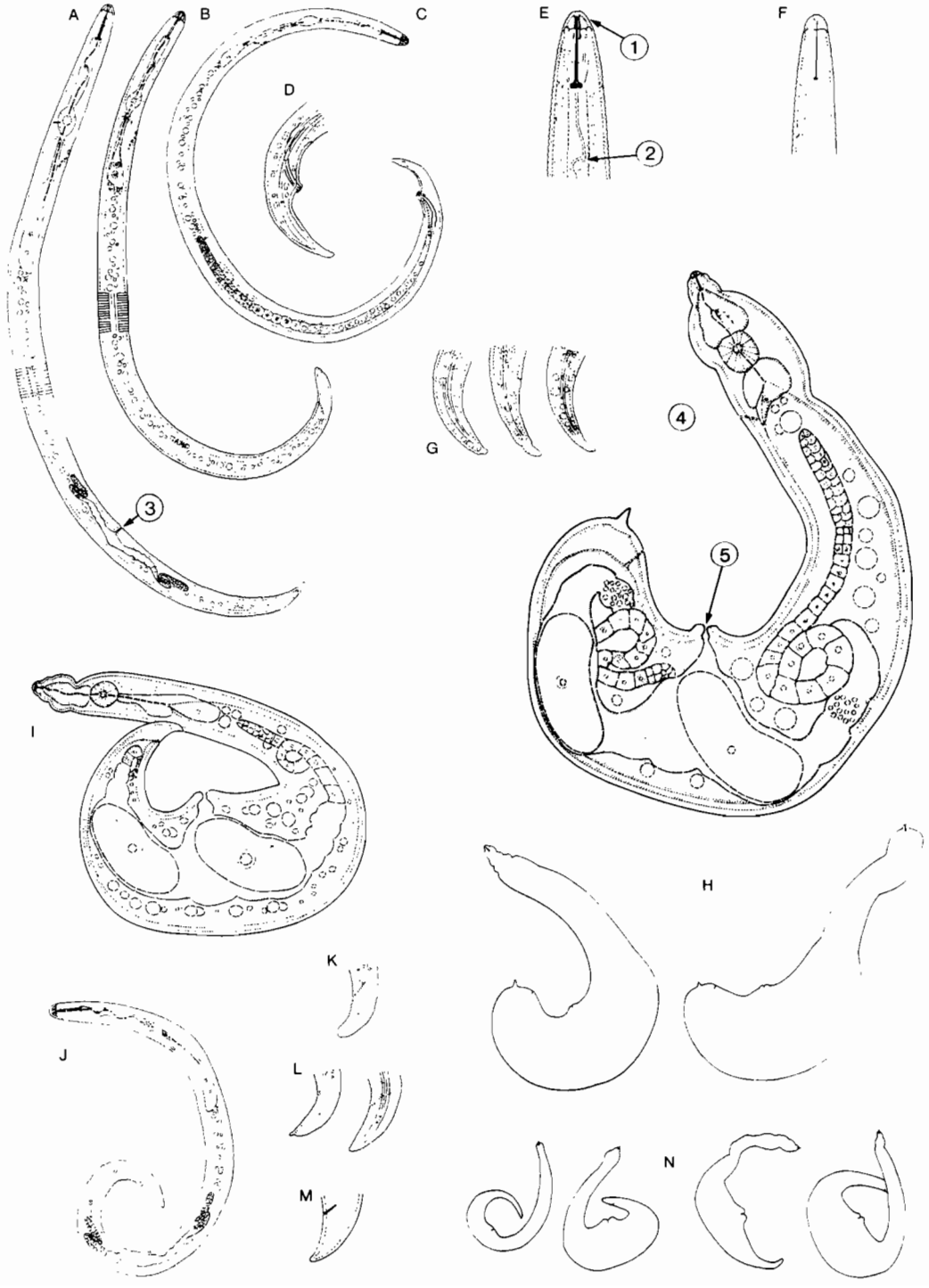
Confusable genus: *Senegalonema*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 1, No. 5; Set 6, No. 83).

Dasgupta, D. R., Raski, D. J. & Sher, S. A. (1968). A revision of the genus *Rotylenchulus* Linford & Oliveira, 1940 (Nematoda: Tylenchidae) *Proceedings of the Helminthological Society of Washington. 35*: 169–192.

Fig. 19. *Rotylenchulus parvus*. I,N: mature females; J: immature female; K: juvenile tail; L,M: immature female tails. *R. reniformis*. A: immature female; B: juvenile; C: male; D: male tail; E: female head; F: male head; G: female tail development; H: mature females.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Tylenchulus Cobb, 1913

Systematic position: Tylenchina, Tylenchulidae

Morphology: Sexually dimorphic. Immature female (free in soil): Body vermiform, ventrally curved posteriorly, small (under 0.5 mm). Head region rounded, continuous with body contour. Cephalic sclerotization weak. **Stylet of medium development** (1) with rounded basal knobs. **Oesophagus with strong median bulb which is not well separated from the procorpus** (2); **glands forming a basal bulb** (3). **Vulva very posteriorly situated** (4); **genital tract single, anteriorly outstretched. Excretory pore very posteriorly situated** (5), slightly anterior to the vulva. Tail conical. **No anus or rectum.** Mature female: **Anterior part embedded in root tissue** (6), **irregular**, slender, **with thin cuticle** (7). **Posterior part**, bursting out of root, **swollen with very thick cuticle** (8) and a pointed postvulvar section; **excretory pore and vulva very posterior** (9). **Excretory cell well developed**, and producing a gelatinous matrix. Genital tract convoluted, with several eggs. **No anus, or rectum.** Male: Body vermiform, short and slender. **Cephalic sclerotization, stylet and oesophagus reduced** (10). Spicules slightly curved. **No bursa.** Tail conical, pointed. Juvenile: Body vermiform. Cephalic sclerotization, stylet and oesophagus similar to those of immature females. Tail long, pointed. Genital primordium differently shaped in male and female juveniles from J2 onwards.

Biology: The eggs are contained in a gelatinous matrix which is produced by the excretory cell. After hatching, male juveniles moult to the adult without feeding whilst female juveniles feed on cortical cells. The immature female penetrates deeper into the root, the anterior end reaching deep into the cortex whilst the posterior section remains in the soil and becomes obese. A highly sophisticated system of trophic nurse cells is initiated around the female head. [Note: a heavily infested citrus root, when carefully rinsed in water, retains a collar of earth adhering to the gelatinous egg-sacs underneath].

Major species: *T. semipenetrans*

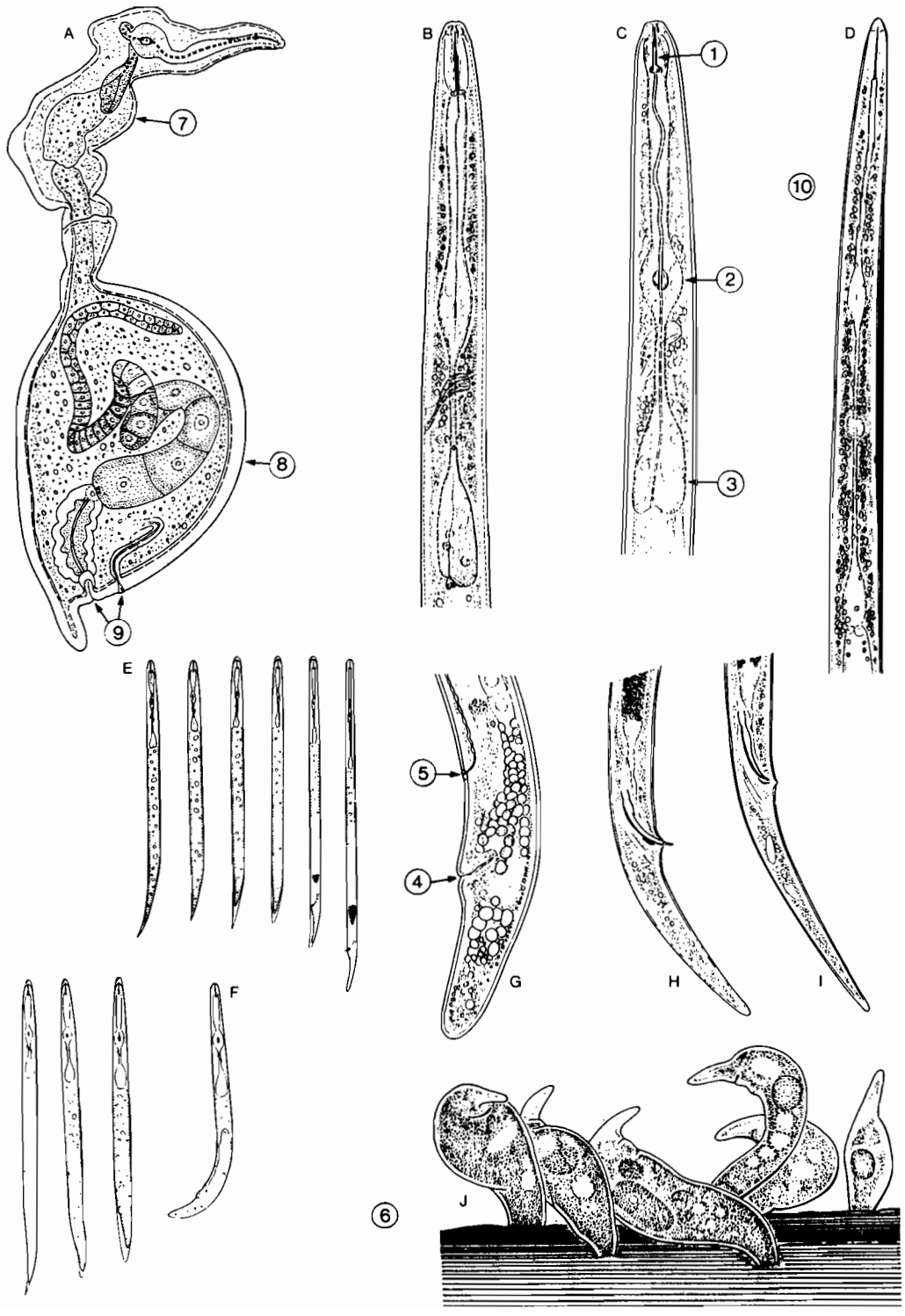
Distribution: Found almost everywhere that citrus is grown on any scale.

Confusable genus: *Trophotylenchulus*

Useful Literature

CIH Descriptions of Plant-parasitic Nematodes, Sets 1–8. CAB International, Wallingford, UK. (Set 3, No. 34).

Fig. 20. *Tylenchulus semipenetrans*. A: mature female; B: juvenile oesophagus; C: immature female oesophagus; D: male oesophagus; E: development of male; F: development of female; G: immature female vulval region: H,I: male tails; J: mature females on root.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Cahier ORSTOM, série Biologie. Luc, M. *11*, 5–131 (Fig. 7 H). *Journal of Nematology*. Sher, S. A. *2* 228–235 (Fig. 18 A-F). *Nematologica*. Sher, S. A. *9*, 267–295 (Fig. 12 K-M); *14*, 243–275 (Fig. 14 M,O). *Phytopathology*. Raski, D. J. *40*, 135–152. (Fig. 16 H). *Phytophylactica*. Jacob, P. J. F. & Heyns, J. *14*, 169–178 (Fig. 10 A,B,E,N). [Reproduced under South Africa government printer's copyright authority 9017 of 5 July 1989]. *Proceedings of the Helminthological Society of Washington*. Dasgupta, D. R., Raski, D. J. & Sher, S. A. *35*, 169–192 (Fig. 19 A-N); Sher, S. A. *35*, 219–237 (Fig. 15 A-G, I-P); Siddiqi, M. R. *33*, 173–177 (Fig. 14 E-G, J). Quimi, V. H. *Studies on the false root-knot nematode* Nacobbus aberrans. Unpublished thesis, University of Reading (Fig. 18 G). *Revue de Nématologie*. Luc, M. & Southey, J. F. *3*, 243–269 (Fig. 1 R,N; 10 C,M); Siddiqi, M. R. *2*, 51–64 (Fig. 1 R N, 10 F-H, K,L,O); *3*, 179–199 (Fig. 8 A-E,G). *Soil and freshwater nematodes*. Goodey, J. B. Methuen. pp 544 (Fig. 20 A). *Systematic Parasitology*. Orton Williams, K. J. *8*, 207–214 (Fig. 8 A-E, G) [Reprinted by permission of Kluwer Academic Publishers]. United States Department of Agriculture. (Fig. 15 H. After Cobb, 1915). All other illustrations courtesy of CAB International.

Chapter 2

Extraction and Processing of Plant and Soil Nematodes

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Introduction

Details are given of the methods for the extraction and handling of plant and soil nematodes. There are many modifications to the basic methods often determined by local supplies of equipment and operating conditions. More detailed information is given in Southey (1986); also, Hooper (1987) discusses factors affecting the curation of nematodes.

Collection and storage

1. Most migratory plant parasitic nematodes are found around plant roots and so rhizosphere samples are preferable. Badly stunted plants may have too small a root system to support many nematodes and samples from nearby, less affected, plants may yield more specimens. Usually few nematodes occur in the top 5 cm of soil which can be discarded from samples. Soil samples and plant material to be examined for nematodes should be kept moist. Polythene bags are excellent containers for samples; soil and/or roots keep well in them but whole plants are best kept separate from soil. Plant tops usually decompose faster than roots and should be in separate bags if they are to be stored for more than a day or two. Warm storage adversely affects the extraction of nematodes from plants and soil, so samples should be kept cool, 10°C if possible, and out of direct sunlight. It is common practice to store samples in refrigerators but low temperature (c. 5°C) can adversely affect the recovery of some nematodes from tropical soils (Whyte & Gowen, 1974). For the fixation/preservation of plants and soils see sections 26 and 28, respectively.

Direct examination of plant material

2. Nematodes can usually be seen by examining small amounts of plant tissue with a stereoscopic microscope at magnifications from 15 to 50x using transmitted and/or incident light. Roots should first be gently washed to remove as much soil as possible. Examine the tissue in water in an open Petri dish or large watch glass, and tease it apart with strong mounted needles. Nematodes released from the tissues will float out and can be collected with a handling needle or fine pipette. Nematodes tend to migrate from damaged tissue and it is often worthwhile to re-examine the sample after 2 or

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds) © CAB International 1990

3 hours. To recover females of root-knot nematodes (*Meloidogyne* spp.) from roots, carefully tease away the tissue with forceps and a fine needle to release the head and neck; avoid puncturing the body. Dissection and storage in 0.9% NaCl helps to avoid the osmotic effect of water which tends to cause females to burst. Staining (sections 26 and 27) helps to differentiate nematodes from plant tissues.

Extraction from plant material

The following methods, based on the Baermann funnel technique, rely on the activity of nematodes to separate them from plant material; they are not therefore suitable for extracting sluggish or sedentary nematodes although the juveniles and males of such forms will usually be recovered. Where possible, plastic or stainless steel rather than brass/bronze gauze, rings or pans should be used because metallic ions, especially copper, released into small volumes of static water can be toxic to nematodes, especially dorylaims (Pitcher & Flegg, 1968). However, brief contact with metal sieves as in the sieving technique (section 16) does not appear to be harmful.

Baermann funnel technique

3. A piece of rubber tubing is attached to the funnel stem and closed with a spring or screw clip. The funnel is placed in a suitable support and almost filled with water. Plant material containing nematodes is chopped into small pieces, placed in a square of muslin cloth, nylon gauze, etc, which is folded to enclose the material, and then gently submerged in the water in the funnel (Fig. 1A). Nematodes emerge from the tissues and sink to the bottom of the funnel stem. After some hours, or overnight, some of the water can be run off and examined for nematodes. Lack of oxygen at the base of the funnel stem often inactivates nematodes obtained by this method but these usually revive in fresh water.

Modified Baermann funnel

4. Modifications of the Baermann funnel are illustrated in Fig. 1(B–E). Lack of oxygen and the possibility of nematodes lodging on the sloping funnel sides can be avoided by using a shallow dish instead of a funnel and by supporting the material to be extracted on a sieve. The sieve is conveniently made from a plastic ring (cut from polythene or perspex cylinder or vinyl drain-pipe), about 6 to 8 cm in diameter and 2 cm deep, with a piece of muslin stretched over one end and held by a rubber band, or secured between two closely fitting rings; alternatively, nylon gauze can be stuck or fused to a plastic ring. A milk filter or paper tissue is then placed in the sieve and the chopped plant material put on it. A circle of muslin or paper tissue placed on top of the material will keep it moist and prevent it from floating. The sieve, with the material to be extracted, is placed in water in a Petri dish or similar container. Small supports, e.g. glass rods or small feet attached to the sieve ring, are used to give a space of about 2 mm between the base of the sieve and the collecting dish (Fig. 1D). The material should be almost awash and, when it is not, more water should be added carefully between the outside of the sieve and the edge of the collecting dish. After a few hours, or overnight, the sieve is gently removed and the contents of the dish examined for nematodes. The sieve can be reimmersed in fresh water for further extraction of the material.

Root incubation technique (Young, 1954; West, 1957)

5. When roots are stored moist or in shallow water, migratory endoparasites tend to leave them. Thick roots (e.g. banana) can be split longitudinally to help nematodes emerge. The roots are put into containers such as screw-cap jars, closed Petri dishes or sealed polythene bags, and kept at about 20 to 25°C. The roots are well wetted or immersed in shallow water before the containers are closed. Tarjan (1967, 1972) improved oxygenation, hence nematode extraction, by wetting roots with water containing 1–3% H_2O_2. It is advisable to remove the nematodes every 24 hours by pouring off the water and rinsing the roots. The extraction can be continued by adding a little more

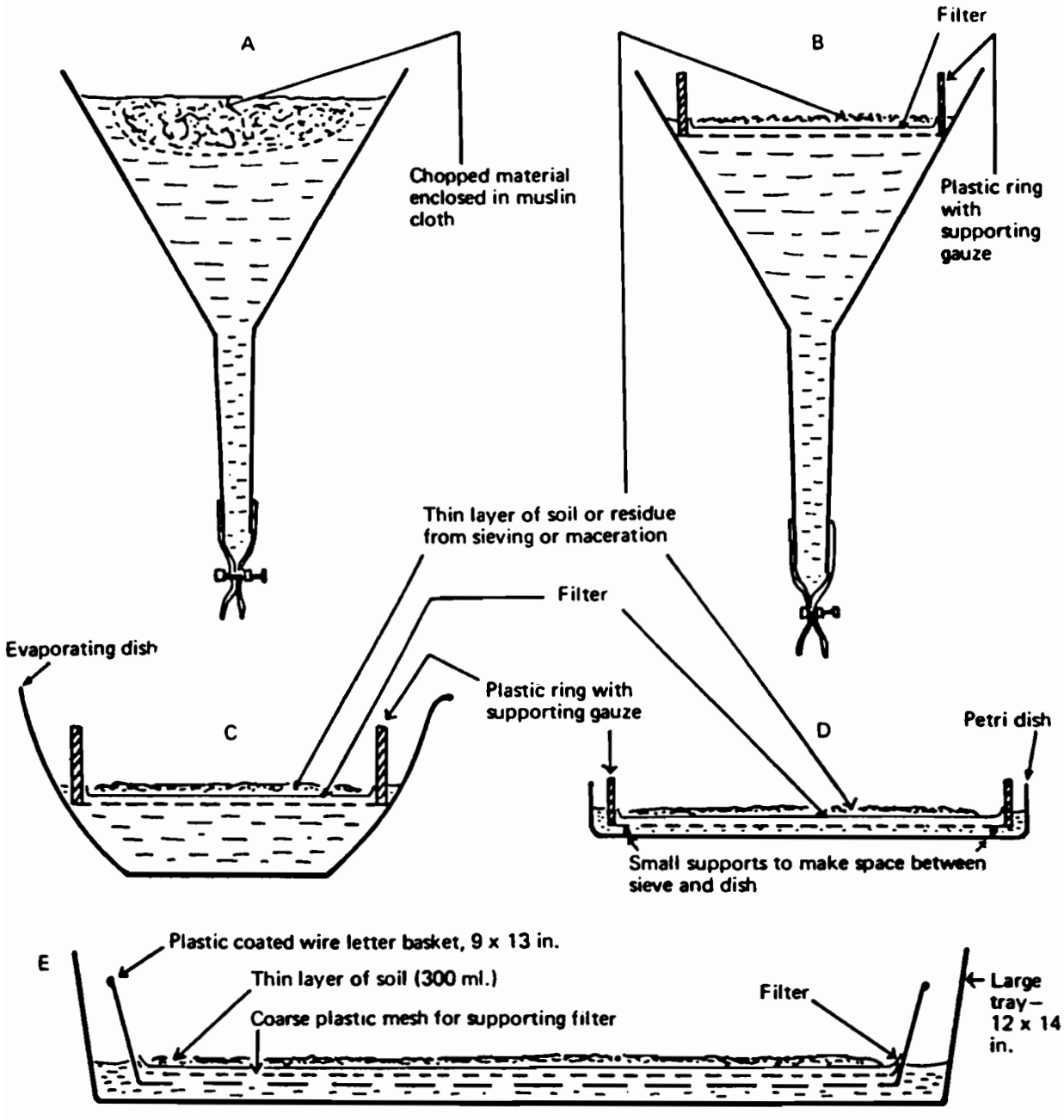


Fig. 1. Baermann funnel and modifications for extraction of active nematodes from chopped plant material, from thin layers of soil, or from residues obtained by sieving or maceration. Filter – cotton wool milk filter, wet strength facial tissue, coarse cotton cloth, or fine woven nylon or terylene cloth. Plastic rings – cut from perspex, polythene or vinyl tubes. Supporting gauze – muslin or nylon cloth held with elastic band, coarse plastic mesh stuck or fused to edge of ring.

water before reclosing the containers. This method extracts root endoparasites such as *Radopholus* and *Pratylenchus* and also the immature stages and males of sedentary parasites but it may take several days to recover a good proportion of the nematodes. Chapman (1957) improved aeration, hence recovery, of *Pratylenchus* by agitating chopped roots in water in flasks on a shaker. Extraction was improved further if chopped roots were shaken in water with 110 ppm of ethoxyethyl mercuric chloride and 50 ppm dihydrostreptomycin sulphate; 90 per cent of recoverable *P. brachyurus* were obtained in four days compared with over two weeks in water alone. Some other chemicals also enhanced recovery at certain concerntrations (Bird, 1971).

Maceration/filtration technique (Fallis, 1943; Stemerding, 1964)

6. This method is often quicker and more efficient than those described in sections 3, 4 and 5. About 5 g of roots are chopped into lengths of one cm or less and then placed in about 100 ml of water and macerated in an electric mixer with revolving knife blades (Waring blender, M.S.E. Atomix, Sunbeam domestic or Dormeyer blender). The maceration time required depends on the type of mixer used and, to some extent, on the type of plant material. Maceration needs to be continued long enough to give nematodes easy egress from the tissues but not to damage or render them immobile. About 5 sec for the macerator to reach full speed, 5 sec at full speed and 5 sec to stop is usually adequate. The suspension from the macerate is poured on to a milk filter or paper tissue supported on a sieve which is then placed, just awash, in water for 24 to 48 hours as in section 4.

Maceration-flocculation-flotation (Escobar & Rodriguez-Kabana, 1980)

7. To extract *Radopholus similis* from banana, the roots are washed and chopped into small pieces and 25 g are macerated in 100 ml water. Then 250 ml of 1M sucrose solution containing 12.5μg/ml of the flocculating agent Separan NP 10 are added and mixed. After standing for 2 min, the clear supernatant is poured through a 400μm-aperture sieve over one with 80μm apertures; the sieves are sprayed with water and nematodes washed from the 80μm sieve into a counting dish.

Maceration-centrifugal flotation (Coolen & D'Herde, 1972; Coolen, 1979)

8. Well washed roots are cut into 0.5 cm pieces, thoroughly mixed in a large volume of water and collected in a sieve. A 5g subsample is homogenized in 250 ml of water with an electric macerator (Waring blender) at about 12 600 rpm for 30 sec. The suspension is then poured on to a 1200μm-aperture sieve resting in a funnel standing in a 500 ml centrifuge tube; the residue on the sieve is carefully washed with a spray before it is discarded. Five ml of kaolin powder is added to the extract in the centrifuge tube and the contents thoroughly mixed with a Vibromixer. Tubes are balanced and centrifuged for 4 min at 1500 *g*; the supernatant is poured off and the residue resuspended in sucrose, $ZnSO_4$ or $MgSO_4$ solution of sp.gr 1.18 (see section 21) with a Vibromixer for at least 30 sec. Tubes are balanced with the appropriate solution and centrifuged for 4 min at 1500 *g*; the supernatant is poured on to a 5μm-aperture sieve and the nematodes and eggs collected in a beaker as described in section 21. De Waele *et al.* (1987) found that efficiency of extraction of *Pratylenchus* from maize roots decreased with increase in sample size and so the root mass extracted should be standardized for comparative studies.

Mistifier technique (Seinhorst, 1950)

9. A continuous fine mist of water is sprayed over the material to be extracted. Nematodes recovered by this method are more active than those extracted by methods 2 to 5 because oxygenation is better, and sap and decomposition products from the material, which inactivate nematodes, are washed away. A spray nozzle, passing about 4.5 l per hour, is usually used. Some systems use an intermittent spray of say 1 min in every 10 min. Oil burner nozzles or gas jets can sometimes be adapted and a water pressure of about 2.8 kg per cm^2 is usually required to give a suitable mist. The plant material to be extracted is finely chopped into pieces 3 to 4 mm long and placed on a milk filter or tissue supported on a mesh as in section 4. Optimum sample size for extraction will

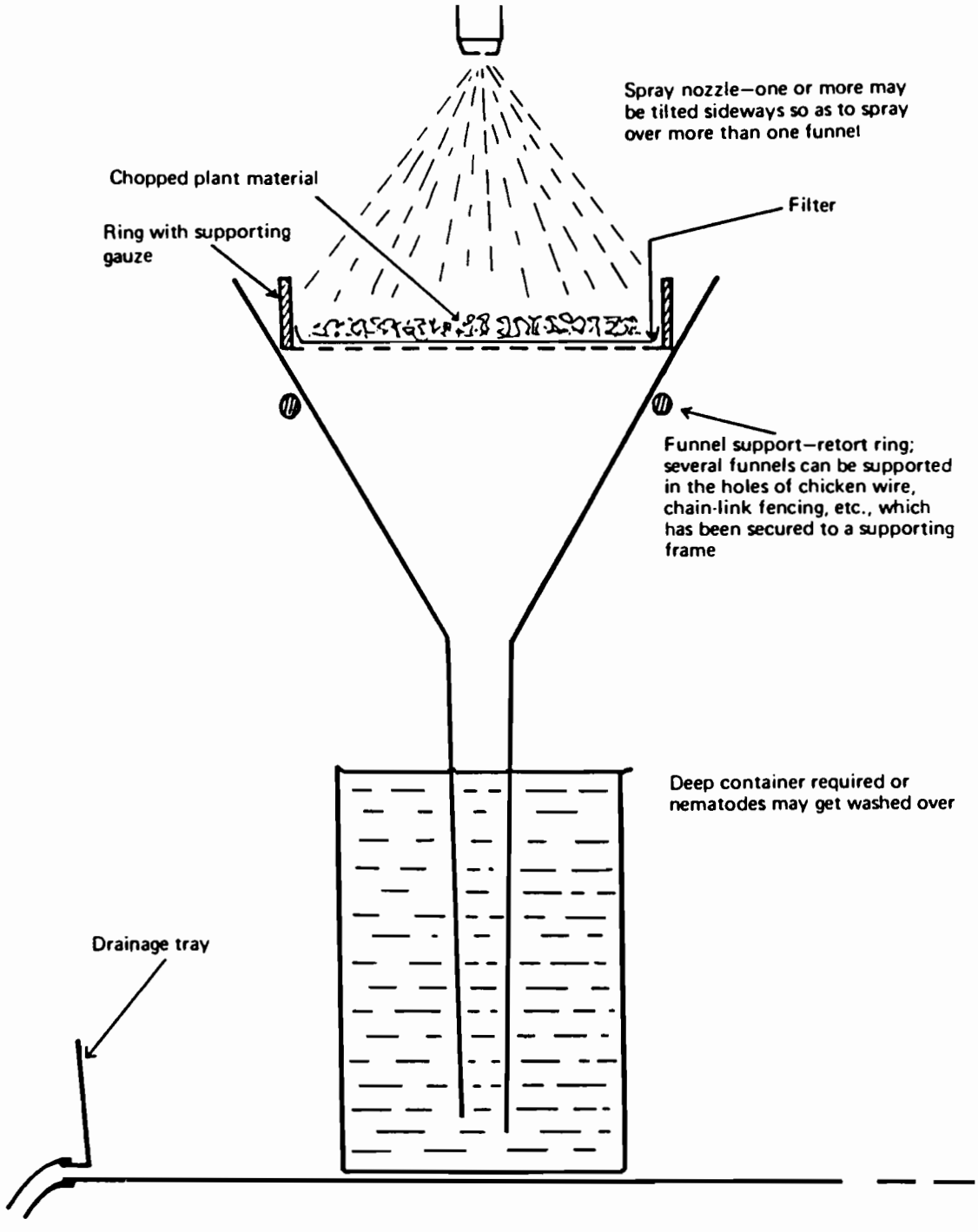


Fig. 2. Mist extraction of active nematodes from chopped plant material. The apparatus may be covered with plastic sheeting to prevent spread of the spray.

depend on sieve diameter and water flow rate; increasing sample size can decrease the efficacy of extraction (De Waele *et al.* 1987). The sieve is placed inside a funnel the stem of which leads to the bottom of a 250 ml collecting beaker so that the overflow of excess water is not sufficient to carry nematodes with it (Fig. 2). Several funnels can be set up on a rack and one or two nozzles can supply all of them. The whole apparatus can be set up on the bench if enclosed with a polythene cover and stood on a drainage tray. For a more elaborate apparatus using collection trays instead of beakers, see Southey (1986). This method is suitable for recovering most active nematodes but not for *Rhadinaphelenchus*, which swims and is lost in the overflowing water.

Extraction of *Rhadinaphelenchus* from coconut stem tissue

10. The material is chopped, well macerated (see section 6) and the suspension transferred to a 2 l conical flask which is then filled with water and allowed to stand for 30 min. The flask is then shaken and inverted with its neck in a vessel of water and the suspension allowed to settle for 30 min (as in section 18 but without a funnel attachment). The contents of the lower vessel are discarded and the flask contents are sieved 4 times through a 63 μm aperture sieve, the residue is washed off each time and collected in a beaker (after Fenwick, 1963).

Sedentary parasitic nematodes

11. Immobile stages, e.g. root-knot females, can be estimated by observing material directly (section 2) or by carefully macerating it as in section 6 and examining it without filtering. Staining before maceration (see sections 26 & 27) helps to differentiate the nematodes from the tissues.

Cleaning and storage of nematode suspensions

Filters

12. The above methods (sections 3 & 4) and some of those for extraction from soil make use of the ability of many nematodes to pass through a filter, thus separating them from plant debris and soil particles. Cotton wool milk filters and wet strength paper handkerchiefs and towels are suitable, as are various types of cotton cloth or muslin. It is necessary to select a filter that retains as much debris as possible but with sufficiently large pores for the nematodes to migrate through. For larger nematodes like *Longidorus* spp., a nylon gauze of about 90 μm aperture, secured to a supporting ring, will often give a clean enough extract. Various grades of lingerie material, nylon or terylene, are also suitable for filters and/or sieves. The author wedges a wet strength viscose filter between two vinyl rings (drain pipe) avoiding the use of a separate filter support.

Storage

13. Many nematodes remain in good condition for several days when stored in shallow water at about 5–10°C. Distilled water is often used but it exerts considerable osmotic stress upon nematodes (Wright & Newall, 1980) and tends to be acid, so Green and Hornsey (1984) recommend the use of water stored over marble chips. Evans (1979) found that *Longidorus leptocephalus* survived much longer in Ringer's solution or fresh tap water direct from the mains than in tap water indirectly from the mains or in distilled water.

Contaminating micro-organisms can be suppressed by adding a few drops of bacteriocide (i.e. 3 drops of 5% streptomycin sulphate solution per 5 ml of nematode suspension).

Extraction from soil

14. Baermann-type techniques, relying on nematode motility to separate them from inert material, require little labour and use simple equipment. Small (10 to 50 ml) samples of soil finely crumbled or passed through a 8 mm aperture sieve can be extracted using methods described in sections 3

and 4 above. The extraction tray (section 15) is now widely used for obtaining active nematodes from larger (300 ml) samples of soil but it is inefficient in recovering some large nematodes such as *Longidorus* or *Xiphinema;* for these nematodes sieving or sieving and filtering are better whereas trichodorids are best extracted using sieving or elutriation techniques. Sieving (section 16) or sieving plus filtering (section 17) are quick methods for assessing the types of nematodes in soil but they are not very quantitative as they are subject to much operator error. The Seinhorst two-flask technique (section 18) is a simple method giving a more efficient and cleaner extract than direct sieving. The fluidising column (section 20) is a very versatile apparatus capable of extracting wet cysts or verminform nematodes from soil or root-knot females from root debris providing the appropriate sized sieves are used to catch the extract and the correct flow rate of water, monitored through a flow meter, is used. Centrifugal extraction (section 21–23) gives the most efficient and quickest extraction of active and sedentary nematodes from soil. Ideally large centrifuge tubes (300–400 ml) are preferable but smaller tubes can be used especially when used in conjunction with a sieving technique (section 23). Demeure and Netscher (1973) noted that to obtain an accurate assessment of *Meloidogyne* in a non-permeable sandy clay soil, where egg masses combined with sand particles, the combined use of sieving, elutriation, centrifugation and mist extraction was necessary.

Extraction trays (Thomas, 1959; Whitehead & Hemming, 1965)

15. A sieve to support the soil is made from a plastic covered letter basket (22 x 32 cm) or other large plastic basket inside which is placed a coarse plastic mesh and on top of this a double layer of muslin cloth, paper tissue, or milk filters. The basket is stood in a collecting tray (large photographic dish, baking dish, glasshouse tray). Up to 300 ml of finely crumbled soil, passed through a 8 mm aperture sieve if necessary, is evenly spread in a thin layer over the filter in the basket. Water is carefully added down the inside edge of the collecting tray until the soil layer looks wet (Fig. 1E). To obtain a clean extract it is important not to move the tray once the water has been added. Space can be saved by making a simple rack to hold the trays and evaporation can be lessened by covering with polythene sheeting. Most nematodes will have collected on the floor of the tray after 24 hours but root-knot juveniles from egg masses or some endoparasites from root fragments may take several days to emerge. The basket is then slowly and carefully removed and the nematode suspension from the tray beneath can be concentrated by pouring into a large, narrow, beaker (one to 1.5 l) and allowed to settle for 4 h or more when the supernatant water can be decanted or syphoned off; or the extract can be concentrated in large (8 cm x 40 cm) glass cylinders having a funnel-like base fitted with a tap or pinch-cock (Whitehead & Hemming, 1965). Alternatively, the suspension can be concentrated by passing it 3 or 4 times through a very fine sieve (<45 μm aperture), washing the nematodes off the sieve each time and collecting them in a vessel.

Sieving technique (Cobb, 1918)

16. Equipment required: 2 deep basins, 25 to 30 cm diameter, or 2 small buckets; seven 15 to 20 cm diameter sieves made with wire mesh (usually phosphor bronze but preferably stainless steel) of 8, 22, 60, 120, 170, 240 and 350 meshes per in, equivalent to an aperture size of 2 mm, 710 μm,250 μm 125 μm, 90 μm, 63 μm, and 45 μm respectively; a small pan about 15 cm diameter and 5 cm deep, and 250 ml-beakers for the residue from each of the sieves used.

Ready-made sieves are expensive. Cheaper ones can be made by buying the wire gauze separately and fitting it to circular plastic dishes or metal baking pans of about 15 to 20 cm diameter from which the base has been removed.

Usually only 3 or 4 of the set of sieves will be used for a particular sample, with the sieves selected to match the size of nematode it is hoped to extract, and to suit the type of soil involved. Most adults of large dorylaims are caught on a 250 μm aperture (60-mesh) sieve, adults of average-size nematodes on a 90 μm aperture (170-mesh) and many juveniles and small adults on a 63 μm aperture (240-mesh). A 45 μm aperture (350-mesh) sieve must be used to recover small juveniles.

Only a proportion of the nematodes are caught when a suspension is poured once through even the finest sieve (65% of nematodes 500 μm long or 25% of those 250 μm long when a suspension is poured once through a 50 μm sieve). It is therefore advisable to pour the suspension 3 or 4 times through the finest sieve in use, collecting the residue off the sieve each time.

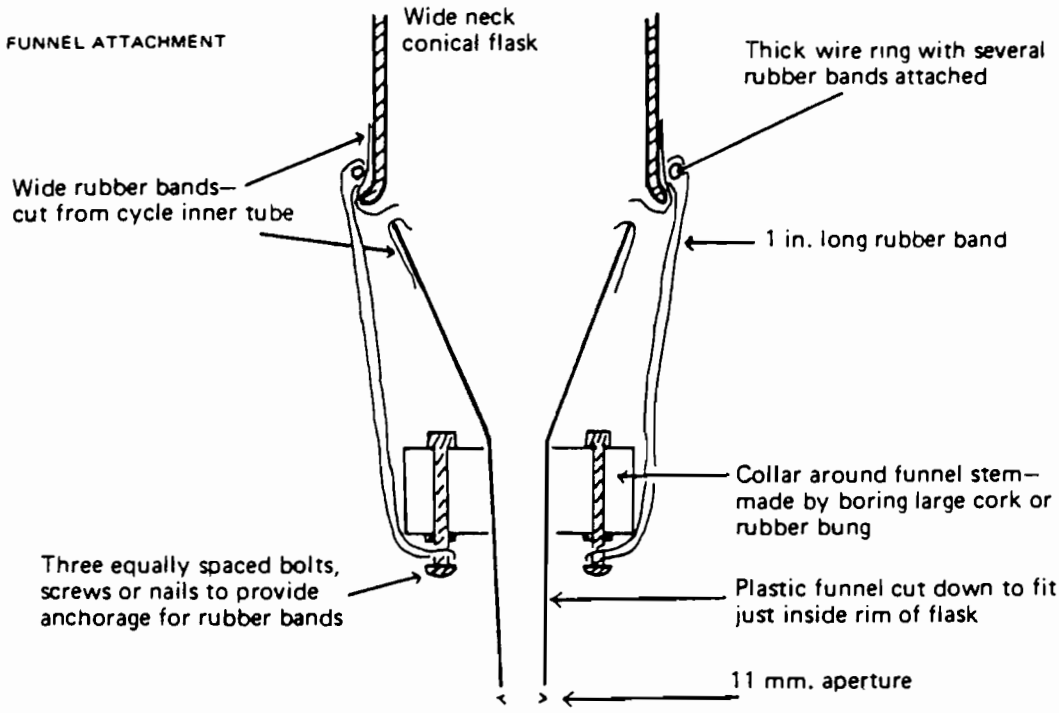
The soil sample (about 200 ml) is placed in basin I, covered with water and any lumps gently broken up. Dry soils should be soaked for a few hours. The mixture is stirred and poured through a 2 mm aperture (8-mesh sieve) into basin II leaving heavy material behind, more water is added to the material in basin I, which is stirred again and poured through the sieve into basin II. Any sediment left is discarded and basin I washed out. The sieve is rinsed over basin II. The residue on this sieve may contain very large nematodes but usually it can safely be discarded. The contents of basin II are stirred, allowed to settle for about 10 sec and then poured through a 710 μm aperture (22-mesh) sieve into basin I, leaving behind heavy soil particles to which more water is added and the process repeated, if desired, but again leaving behind heavy material. The sieve over basin I is rinsed; the residue on this sieve may contain only a few large nematodes but this often depends on how much debris is present. To collect the residue, the sieve is stood on edge in the 15–20 cm-pan and tilted with its underside uppermost; a gentle stream of water is used to wash the residue into the pan. The pan contents are then decanted into a beaker, labelled "710 μm aperture or 22-mesh", leaving behind any heavy particles. Basin II is cleaned and the process repeated using 250 μm, 125 μm and 90 μm aperture (60-, 170- and 240-mesh) sieves and collecting the residues, as described above, in appropriately labelled beakers. If the contents of the beakers appear cloudy it is because the residue on the sieve was inadequately rinsed. If necessary the contents should be poured back on to the sieve and rinsed again over the basin containing the remaining suspension before proceeding to the next sieve in the series.

Fine sieves are easily clogged but this can partially be avoided by pouring the suspension on a sieve inclined at an angle of about 30° to the horizontal. Gently patting the underside of the sieve into the water in the basin below and lifting it in and out a few times will help to clear it.

The contents of the collecting beakers are allowed to settle for one to 2 h and the supernatant liquid is carefully decanted or syphoned off leaving about 40 ml in the bottom which can be examined for nematodes (see section 29).

Sieving and filtering

17. Sieving alone often fails to result in an extract clear enough to examine for nematodes, especially from soils that contain much debris. Some workers make a quick extraction with sieves as described in section 16, then pool the residues from the sieves in one beaker and leave them to settle for 2 hours. The supernatant liquid is carefully poured or syphoned off and the remaining suspension is poured on to a milk filter or paper tissue supported on a sieve as described in section 4. Other workers prefer to stand the sieve in shallow water in a Petri dish which is allowed to overflow when the suspension is added. The sieve with its residue is then placed just awash in a funnel or in a shallow dish as described in sections 3 and 4. Most nematodes pass through the filters in 24 hours and can be collected almost free from debris. For the extraction of larger nematodes (e.g. *Longidorus*/*Xiphinema*) Flegg (1967) gently crumbled 200 cm^3 of soil and soaked in water for 1 h stirring intermittently. The suspension is then washed through a 4 mm aperture sieve, to remove coarse debris, into a 5 l bucket which is almost filled with water and stirred vigorously to suspend particles. After standing for 25 sec the supernatant is poured through three 150 μm aperture sieves. The residue on the sieves is thoroughly rinsed with a gentle stream/spray of water before collecting in a beaker. More water is added to the bucket, the suspension is stirred vigorously and, after settling for 15 sec, poured through the same sieves rinsing and collecting the residue as before. The combined residues are stirred gently and poured on to a 90 μm aperture, polythene supported, nylon sieve which is placed in water in a funnel or shallow dish as above.



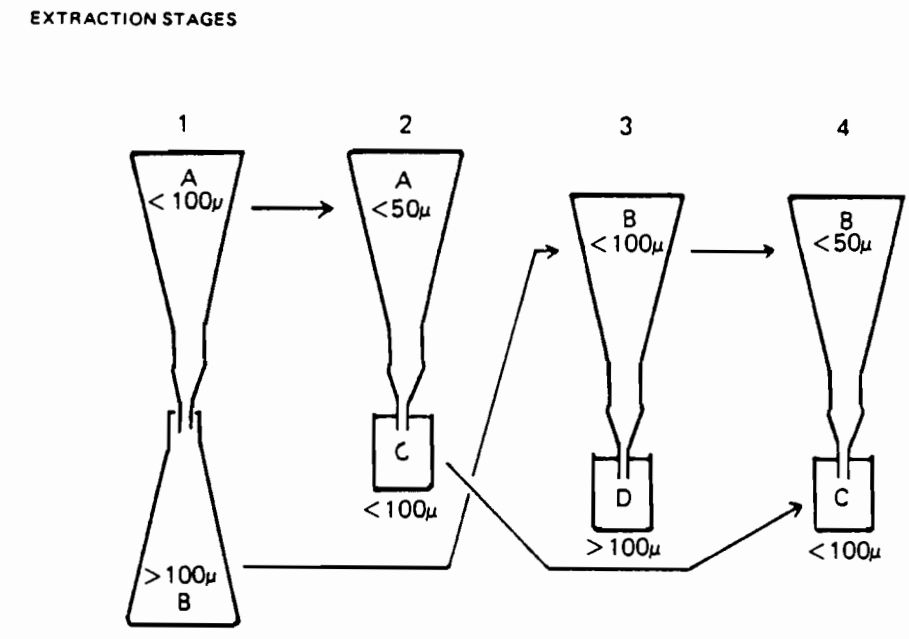


Fig. 3. Seinhorst two-Erlenmeyer-flask soil extraction technique. Progress in the stages of extraction are shown. With easier soils, stages (2) and (4) may be omitted and only the contents of (A) and (B) are then sieved.

Seinhorst two-Erlenmeyer-flask technique (Seinhorst, 1955)

18. This simple but very efficient technique is widely used and often gives a clean extract that can be examined direct without the need to filter. It is therefore useful for extracting rather sluggish nematodes such as *Criconema* which do not readily pass through a filter.

Two wide necked 2-litre Erlenmeyer (conical) flasks are needed, preferably with a standard ground glass joint at the neck on to which can be fitted a gradually tapered funnel with a stem aperture of about 11 mm. Alternatively plastic flasks and funnels can be used; the funnel can be cut down to fit just inside or outside the rim of the flask to which it is simply attached using a wide rubber band cut from a cycle tyre inner-tube. Tensions involved in making the attachment could fracture the neck of glass flasks and for them the following system may be used: a wide rubber band is fitted around the rim of the flask so that it slightly overlaps the flask opening; a similar band is fitted around the rim of the plastic funnel. The bands help to give a water-tight seal. The funnel is secured to the flask by attaching 3 equally spaced rubber bands, which are fixed on a wire ring around the flask neck, on to screw heads fixed in a collar around the top of the funnel stem (see Fig. 3). Alternatively, large (1.5–2 l) drink bottles, preferably plastic, with gradually sloping shoulders can be used instead of conical flasks. The plastic funnel connectors used to fix shower equipment to water taps can be adapted to provide the funnel. Two retort stands are each fitted with a retort ring in which an inverted flask can be supported; about one third of the retort ring is cut away so that the flask can be inserted while holding a finger over the attached funnel outlet. Two 250 ml and two 400 ml beakers plus one, or more, 90 μm and 50 μm-aperture sieves are also required.

The soil sample, usually 200 cm^3, is thoroughly mixed with water and transferred to flask (A) by passing it through a hemispherical, 2 mm aperture, domestic type sieve resting in a large funnel. Any residue left on the sieve is well rinsed before being finally discarded. The flask is topped up with water and the funnel attached. With a finger over the funnel stem the whole is shaken and then quickly inverted into the top of a similar flask (B) previously filled with water; the finger being removed as the funnel stem enters the water. The soil particles sediment out differentially. This and subsequent stages, where each flask is inverted over a 400 ml beaker of water, are shown in Fig. 3. At each change, shake the flask before putting it into its new position. Each stage is allowed to run 10 min, the figures on the containers (A, B, C & D) show the size of soil particle to be found in each at the end of the prescribed time. Pour the contents of (A) and (B) through a 50 μm aperture sieve, and (C) through a 90 μm sieve at least 3 times, or through 3 sieves, rinse and collect the residue each time as described in section 16. The second beaker (D) contains practically no nematodes and is discarded. This procedure can be speeded by omitting stages 2 and 4 (Fig. 3); the contents of both flasks are then passed through a bank of 6 sieves, the uppermost of 90 μm aperture and the remaining five of 50 μm aperture.

Elutriation techniques

19. These techniques use an upcurrent of water to separate nematodes from soil particles and hold them in suspension. They give a cleaner extraction than that obtained by direct sieving and some will extract from larger soil samples than does the two-Erlenmeyer-flask method, although they are not any more efficient. Flow rates can readily be adjusted to suit soil type and the size of nematode to be extracted. Of the models that have been developed (Seinhorst, 1956; Tarjan *et al.*, 1956; Oostenbrink, 1960) the No. III model of Oostenbrink is often used because it is robust and easily operated and cleaned. Oostenbrink (1960) or Southey (1986) should be consulted for details.

Fluidising column (Trudgill *et al.*, 1973)

20. This is a simple, robust, versatile elutriator. The modified version (Figs 4 & 5) used at Rothamsted has an internal diameter of 7.5 cm and a column height of 42 cm above the disc. It is constructed from a plastic (perspex) cylinder which fits tightly into a short cylindrical base sealed by an O ring. The base contains a plastic sintered plate and water is introduced beneath the plate, through a side arm with a perforated end piece. By varying the water flow rate, preferably with a flow meter, all

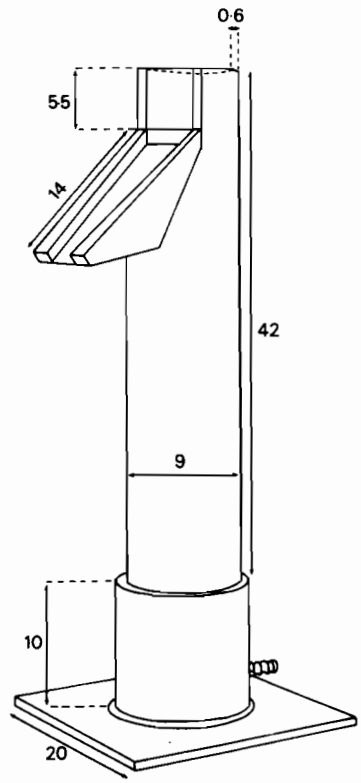


Fig. 4. Fluidising column, with dimensions in cms (from Trudgill *et al.*, 1973) reproduced with permission from *Nematologica*)

types and sizes of nematodes can be recovered. Up to 200 cm^3 of soil can be extracted, it is mixed in water and passed through a coarse sieve (8 mm aperture). The prepared sample is added with the column about one third full of water. The upward water flow, through the sintered plate, is adjusted to a rate of about half that required to wash over the nematodes and is allowed to run for 3 min to mix and fluidise the suspension, then for a further 3 min at the full rate to extract the desired nematodes. The overflow from the column is caught on a sieve or bank of sieves of appropriate size. In order to obtain reasonably clean extracts the flow of water through the column needs careful control.

Trudgill *et al.*, (1973) give a terminal velocity (settling rate) of 0.11 cm/sec for *Longidorus leptocephalus* adults and 0.01 for cyst nematode (heteroderid) juveniles. Thus for a column with a 3.75 cm radius the least flow to extract longidorids would be $\pi\chi$ $(3.75)^2$ (area of the disc) x 0.11 (settling rate) x 60 (sec to min) = 291 ml/min; for heteroderid juveniles the flow rate would be 29 ml/min. In practice, about twice these flow rates should be used to ensure a good recovery of nematodes; so the apparatus should be run at approximately 300 or 30 ml/min for 3 min then at 600 or 60 ml/min for longidorids or heteroderid juveniles, respectively. Longidorid adults would be caught on a 150 μm aperture sieve and heteroderid juveniles on one with 53 μm apertures. Extracts

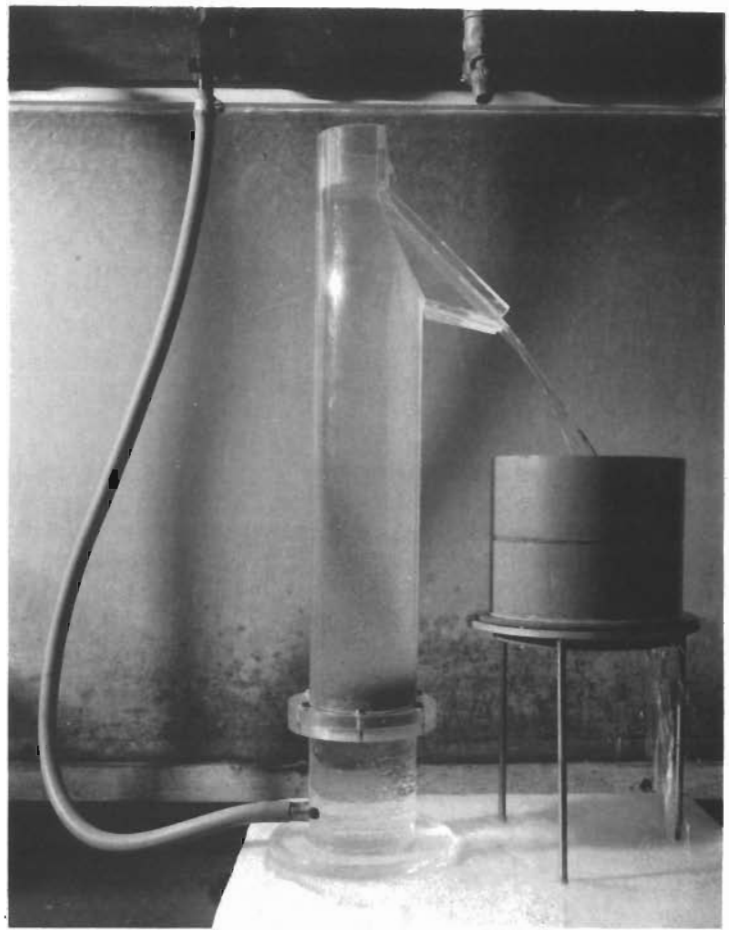


Fig. 5. Fluidising column in operation (Photo: Rothamsted Experimental Station).

from the sieves can be concentrated and cleaned as in section 12. Much faster flow rates (3.5 l/min for 3 min then 7 l/min for 3 min) are required to extract heteroderid females and cysts from moist soils; the extract is caught on a 250 μm aperture sieve after passing through a 840 μm sieve to remove coarse debris.

Centrifugal flotation

21. Nematodes can be extracted from soil and organic debris by floating them out in a solution of specific gravity (sp.gr.) greater than their own. As the method does not rely on the mobility of nematodes it is extremely useful for extracting sluggish forms such as criconematids as well as dead, molting, or fixed nematodes and eggs. Centrifugal flotation is a generally more efficient nematode extraction method than Baermann, sieving or elutriation techniques. This method is often used to clean extracts obtained by sieving or elutriation. Solutions of sucrose, $MgSO_4$ or $ZnSO_4$ are mostly used but nematodes may be distorted or even killed by osmotic stress and they should be rinsed with water or put into excess water as soon as possible to aid their recovery. A solution with a specific gravity of about 1.18 (484 g of cane sugar dissolved in water and made up to 1 l) is suitable. The specific gravity of a solution should be checked just prior to its use as changes in temperature

and microbial activity can cause a considerable decrease in concentration. The suspensions recovered are usually so clean that they can be caught on very fine sieves (5–10 μm aperture nylon gauze).

Direct extraction from soil (Caveness & Jensen, 1955; Dunn, 1971)

22. The soil sample should be mixed and, if necessary, passed through a 1 cm-aperture sieve to remove stones or coarse debris. Each 20 cm^3 subsample of soil is placed in a 100 ml centrifuge tube and water added (and 1 cm^3 of kaolin powder if desired) up to 2 cm from the tube brim. The contents are shaken vigorously or thoroughly mixed using a Vibromixer. The tubes are balanced by adding water and centrifuged at about 1800 *g* for 4 min after which the centrifuge must be carefully braked to avoid vibrations that will disturb the sediment pellet. The superantant is discarded and the tube almost filled with suspending solution (sp.gr. 1.18) and shaken vigorously or vibromixed to resuspend the pellet. Tubes are balanced by adding more solution then re-centrifuged (1800 *g*, 4 min) and the supernatant poured into excess water (about 1:5) in a measuring cylinder. The inside of the centrifuge tube is rinsed to free any nematodes but without disturbing the soil pellet and the rinsings are added to the main extract. After about 2 h the supernatant is poured or drawn off and the remainder (c.20 cm^3) examined in a suitable counting dish. Alternatively, the supernatant solution from the centrifuge tube can be poured through a fine (5 μm aperture) sieve the sievings being quickly rinsed with water before collecting in a beaker or counting dish.

Sieving/centrifugation

23. Jenkins (1964) modified Caveness and Jensen's (1955) technique (22) to handle larger soil samples. 100–150 cm^3 soil are washed through a 840 μm aperture sieve into a bucket, and made up to about 6 l with water. After stirring, the suspension is allowed to settle for 30 sec before the supernatant is decanted through a 52 μm aperture sieve. The bucket is refilled and the process repeated. The sievings are collected in two 50 ml centrifuge tubes which are balanced before spinning at 1750 rev/min for 4–5 min. The supernatant is poured off and replaced by sucrose solution (sp.gr. 1.18). The tubes are balanced, shaken, and spun for 1/2–1 min. The supernatant is poured through sieves of 53 μm aperture or less and the sievings are washed before collection in a beaker for examination. Extracts obtained by elutriation (section 19 *seq.*) can also be cleaned using this Jenkins modification. Gooris and D'Herde (1972) and Demeure and Netscher (1973) described more elaborate methods for extracting *Meloidogyne* stages including egg masses.

Flotation, flocculation and sieving technique (Byrd *et al.*, 1966)

24. In this method flocculating chemicals are used instead of centrifugation to separate soil particles from suspension in 1.0 M (342 g/l solution) sucrose solution. Separan is an effective flocculating agent irrespective of soil type or pH. Ferric chloride ($FeCl_4$) can be used but the concentration is critical and must be varied according to soil type and pH. This method takes only 1–3 min per sample and gives good yields of *Xiphinema*, trichodorids and spiral nematodes, but small forms such as *Criconemoides* may be trapped in the flocculated material and lost.

Fifty cm^3 of soil are placed in a 600 ml beaker and made up to 350 ml with 1.0 M sugar solution containing 12.5 ppm of Separan. This is gently stirred with a mechanical stirrer (1600 rev/min) for 20 s and then allowed to settle for 2–5 min. The nematode suspension is then poured through a 355 μm aperture sieve set over one of 45 μm aperture. The residue on the sieves is rinsed and washed into a beaker; the contents are swirled, allowed to settle for a few seconds, and then poured back on to the 45 μm aperture sieve leaving behind heavier particles. The nematodes are then washed from the sieve into a beaker with about 25 ml water. Rodriguez-Kabana and King (1975) found that blackstrap molasses were cheaper and, because of higher viscosity, more effective than sucrose for extracting nematodes.

Mishra *et al.* (1977) pooled soil extracts obtained by sieving (16) into a beaker, mixed in 0.2% Separan CP–7 and after allowing particles to settle for 1 min decanted the supernatant through a 50 μm aperture sieve to recover the nematodes. The process is repeated three or more times on the

residue left in the beaker. This modification avoids the use of a sucrose solution and, because sieved extracts only are treated, larger volumes of soil can be handled initially. Rush (1970) extracted *Xiphinema americanum* from soil using Separan without sucrose.

Extraction of heteroderid cysts from dry soils

25. The saccate dead females, 'cysts', containing embryonated eggs for the next generation, of heteroderid nematodes float when they are dried and so they can be readily extracted from dried soils.

The soil sample is air dried and passed through a 4 mm aperture sieve. A 50 cm^3 sample of the dried soil is placed in a one-litre conical flask, half filled with water and shaken vigorously. The flask is filled to just below its lip and allowed to stand for 10 min. Any cysts present will float to the surface with other soil debris and can be pipetted off or collected on a fine brush for further examination. Alternatively the float can be poured on to a filter paper in a funnel, the water drained off, and the paper examined for cysts most of which will occur along the 'tide mark' left at the upper water level.

Fixation/staining of plant tissue

Fixation

26. Roots and shoot tissue can be fixed for storage, subsequent examination or staining by adding to them preferably hot (60 to 70°C) F.A. 4:1 (section 33) or 5% formalin (2% formaldehyde solution). Alternatively fresh material can be put directly into hot lactophenol/lactoglycerol (section 27), this softens tissues and is particularly helpful in the recovery of *Meloidogyne* females from roots. *Meloidogyne* egg masses can be detected on roots by soaking in phloxine-B stain (0.15 g per 1 water) for 15–20 min, rinsing and examining them in water; the gelatinous matrix of the egg sac is stained red (Holbrook *et al.* 1983) although a few species, eg. *M. artiellia,* do not stain well.

Staining in lactophenol/lactoglycerol

27. Athough lactophenol (section 36) has been widely used in the past it is now recognised that phenol fumes are a danger to health. To avoid using phenol, Bridge *et al.* (1982) recommended the use of lactoglycerol; this is a solution of equal volumes of glycerol, lactic acid and distilled water plus 0.05% acid fuchsin or 0.05% methyl blue stain. Plant material is gently washed free from soil or debris and any thick material should be sliced thinly before staining. The infected material is plunged into gently boiling lactoglycerol, this should be in a deep beaker as frothing occurs when material is added. Several small samples can be stained in the one operation by wrapping each in a piece of muslin cloth. The material is boiled for 3 min and allowed to cool in the stain and washed well in water before it is cleared in equal volumes of glycerol and distilled water (acidified with a few drops of lactic acid). Depending upon the type of material, differentiation may take from several hours to 2–3 days but the stained nematodes should eventually be seen in largely unstained tissue; more rapid differentiation can be obtained by boiling in acidified lactoglycerol for a few minutes. A microwave oven can be used for boiling solutions.

Fixation of soil samples before extraction

28. Elmiligy and De Grisse (1970) mixed hot fixative (100 ml of 40% formaldehyde + 10 ml glycerol + 890 ml distilled water at about 80°C) with soil samples. Fixed soils are extracted using centrifugal flotation (section 21–23). This method is useful in preventing population changes during storage and avoids the quarantine restrictions applicable to live material.

Examination of nematode suspensions

29. A good stereoscopic microscope with a range of magnifications 10x to 100x, a fairly flat field and good resolution are essential. Illumination by transmitted light should be as even as possible; small frosted strip-light tubes are suitable.

All or part of the extracted suspension, according to its density, is placed in an open counting dish and examined under the microscope. When samples are taken with a pipette it should have a wide outlet to prevent debris clogging it. Petri dishes or flat-bottomed Syracuse watch glasses are often used and a grid is etched, or scratched with a marking diamond, on the inside of the base to act as a guide when searching (Fig. 6C & E). Disposable plastic Petri dishes can be used on which a grid is easily scratched with a needle. Merny and Luc (1969) describe an open plastic dish 5 ml capacity, with sloping sides to minimise the effect of the meniscus; the base is marked in 2 mm squares (Fig. 6D). Some dishes have channels/ridges on the base which restrict the movement of nematodes: the Doncaster (1962) dish (Fig. 6B) with concentric channels holds up to 40 ml; De Grisse (1963) moulded a rectangular dish with ridges and Bridge (unpubl., see Fig. 6A) designed a 5 ml plastic dish with a ridged base which is readily made by injection moulding. Fixed capacity, usually 1 ml, covered counting slide chambers are useful for routine counts when immediate access to nematodes within the suspension is not required. Examples are the Peters 1 ml counting slide made in glass by Hawksley (Fig. 6F) and the Fenwick multichamber slides which can be made in plastic (Doncaster *et al.*, 1967; Southey, 1986). To be sure of searching over the whole area of the dish, the space between the grid lines should be a little less than the field width of the microscope at the magnification being used. Thus, a dish with an extract containing large nematodes (*Xiphinema* etc.) which would be examined at about 15x magnification, would have guide lines about 1 cm apart, whereas extracts containing average size nematodes would be examined at about 50x and have lines about 3 mm apart. Some workers prefer to examine extracts in a dish with a thin base (e.g. disposable plastic Petri dish) using the low/medium power objectives of an inverted, compound microscope when nematodes can be seen in more detail. A hand tally counter or bank of counters are useful aids for counting different genera.

Handling nematodes

30. Small batches of nematodes can be selected and transferred from a suspension by using a fine pipette. Selection of individual specimens requires a handling needle. This is a dissecting needle to the end of which is attached, with cellulose glue, a nylon tooth-brush bristle, sharpened bamboo splinter, eyebrow hair, fine wire or small wire loop. Old curved nylon tooth-brush bristles are recommended as they can be tapered to the desired thickness with a sharp scalpel and they are not so easily damaged as other types. The quill and shaft of a moderate sized feather also make a convenient handling tool, the feather vane is removed and the thin end of the shaft shaped/sharpened; the thicker quill end can also be used but the hollow core should be blocked off to prevent loss of nematodes up the quill by surface tension. Many beginners have difficulty in picking up nematodes with a bristle. To do this the nematodes should be in shallow water, near the centre of the dish, and the lowest convenient microscope magnification should be used to give the greatest possible depth of focus and working distance. While viewed with the stereoscopic microscope the handling needle is used to lift the nematode to the surface of the water, the bristle is then held immediately underneath the nematode and quickly flicked up so that the nematode is pulled out through the meniscus. Avoid using too fine and smooth a bristle as it will not have enough drag to bring the nematode up with it through the meniscus. The surface tension can be removed by adding a small drop of soap or detergent on a needle.

Killing and fixing nematodes

31. A few specimens can be killed by transferring them to a drop of water on a 26 x 76 mm glass slide which is then heated over a small flame for a few seconds until the nematodes suddenly

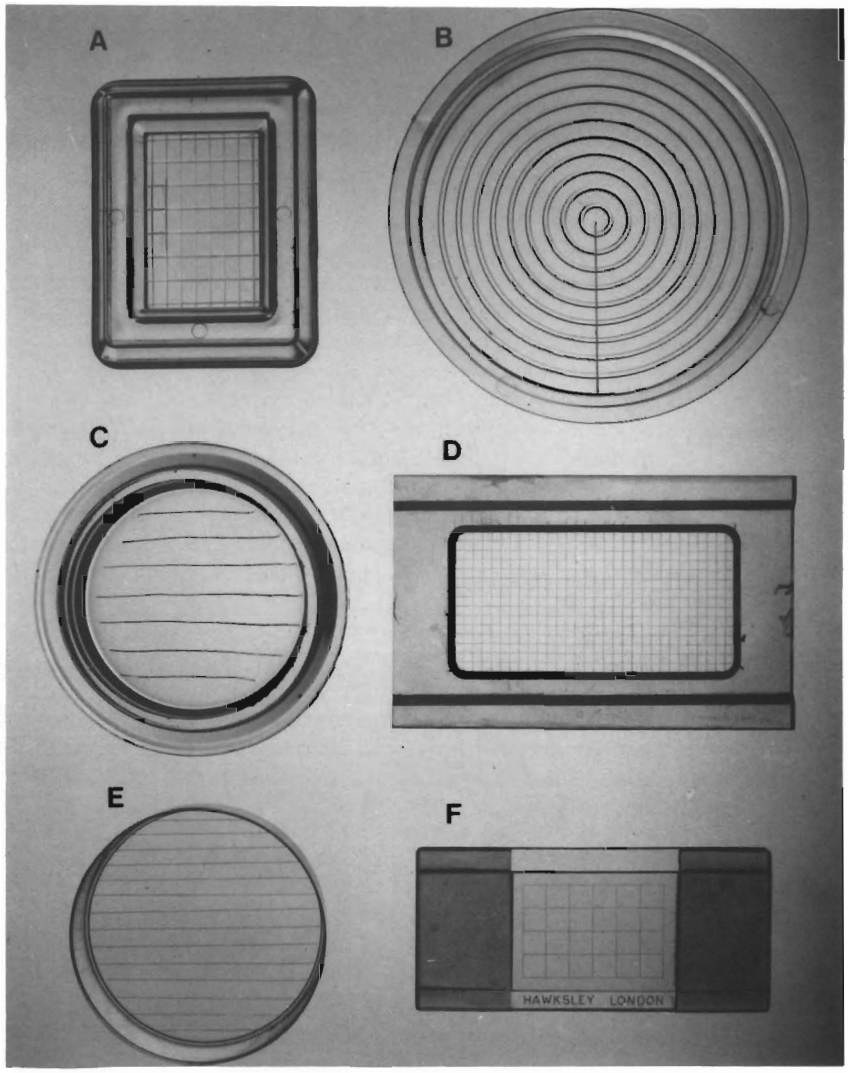


Fig. 6. Examples of counting slides/dishes:
A, Moulded plastic dish, 5 ml, with sloping sides and ridged grid (made at Rothamsted Experimental Station from a design by Bridge (unpublished); B, Moulded plastic dish, 40 ml, with concentric ridges (made at Rothamsted Experimental Station after the design by Doncaster, 1962); C, Flat bottomed glass dish, 15 ml, base lines cut with a glass writing diamond; D, 5 ml plastic dish as produced by ORSTOM (Merny & Luc, 1969); E, 50 mm diameter plastic Petri dish marked for examination at 20–40 X; F, Peter's 1 ml counting slide in glass as made by Hawksley. (Photo: Rothamsted Experimental Station)

straighten out – killed by the heat. Killing on a controlled hot plate at 65–70°C is most effective and prevents damage to specimens due to over-heating. The specimens are transferred to fixative or fixed on the slide by adding an equal-sized drop of double strength fixative (section 32).

The following method is recommended for killing and fixing nematodes: specimens are concentrated in about 3 ml of water in a tube, either by centrifuging or by letting them settle. The tube is shaken to disperse the nematodes and stood in a beaker of water at 65°C for 2 to 3 min, preferably the temperature is monitored with a thermometer in the suspension, then an equal volume of double strength fixative is added.

An alternative method is to collect the nematodes in a very small drop of water in a glass block or small deep watch glass. Formal acetic (or propionic) fixative 4:1 (preferably plus 2% glycerol) is heated to about 99°C and an excess, 3 to 4 ml, is quickly added to the nematodes; this kills and fixes them in the one process (Seinhorst, 1966). The fixative can be heated in a small tube stood in boiling water for a few minutes. This method gives a very good fixation of glands and gonads. Nuclei tend to expand and are more easily seen. Although, specimens appear rather dark as soon as they are fixed, processing to lactophenol or glycerol will eventually clear them.

Fixatives

32. Solutions of 5 to 10% formalin (2 to 4% formadehyde), preferably plus 2% glycerol, are often used. The addition of a small amount of powdered $CaCO_4$ to the stock solution is recommended as this neutralizes the free formic acid which can cause darkening and granulation of tissues. Alternatively the formic acid can be neutralized using triethanolamine as in TAF fixative (section 34).

33. Formal acetic (F.A.) or Formal propionic (F.P.) 4:1

formalin (40% formaldehyde)	10 ml
glacial acetic acid (or propionic acid)	1 ml
(glycerol	2 ml)
distilled water up to	100 ml

As noted by Golden in Hooper (1970), the addition of 2% glycerol to the above means that nematodes can be brought direct from fixative to glycerol by slow evaporation (see section 37). Also as noted by Hooper (1987) nematodes stored in vials will eventually end up in glycerol should the fixative evaporate.

34. TAF (Courtney, Polley & Miller, 1955)

formalin (40% formaldehyde)	7 ml
triethanolamine	2 ml
distilled water	91 ml

TAF fixative is often used because it has the advantage over formalin or F.A. (F.P.) 4 : 1 in that nematodes retain their life-like appearance for several hours. However, as noted by Hooper (1987), TAF is not a good long term preservative as some degeneration of nematode cuticle can occur during prolonged storage and so the transfer to, or the addition of an excess of F.A. (F.P.) 4 : 1 plus 2% glycerol is recommended.

Double strength fixatives are made up using half the amount of water indicated above.

Nematodes will be spoiled if put alive into cold fixative. Alcoholic fixatives should be avoided as they usually shrink nematodes; well fixed specimens have a smooth outline whereas distorted specimens are rarely worth keeping.

Nematodes can be stored in fixative indefinitely. Vials containing them should be labelled with identity of nematode if known, source, locality, fixative used and date of fixation.

Processing and mounting nematodes

35. In fixed nematodes, much of the internal body contents, especially gonad structure, may be obscured by the granular appearance of the intestine. Specimens can be cleared by processing to lactophenol, lactoglycerol or glycerol, which are also suitable mountants. As noted earlier, phenol is a dangerous poison and so lactophenol should be used with caution. Some workers prefer to use lactoglycerol (section 27) instead. It is quicker than processing to glycerol to make mounts in lactophenol/lactoglycerol, which, if well sealed, may last many years; also, especially if a stain is used, some features are more readily seen than in glycerol. However, for permanent collections specimens are usually processed to and mounted in glycerol but as noted by Hooper (1987) mounted specimens can deteriorate and the storage of some representatives in glycerol in vials is recommended.

Lactophenol method (Franklin & Goodey, 1949)

36. Lactophenol

Phenol liquid	50 ml
Lactic acid	50 ml
Glycerol	100 ml
Distilled water	50 ml

Cotton blue (methyl blue) stain 0.05% for staining roots, (0.0025 to 0.01% for staining specimens) is dissolved in the water before mixing with other reagents. Acid fuchsin stain (red) is preferred by some workers especially for staining nematodes in plant tissue.

A cavity slide almost filled with lactophenol, plus blue stain if desired, is heated on a hot plate to about 65°C (a brass plate over a small flame can be used as a hot plate); when the lactophenol is hot, a handling needle is used to transfer to it nematodes that have been fixed for several hours or overnight. The hot slide should be examined with a stereoscopic microscope after 2 to 3 min by which time the specimens should have cleared. The slide can be re-heated if more clearing is required. If cotton blue stain is being used the slide should be heated until the specimens are of a mid-blue colour; they should then be transferred to clear lactophenol or to lactophenol with 0.0025% cotton blue stain. Some nematodes, such as hoplolaims and criconematids, do not stain readily but the internal contents do clear. Fixed nematodes should not be put into cold lactophenol as they are often irreversibly distorted. Esser (1973) describes a 4 min lactophenol fixation/processing method.

Glycerol

37. Slow method

Specimens in fixative plus glycerol in deep glass blocks (section 31) with a loose fitting cover will, after two or three weeks at room temperature, end up in glycerine due to evaporation of the fixative. The process can be speeded up in an oven at 30–40°C but the container needs to be well covered to ensure that the evaporation takes several days. Golden (in Hooper, 1970) recommends the addition of a few drops of picric acid which helps to prevent clearing and fading of nematode stylets and the growth of moulds.

Specimens in fixative without glycerol can be transferred to about 2 ml of a solution of 1.5% glycerol in distilled water in a small watch glass or cavity block. A trace of picric acid, copper sulphate or thymol should be added to the solution to prevent the growth of moulds. The watch glass is placed in a small airtight container together with a small tube (50 x 12 mm) of desiccant such as calcium chloride or silica-gel and kept at 25–30°C. The water should have been absorbed after about 4 weeks. It is important not to rush the process or specimens may become distorted (after Thorne, 1961).

38. Rapid method (Seinhorst, 1962)
Fixed specimens are transferred to a small concave glass dish of 2 to 4 ml-capacity containing about 0.5 ml of the following solution:

96% ethanol	20 ml
Glycerol	1 ml
Distilled water	79 ml

The dish with nematodes is placed into a closed glass vessel containing an excess (e.g. 1/10 volume of vessel) of 96% ethanol. The dish is supported above the ethanol on a platform or grid. After 12 hours or more in an oven at 40°C, the specimens will be in a mixture of mainly ethanol, with some glycerol

The dish is removed from the vessel and filled with a solution of 5 parts glycerol and 95 parts of 96% ethanol and placed in a partly closed Petri dish in an oven at 40°C until the ethanol has evaporated. This should take at least 3 hours, the nematodes are then in pure glycerol and can be mounted.

Note
Nematodes processed to lactophenol or glycerol are very soft and should be handled carefully, preferably using a mounted eyebrow hair or similar soft bristle.

Mounting nematodes

39. Glass slides, 26 x 76 mm, are often used but the Cobb-type aluminium, double coverglass, slides (see Southey, 1986) are preferable as they can be stacked upon each other and are more easily handled for storage and transit. Glass slides with thick card labels at each end may also be stacked.

40. Temporary mounts in fixative
Some important features of nematodes are most readily seen in freshly killed/fixed specimens mounted in TAF (section 34). Refractive structures are often more distinct than in specimens fixed for some time or processed to lactophenol or glycerol. Place the specimens, plus similar sized glass fibres or fine wire (stainless steel), in a small, bold drop of fixative, drop a cover-glass on to it, blot off excess fixative from around the coverglass with a tissue if necessary but take care not to displace the specimens, seal the cover glass down with molten wax or slide ringing compound. In spite of a good seal, mounts in fixative usually start to dry out after a few days.

41. Permanent mounts
A small drop of lactophenol or anhydrous glycerol is placed in the centre of a clean slide and nematodes of about equal diameter are transferred to it, using a handling needle, and arranged in the centre of the drop so that they are touching the slide surface, not floating. Three pieces of glass fibre, equal in diameter to the nematodes and about 1 mm long, for coverslip supports are arranged around the inside edge of the drop. It is helpful to have glass fibre suitable for supports ready in a dish of the appropriate mountant. Small pieces can be selected under a microscope and handled as if they were nematodes. Pieces of fine nickel-chrome or stainless steel wire can also be used particularly for fatter nematodes.

A clean coverslip (19 mm diameter circle No. 1) held with fine forceps is warmed over a small flame and lowered on to the drop. A mounted needle held in the other hand can be used to help prevent the coverslip from sliding sideways when it is applied. It helps to prevent air bubbles from being trapped if the drop is kept as hemispherical as possible before applying the coverslip. The drop should be of such a size that it is only just covered by the coverslip. A good seal cannot be obtained if there is excess mountant around the coverslip edge. The coverslip is fixed down at 3 points using 'Zut', 'Glyceel', 'Permount' or similar sealant; nail varnish is a good substitute. When the drops have dried, the coverslip is ringed, using a small soft brush, with a thick but fairly narrow band of the sealant making sure there is sufficient on the coverslip as well as on the slide. Repeat

the process when the first ring has dried to give a good seal. The brush can either be kept in the sealant or in a tube of solvent (*n*-butyl acetate).

42. Wax-ring method of sealing mounts (after de Maesener & d'Herde, 1963)
In this method a small drop of mountant is surrounded by a wax ring which serves as a seal and cover glass support. If the central area occupied by the mountant is likely to exceed a quarter of the coverglass area then additional supports should be used. To make the wax ring a 1.5 cm diameter tube is heated in a flame, dipped in paraffin wax (M.P. 60°C) or wax mixture (8 parts wax to 3 parts petroleum jelly) and applied to the centre of the slide. The tube may be glass with the end ground flat or, better, a 10 cm-long stainless steel or copper tube with a large cork around one end for a heat-proof handle. For square cover-glasses, molten wax can be applied to the slide with a brush to form a matching hollow square. Specimens, and supports if necessary, are arranged as in section 41, in a small drop of mountant, rather smaller than described in section 41. A 19 mm diameter cover-glass is applied and the slide placed on a hotplate at 65°C for a few seconds or in an oven at 70–80°C for a few minutes. Instead of a wax ring, Siddiqi (1986) recommends the use of three small lumps of wax, each about the size of the mounting drop, arranged around the drop and the coverglass is placed on the lumps and the slide then heated. The wax melts allowing the cover-glass to settle down and confines the glycerol to the centre of the mount. It is important to retain an hemispherical drop of mountant before applying the cover-glass or the wax may swamp the specimens; as soon as the wax melts press lightly with a mounted needle on the cover-glass to make sure it has settled far enough; thick mounts prevent oil-immersion objectives being used. The wax will set rapidly when the slide is placed on a cool surface. A secondary seal of cover-glass cement is desirable to prevent drying out and to prevent immersion oil dissolving the wax.
43. Esser (1974) obtained a good seal by ringing the small drop of mountant containing the specimens with free-flowing Zut (Glyceel). A 15 mm diam. cover-glass is applied and lightly pressed down with a needle to exclude any air between the mountant and the glyceel; the smaller the cover-glass the easier it is to exclude air bubbles. The resulting wide surrounding band of 'Zut' eventually dries and provides a very effective seal.

Posterior cuticular patterns of *Meloidogyne* spp.

44. The cuticular markings surrounding the vulva and anus (posterior cuticular pattern or 'perineal' pattern) of females of *Meloidogyne* spp. are used in their indentification (Taylor *et al.*, 1955; Franklin, 1962). Fresh or fixed, galled roots are stained in cotton-blue lactophenol or lactoglycerol (section 27) and allowed to differentiate. Females stained in fresh root material are preferable because their body contents are more easily removed (Franklin, 1962). About 20 females are dissected out and transferred, using fine-pointed forceps, to 45% lactic acid on a transparent plastic (e.g. perspex) slide. Alternatively they may be transferred as a group by fine pipette, then, working at a magnification of at least x32, preferably more, the swollen female is speared at the neck end with a very sharp, fine needle and, held so the posterior end is cut off with an oculist's scalpel or sharp Borradaile needle; a hypodermic needle mounted on a handle also serves as a very good cutting tool. The inner tissue is carefully removed by lightly brushing with a flexible bristle. The cuticle is transferred to a drop of glycerol where it is trimmed to a size slightly greater than the pattern which is then transferred to a drop of glycerol on a clean glass slide. The posterior patterns, outside uppermost, are arranged in one or two neat rows and a cover-glass is applied and sealed. Supports are optional. At least 10 specimens from a population should be examined; the patterns can usually be seen satisfactorily at a magnification of about x500 but for species having small or indistinct patterns an oil-immersion objective and higher magnification may be needed. As noted by Taylor (1987), the lip region shape and the position of the excretory pore in mature females are an aid to the identification of *Meloidogyne* species. Gerber and Taylor (1988) give details of preparation and mounting so as to show the anterior end and perineal pattern on the one specimen. The preparation is similar to that described above for perineal patterns only but the mature female is pierced once or twice in the mid body

region and the body contents carefully squeezed out so as not to damage the neck or posterior end. The female is then orientated with the perineal pattern to one side and, using a fine scalpel or hypodermic needle, the posterior quarter of the body, without the pattern, is cut away taking care not to damage the pattern. The prepared specimens are then mounted in glycerol with the cut opening underneath and the perineal pattern uppermost. For additional information on preparation methods for culturing and identification of *Meloidogyne* spp. see Barker *et al.* (1985) or Jepson (1987).

Vulval cones of cyst nematodes

45. The structure of the vulva, fenestra and associated internal structures as well as the general shape of cysts, are used for identifying heteroderids (Hesling, 1978). Dry cysts should be soaked in water for up to 24 h before dissection. A moist cyst is placed on a perspex slide on the stage of a stereomicroscope and the posterior end cut off so that the fenestral area is in the centre of the cut piece. If necessary, the cut end is trimmed so that it is no more than 5–10 times the fenestral area. Using very fine forceps and a flexible probe [eyebrow or fine toothbrush bristle mounted on the end of a dissecting needle (section 30)], any adhering body contents, e.g. eggs, are cleaned out taking particular care not to damage the structures associated with the vulva. Thick-walled and heavily pigmented species, bleached for a few minutes in 90 volume H_2O_2 often have more visible structures. (Bleaching should be watched carefully to avoid over bleaching or a weaker (40 vol.) solution used for a longer time). The cleaned vulval cones are washed in distilled water and then passed through 70, 95 and 100% ethanol to clove oil; cleared in clove oil and mounted in Canada balsam. The cover-glass is supported with pieces of glass rod or broken cover-glass thick enough to prevent crushing. Vulval cones may also be mounted in 'Euparal', after passage through 70% ethanol and isobutanol, or direct in glycerine jelly and sealed.

References

Barker, K.R., Carter, C.C. & Sasser, J.N. (1985). *An advance treatise on* Meloidogyne *Volume II: Methodology.* Raleigh, North Carolina, Department of Plant Pathology, North Carolina State University & United States Agency for International Development. 223 p.

Bird, G. W. (1971). Influence of incubation solution on the rate of recovery of *Pratylenchus brachyurus* from cotton roots. *Journal of Nematology*, 3: 378–385.

Bridge, J., Page, S. & Jordan, S. (1982). An improved method for staining nematodes in roots. *Report of Rothamsted Experimental Station for 1981,* Part 1:171.

Byrd, D.W., Nusbaum, C.J. & Barker, K.R. (1966). A rapid flotation-sieving technique for extracting nematodes from soil. *Plant Disease Reporter* 50:945–957.

Caveness, F.E. & Jenson, H.J. (1955). Modification of the centrifugal-flotation technique for the isolation and concentration of nematodes and their eggs from soil and plant tissue. *Proceedings of the helminthological Society of Washington* 22:87–89.

Chapman, G.W. (1957). The effects of aeration and temperature on the emergence of species of *Pratylenchus* from roots. *Plant Disease Reporter*, 41: 836–841.

Cobb, N.A. (1918). Estimating the nema population of the soil. *Agricultural Technology Circular 1, Bureau of Plant Industry, United States Department of Agriculture.* 48 p.

Coolen, W.A. (1979). Methods for the extraction of *Meloidogyne* spp. and other nematodes from roots and soil. In: Lamberti, F. & Taylor, C.E. (Eds) *Root-knot nematodes* (Meloidogyne *species*) *systematics, biology and control.* London & New York, Academic Press: 317–329.

Coolen, W.A. & d'Herde, C.J. (1972). *A method for the quantitative extraction of nematodes from plant tissue.* Ghent, State Agriculture Research Centre: 77 p.

Courtney, W.D., Polley, D. & Miller, V.L. (1955). TAF, an improved fixative in nematode technique. *Plant Disease Reporter* 39:570–571.

Demeure, Y. & Netscher, C. (1973). Méthode d'estimation des populations de *Meloidogyne* dans le sol. *Cahiers ORSTOM Sér. Biol.* No. 21:85–90.

Doncaster, C.C. (1962). A counting dish for nematodes. *Nematologica* 7:334–336.

Doncaster, C.C., Edwards, B.S. & Shepherd, A.M. (1967). A labour-saving method of making Fenwick multi-chamber counting slides for nematodes. *Nematologica* 12:644.

Dunn, R.A. (1971). Comparison of two centrifugal flotation techniques with Seinhorst elutriation for efficiency of nematode extraction from soil. *Journal of Nematology* 3:308–309 (Abstract).

Elmiligy, I.A. & De Grisse, A. (1970). Effect of extraction technique and adding fixative to soil before storing on recovery of plant parasitic nematodes. *Nematologica* 16:353–358.

Escobar, J. & Rodriguez-Kabana, R. (1980). Comparacion de un metodo de flotacion con uno de tamizado para la determinacion de *Radopholus similis* en raices de banana. *Nematropica* 10:86–88.

Esser, R.P. (1973). A four minute lactophenol fixation method for nematodes. *Plant Disease Reporter* 57:1045–1046.

Esser, R.P. (1974) Zut as a cover glass support for nematodes. *Nematologica* 19 (Year 1973): 566–567.

Evans, K. (1979). Nematode problems in the Woburn Ley-Arable Experiment, and changes in *Longidorus leptocephalus* population density associated with time, depth, cropping and soil type. *Report of Rothamsted Experimental Station for 1978, Part 2,* 27–45.

Fallis, A.M. (1943). Use of the Waring blender to separate small parasites from tissue. *Canadian Journal of Public Health* 34:44.

Fenwick, D.W. (1963). Recovery of *Rhadinaphelenchus cocophilus* (Cobb 1919) Goodey, 1960 from coconut tissues. *Journal of Helminthology* 37:11–14.

Flegg, J.J.M. (1967). Extraction of *Xiphinema* and *Longidorus* species from soil by a modification of Cobb's decanting and sieving technique. *Annals of applied Biology* 60:429–437.

Franklin, M.T. (1962). Preparation of posterior cuticular patterns of *Meloidogyne* spp. for identification. *Nematologica* 7:336–337.

Franklin, M.T. & Goodey, J.B. (1949). A cotton blue-lactophenol technique for mounting plant-parasitic nematodes. *Journal of Helminthology* 23:175–178.

Gerber, K. & Taylor, A.L. (1988). A simple technique for mounting whole root-knot nematode females. *Journal of Nematology* 20, 502–503.

Gooris, J. & d'Herde, C.J. (1972). *A method for the quantitative extraction of eggs and second stage juveniles of Meloidogyne* spp. *from soil.* Ghent State Agricultural Research Centre, 36 p.

Green, C.D. & Hornsey, J. (1984). Apparatus for collecting and surface sterilising nematodes and similar small aquatic organisms. *Nematologica* 29 (year 1983): 362–365.

De Grisse, A. (1963). A counting dish for nematodes excluding border effect. *Nematologica* 9:162.

Hesling, J.J. (1978). Cyst nematodes : morphology and identification of *Heterodera, Globodera and Punctodera.* In: Southey, J.F. (Ed.) *Plant nematology* Reference Book, Ministry of Agriculture Fisheries and Food, No. 407 (GDI), London, Her Majesty's Stationery Office: 125–155.

Holbrook, C.C., Knauft, D.A. & Dickson, D.W. (1983). A technique for screening peanut for resistance to *Meloidogyne arenaria. Plant Disease* 67:957–958.

Hooper, D.J. (1961). A method for attaching the funnel to the flask for use in the Seinhorst two-Erlenmeyer-flask soil extraction technique. *Nematologica* 6:336.

Hooper, D.J. (1970). Handling, fixing, staining and mounting nematodes. In: Southey J.F. (Ed.) *Laboratory methods for work with plant and soil nematodes.* Ministry of Agriculture, Fisheries and Food Technical Bulletin 2. London, Her Majesty's Stationery Office: 39–54.

Hooper, D.J. (1987). Observations on the curation of plant and soil nematodes. *Nematologica* 32 (Year 1986): 312–321.

Jenkins, W.R. (1964). A rapid centrifugal-flotation technique for separating nematodes from soil. *Plant Disease Reporter* 48:692.

Jepson, S.B. (1987). *Identification of root-knot nematodes (*Meloidogyne *species*). Farnham Royal, England, CAB International: 265 p.

de Maeseneer, J. & d'Herde, J. (1963). Méthodes utilisées pour l'étude des anguillules libres du sol. *Revue de l'Agriculture Bruxelles* 16:441–447.

Merny, G. & Luc, M. (1969). Les techniques d'échantillonnage des peuplements de nématodes dans le sol. In: Lamotte, M. & Bourlière, F. (Eds.) *Problémes d'écologie: l'échantillonnage des peuplements animaux des milieux terrestres* . Paris, Masson et Cie: 237–272.

Mishra, S.D., Vijayalakshmi, K. & Seshadri, A.R. (1977). A rapid sieving-sedimentation method for extracting nematodes from soil. *Indian Journal of Nematology* 5 (Year 1975): 259–260.

Oostenbrink, M. (1960). Estimating nematode populations by some selected methods, In: Sasser, J.N. & Jenkins, W.R. (Eds.) *Nematology. Fundamentals and recent advances with emphasis on plant-parasitic and soil forms.* Chapel Hill, USA., Univ. N. Carolina Press: 85–102.

Pitcher, R.S. & Flegg, J.J.M. (1968). An improved final separation sieve for the extraction of plant-parasitic nematodes from soil debris. *Nematologica* 14:123–127.

Rogriguez-Kabana, R. & King, P.S. (1975). Efficiency of extraction of nematodes by flotation-sieving using molasses and sugar and by elutriation. *Journal of Nematology* 7:54–59.

Rush, M.C. (1970). Transmission of tobacco ringspot virus from native host to *Cucumis sativus* by *Xiphinema americanum. Phytopathology* 60:917–918.

Seinhorst, J.W. (1950). De betekenis van de toestand van de grond voor het optreden van aantasting door het stengelaaltje (*Ditylenchus dipsaci* (Kühn) Filipjev). *Tijdschrift over Plantenziekten* 56:289–348.

Seinhorst, J.W. (1955). Een eenvoudige methode voor het afscheiden van aaltjes uit grond. *Tijdschrift over Plantenziekten* 61:188–190.

Seinhorst, J.W. (1956). The quantitative extraction of nematodes from soil. *Nematologica* 1:249–267.

Seinhorst, J.W. (1962). On the killing, fixation and transferring to glycerin of nematodes. *Nematologica* 8:29–32.

Sienhorst, J.W. (1966). Killing nematodes for taxonomic study with hot F.A. 4 : 1. *Nematologica* 12:178.

Siddiqi, M.R. (1986). *Tylenchida parasites of plants and insects.* Farnham Royal, UK, Commonwealth Agricultural Bureau: 645 p.

Southey, J.F. (Ed.) (1986). *Laboratory methods for work with plant and soil nematodes.* Reference Book Ministry of Agriculture Fisheries and Food No. 402. London, Her Majesty's Stationery Office: 202 p.

Stemerding, S. (1964). Een mixer-wattenfilter methode om vribeweeglijke endoparasitaire nematodes uit wortels te verzamelen. *Verslagen Plantenziektenkundigen Dienst,* No. 141 (Jaarboek 1963): 170–175.

Tarjan, A.C. (1967). Influence of temperature and hydrogen peroxide on the extraction of burrowing nematodes from citrus roots. *Plant Disease Reporter* 51:1024–1028.

Tarjan, A.C. (1972). Observations on extracting citrus nematodes, *Tylenchulus semipenetrans,* from citrus roots. *Plant Disease Reporter* 56:186–188.

Tarjan, A.C., Simanton, W.A. & Russell, E.E. (1956). A labor-saving device for the collection of nematodes. *Phytopathology* 46:641–644.

Taylor, A.L. (1987). Identification and estimation of root-knot nematode species in mixed populations. *Bulletin 12, Florida Department of Agriculture & Consumer Services,* Gainsville, Florida, 73 p.

Taylor, A.L., Dropkin, V.H. & Martin, G.C. (1955). Perineal patterns of root-knot nematodes. *Phytopathology* 45:26–34.

Thomas, H.A. (1959). On *Criconemoides xenoplax* Raski, with special reference to its biology under laboratory conditions. *Proceedings of the helminthological Society of Washington* 26:55–59.

Thorne, G. (1961). *Principles of nematology.* New York, McGraw Hill Book Co. Inc.: 553 p.

Trudgill, D.L., Evans, K. & Faulkner, G. (1973). A fluidising column for extracting nematodes from soil. *Nematologica* 18 (Year 1972): 469–475.

De Waele, E., De Waele, D. & Wilken, R. (1987). Effect of root mass on the efficacy of methods for extracting root-lesion nematodes from maize roots. *Phytophylactica* 19:473–474.

West, J.A. (1957). Recommended changes in recovery techniques for burrowing nematode. *Plant Disease Reporter* 41:600–602.

Whitehead, A.G. & Hemming, J.R. (1965). A comparison of some quantitative methods of extracting small vermiform nematodes from soil. *Annals of applied Biology* 55:25–38.

Whyte, E.B. & Gowen, S.R. (1974). Recovery of nematodes from banana roots and soil samples. *Nematropica* 4:27–41.

Wright, D.J. & Newall, D.R. (1980), Osmotic and ionic regulation in nematodes. In: B.M. Zuckerman (Ed.) *Nematodes as biological models Vol. 2*. New York, Academic Press: 143–164.

Young, T.W. (1954). An incubation method for collecting migratory endoparasitic nematodes. *Plant Disease Reporter* 38:794–795.

Chapter 3

Nematode Parasites of Rice

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Rice is the most important food crop in the world being the staple food for more than half of the world's population, predominantly in Asia where more than 90% of the world's rice is grown and consumed. It is a very versatile crop and there are many types of rice adapted to various environments and cultivation practises.

Essentially there are five major rice growing environments (Khush, 1984), which have a profound impact on the plant parasitic nematode fauna and their concomitant damage.

Irrigated
About 53% of the world rice area is irrigated and provides up to 75% of the total world rice production. Irrigated (inundated) areas have good water control and rice is flooded throughout the growing season.

Rainfed lowland
Approximately 31% of the world rice area is planted in rainfed lowland areas. Rainfed lowlands have a wide variety of growing conditions related to depth and duration of standing water on the crop. The fields are bunded but are entirely dependent on rainfall.

Deepwater
Areas classified as deepwater occur in the river deltas of South and Southeast Asia occupying about 3% of the world rice area. There is no water control and flooding occurs only during part of the growing season when water depths vary to over 3 m.

Tidal wetlands
Tidal wetlands occur near sea coasts and inland estuaries and are directly or indirectly influenced by tides.

Upland
Upland rice is grown in soils without surface water accumulation. It is rainfed without any water control. Upland rice occupies approximately 13% of the world rice area and yields are generally low. Most rice in Africa and Latin America is upland.

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

TABLE 1. Plant nematode genera and species known or suspected to cause yield loss in rice and means of spread

NEMATODES	RICE AFFECTED	MEANS OF SPREAD
FOLIAR PARASITES		
Aphelenchoides besseyi	Upland, Irrigated, Lowland & Deepwater	Seed, Stem & Panicles, Soil
Ditylenchus angustus	Lowland & Deepwater	Stem & Panicles, Soil
ROOT PARASITES		
Criconemella onoensis	Upland, Irrigated & Lowland	Soil
Heterodera elachista	Upland & Irrigated	Soil & Roots
H. oryzae	Upland & Irrigated	Soil & Roots
H. oryzicola	Upland & Irrigated	Soil & Roots
H. sacchari	Upland & Irrigated	Soil & Roots
Hirschmanniella belli	Irrigated, Lowland & Deepwater	Soil & Roots
H. gracilis	Irrigated, Lowland & Deepwater	Soil & Roots
H. imamuri	Irrigated, Lowland & Deepwater	Soil & Roots
H. mexicana	Irrigated, Lowland & Deepwater	Soil & Roots
H. mucronata	Irrigated, Lowland & Deepwater	Soil & Roots
H. oryzae	Irrigated, Lowland & Deepwater	Soil & Roots
H. spinicaudata	Irrigated, Lowland & Deepwater	Soil & Roots
Hoplolaimus indicus	Upland & Irrigated	Soil & Roots
Meloidogyne graminicola	Upland, Irrigated, Lowland & Deepwater	Soil & Roots
M. incognita	Upland & Irrigated	Soil & Roots
M. javanica	Upland & Irrigated	Soil & Roots
M. arenaria	Upland & Irrigated	Soil & Roots
M. oryzae	Irrigated	Soil & Roots
M. salasi	Irrigated	Soil & Roots
Paralongidorus australis	Upland & Irrigated	Soil
Pratylenchus brachyurus	Upland	Soil & Roots
P. indicus	Upland	Soil & Roots
P. sefaensis	Upland	Soil & Roots
P. zeae	Upland	Soil & Roots
Xiphinema ifacolum	Upland	Soil

Nematodes of Rice

Many genera of parasitic nematodes are associated with rice, but not all are of proven or potential economic importance (Table 1). They have diverse parasitic habits, but all cause mechanical damage and/or malfunctions of the physiological processes involved in plant development, resulting in poor growth and yield loss. Some species cause damage in all rice environments whilst others are more restricted (Table 1). Nevertheless, rice nematodes can be conveniently divided into two groups depending on their parasitic habits: the foliar parasites, feeding on stems, leaves and panicles; and the root parasites.

Foliar Parasites

Aphelenchoides besseyi

Aphelenchoides besseyi is seed borne and causes the disease 'white tip'. It is very widely distributed and now occurs in most rice growing areas (Ou,1985).

Symptoms

Susceptible plants can be symptomless but in general yield loss only occurs in plants showing some symptoms. During early growth, the most conspicuous symptom is the emergence of the chlorotic tips of new leaves from the leaf sheath (Fig. 1). These tips later dry and curl, whilst the rest of the leaf may appear normal. The young leaves of infected tillers can be speckled with a white splash pattern, or have distinct chlorotic areas. Leaf margins may be distorted and wrinkled but leaf sheaths are symptomless (Plate 1C).

Viability of infected seed is lowered, germination is delayed (Tamura & Kegasawa, 1959*b*) and diseased plants have reduced vigour and height (Todd & Atkins, 1958). Infected panicles are shorter, with fewer spikelets and a smaller proportion of filled grain (Dastur, 1936; Yoshii, 1951; Todd & Atkins, 1958).

In severe infections, the shortened flagleaf is twisted and can prevent the complete extrusion of the panicle from the boot (Yoshii & Yamamoto, 1950*a*; Todd & Atkins, 1958). The grain is small and distorted (Todd & Atkins, 1958) and the kernel may be discoloured and cracked (Uebayashi *et al.*, 1976) (Fig. 2). Infected plants mature late and have sterile panicles borne on tillers produced from high nodes.

Biology

When seed infected with *A. besseyi* is sown, the anabiotic nematodes rapidly become active and are attracted to meristematic areas. During early growth, *A. besseyi* is found in low numbers within the innermost leaf sheath, feeding ectoparasitically around the apical meristem (Yoshii & Yamamoto, 1950*b*; Goto & Fukatsu, 1952; Todd & Atkins, 1958). The main stem is frequently more infected than subsequent tillers (Goto & Fukatsu, 1952). A rapid increase in nematode numbers takes place at late tillering (Goto & Fukatsu, 1952) and is associated with the reproductive phase of plant growth (Huang & Huang, 1972). Nematodes are able to enter spikelets before anthesis, within the boot, and feed ectoparasitically on the ovary, stamens, lodicules and embryo (Dastur, 1936; Huang & Huang, 1972). However, *A. besseyi* is more abundant on the outer surface of the glumes and enter when these separate at anthesis (Yoshii & Yamamoto, 1950*b*). As grain filling and maturation proceed, reproduction of the nematode ceases, although the development of J3 to adult continues until the hard dough stage (Huang & Huang, 1972). The population of anabiotic nematodes is predominantly adult female (Huang *et al.*, 1979). These nematodes coil and aggregate in the glume axis. More nematodes occur in filled grain than in sterile spikelets (Yoshii & Yamamoto, 1950*b*) and infected grain tends to occur more towards the middle of the panicle (Goto & Fukatsu, 1952).

A. besseyi is amphimictic (Huang *et al.*, 1979) and males are usually abundant, however reproduction can be parthenogenetic (Sudakova & Stoyakov, 1967). The optimum temperature for oviposition and hatch is 30°C. At 30°C the life cycle is 10 ± 2 days and lengthens significantly at temperatures < 20°C (Huang *et al.*, 1972). No development occurs below 13°C (Sudakova, 1968).

Races and pathotypes

Host races of *A. besseyi* are thought to exist although there is very little evidence except that strawberry plants are not infected by *A. besseyi* from chrysanthemum (Noegel & Ferry, 1963). During several years of screening for resistance to *A. besseyi* in the USA (Cralley, 1952; 1954; Atkins & Todd, 1959) the existence of pathotypes was not discussed as a problem. Differences in susceptibility between years and locations were attributable to environmental factors.

Survival and dissemination

A. besseyi aggregate in the glume axis of maturing grain and slowly desiccate as kernel moisture is lost. They become anabiotic and are able to survive for 8 months to 3 years after harvest (Cralley, 1949; Yoshii & Yamamoto, 1950*b*; Todd, 1952; Todd & Atkins, 1958). Survival is enhanced by aggregation and a slow rate of drying (Huang & Huang, 1974), but the number (Yoshii & Yamamoto,

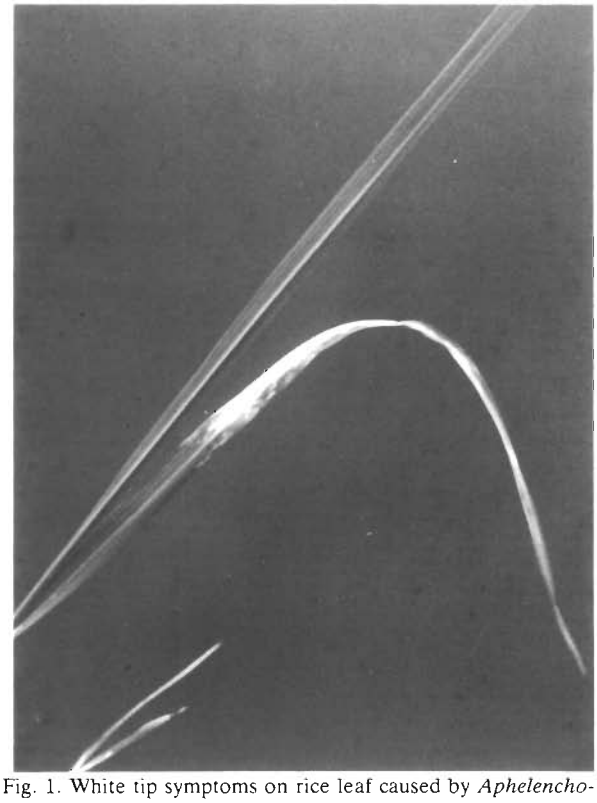

Fig. 1. White tip symptoms on rice leaf caused by *Aphelenchoides besseyi*.

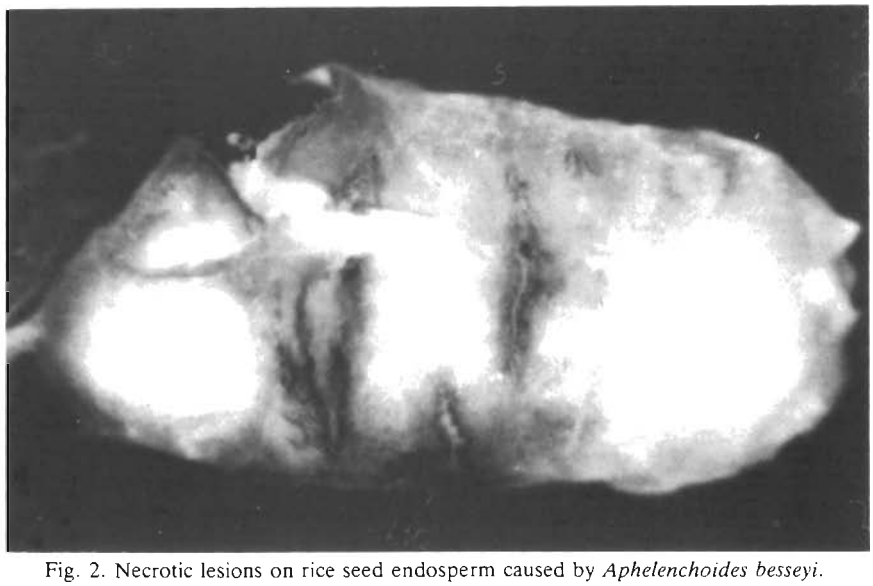

Fig. 2. Necrotic lesions on rice seed endosperm caused by *Aphelenchoides besseyi*.

1950*b*; Sivakumar, 1987*a*) and infectivity (Cralley & French, 1952) of nematodes is reduced as seed age increases. It is ironic that good seed storage conditions probably prolong nematode survival.

A. besseyi is not thought to survive long periods in soil between crops (Cralley & French, 1952; Yamada *et al.*, 1953) although anabiotic nematodes may survive on rice husks and plant debris. Sivakumar (1987*b*) found *A. besseyi* reproducing on *Curvularia* and *Fusarium* in straw after harvest.

The principle dispersal method for *A. besseyi* is seed. The inadvertent dissemination of infected seed must account for its world wide distribution. On a local scale *A. besseyi* can be transmitted in flood water in lowland rice (Tamura & Kegasawa, 1958; Uebayashi & Imamura, 1972) but the survival of nematodes in water decreases as temperature increases from 20° to 30°C (Tamura & Kegasawa, 1958). High seeding rates in infected seed beds also facilitates local dispersal (Kobayashi & Sugiyama, 1977).

Environmental factors affecting parasitism

A. besseyi is able to infect rice in most environments, but infection and damage is generally greater in irrigated lowland and deep water than in upland. In Brazil, Silveira *et al.* (1977) found significantly more infestations in irrigated rice than in upland, and in Japan infection was greater in flooded conditions (Tamura & Kegasawa, 1959*a*).

A. besseyi is active and feeds at a relative humidity greater than 70% (Tikhanova, 1966) and consequently, a high relative humidity during the reproductive phase of the crop is required for migration into the panicle (Sivakumar, 1987*b*) and favours symptom development (Dastur, 1936).

Other hosts

The host range encompasses more than 35 genera of higher plants (Fortuner & Williams, 1975). The wild annual rice *Oryza breviligulata* A. Chev. & Roehr. and *Oryza glaberrima* Steud. are good hosts. Other important hosts include some common weeds of rice fields e.g. *Cyperus iria* L., *Setaria viridis* Beauv. and *Panicum sanguinale* L. (Yoshii & Yamamoto, 1950*b*), and food crops such as *Dioscorea trifida* L. (yam), *Ipomoea batatas* (sweet potato), *Allium cepa* L. (onion), *Zea mays* L. (maize) and *Colocasia esculenta* L. (taro). In addition, many saprophytic and pathogenic fungi are good hosts e.g. *Alternaria* spp., *Curvularia* spp., *Fusarium* spp., *Helminthosporium* spp., *Nigrospora* sp., *Sclerospora* sp. and *Botrytis cinerea*. Rao (1985) found that *A. besseyi* survived but did not multiply on the rice blast fungus, *Pyricularia oryzae*, and Iyatomi and Nishizawa (1954) reported that *A. besseyi* can feed and reproduce on the stem rot fungus *Sclerotium oryzae*.

Disease complexes

The involvement of *A. besseyi* in disease complexes is not widely researched. In Bangladesh, *A. besseyi* occurs with *Ditylenchus angustus* (Timm, 1955) and *Meloidogyne graminicola*, but little is known of their associations. In pot tests the effects of *A. besseyi* and *M. graminicola* on yield of flooded rice were additive but *M. graminicola* infected plants had more *A. besseyi*/seed at harvest than those with *A. besseyi* alone (Plowright, 1986).

A. besseyi appears to influence the symptom development of some fungal pathogens of rice. Nishizawa (1953*a*) found that *A. besseyi* reduced the severity of *Sclerotium oryzae* (stem rot) symptoms and Tikhanova and Ivanchenko (1968) observed that the deterioration of *Pyricularia oryzae* (blast) infected leaves was accelerated by *A. besseyi* which reproduced in the blast lesions. In both reports, the concomitant infection of the fungus and *A. besseyi* reduced yield more than either organism separately. McGrawley *et al.* (1984) found that the *S. oryzae* disease rating and population density of *A. besseyi* on rice cv Nova 76 was increased by concomitant infection of both organisms and their effect on yield was synergistic. Symptom expression, yield loss and the population dynamics of *A. besseyi* varied between rice cultivars.

Rice kernels infected by *A. besseyi* are predisposed to secondary infection by saprophytes such as *Enterobacter agglomerans* which causes black, wedge-shaped spots on grain (Nishizawa, 1976; Uebayashi *et al.*, 1976)

Economic importance and population damage threshold levels

A. besseyi is widely distributed because of its dissemination in seed, but its importance varies between regions, countries and localities. Within a locality the incidence and severity of the disease can change from year to year and is strongly influenced by cultural practises and local rice types.

Damage in a susceptible cultivar largely depends on the percentage of infested seed sown and the number of *A. besseyi*/infested seed. With few exceptions, the former has rarely been determined despite its importance in governing the number of infection loci in a field. Generally, population densities/seed number or weight are counted. Fukano (1962) determined an economic damage threshold density (300 live nematodes/100 seed) which provides a useful basis for damage prediction since in many countries very little information on the current pest status of *A. besseyi* exists.

Yield loss data for *A. besseyi* have been widely reported. In the 1950's typical figures for susceptible cvs in the USA were 17.5%, 4.9% and 6.6% in different years (Atkins & Todd, 1959) and 10–30% in Japan (Yamada & Shiomi, 1950; Yoshii & Yamamoto, 1950*a*; Yoshii, 1951). *A. besseyi* has been controlled in the USA by seed treatment and resistant cvs and is no longer a pest (Hollis & Keoboonrueng, 1984). *A. besseyi* also disappeared from Japan but has re-occurred, the economic value of infected discoloured grain being reduced if infection exceeds 0.7% (Inagaki, 1985).

A. besseyi damage has been reported from deep water rice in Bangladesh. More than 50% of fields are infected and the panicle weight of heavily infected plants (650 nematodes/100 seed) was a third that of less infected plants (112 nematodes/100 seed) (Rahman & McGeachie, 1982; Rahman & Taylor, 1983). In contrast, local cultivars in Thailand appear to be tolerant of *A. besseyi* and no symptoms have been observed despite widespread infection (Buangsuwon *et al.*, 1971).

Economic loss in the Philippines has not been reported, but infection varies according to year, season and cultivar (Madamba *et al.*, 1974). Levels of infested seed are generally low (4.7–7% over 5 years) (Madamba *et al.*, 1981) and severe damage is unlikely as high numbers of *A. besseyi* (210–5300/100 seed) are not always associated with a high percentage of infested seed.

A. besseyi is thought to be an important pest in India. Rao (1976) reported severe symptoms in the field, but accurate yield loss assessment is lacking. Muthukrishnan *et al.* (1974) observed that plants sometimes recover after early severe damage and computed losses of 0.2–10%. Infestation levels in Sri Lanka are not considered important (Lamberti & Ekanayake, 1980).

In Africa, *A. besseyi* is widespread, particularly in west and central Africa, Madagascar and the Comoro Islands (Barat *et al.*, 1969). White tip is very likely to be causing significant yield loss in the mangrove swamp rice of Sierra Leone, where the widely grown cultivars are very susceptible to *A. besseyi* (3000–10 000 *A. besseyi*/100 seed) and the incidence and severity of the disease is increasing (Fomba, 1984). Yield loss is also likely in Tanzania where levels of infested seed are very high (2–82%) and average 68 *A. besseyi*/infested seed (Taylor *et al.*, 1972), and in Madagascar where Vuong (1969) considered that all seed was infested above the Fukano (1962) threshold. *A. besseyi* is not a problem in Zimbabwe (Anon., 1972) and Ghana (Addoh, 1971). In Nigeria, it is very widespread but typical symptoms have not been observed. Infestation levels can be 2–400/100 seed but are commonly < 100/100 seed (Babatola, 1984). In the USSR the yield loss of a susceptible cultivar was 54%. *A. besseyi* infested seed (80%) gave rise to only 31% damaged plants in the field (Popova, 1984). Yield loss in central-west Brazil would seem unlikely with the infestation levels (10–140/100 seed) given by Huang *et al.* (1977) unless grain has a high percent infestation.

Control measures

Preventing dispersal of *A. besseyi* requires the elimination of nematodes from seed e.g. by hot water or chemical seed treatments. Resistant cultivars and cultural methods have been used to reduce infection below damage thresholds, and tolerant cultivars avoid yield loss without nematode control. Stubble burning prevents transmission of *A. besseyi* in straw and chaff but would have to be used in conjunction with other control measures.

Hot water treatment

There are numerous references on the hot water treatment of rice seed (Cralley, 1949, 1952; Yoshii & Yamamoto, 1950*c*, 1951; Todd & Atkins, 1958; Borovkova, 1967). The most effective control requires seed to be pre-soaked in cold water for 18–24 hours, then immersed in water at 51–53°C for 15 minutes. Higher temperatures (55–61°C for 10–15 min) are required if seed is not pre-soaked. The temperature and duration of treatment must be closely monitored, and after treatment the seed must be dried at 30–35°C or sun dried if stored, but otherwise can be sown directly in the field. For quarantine purposes at the International Rice Research Institute, seed is soaked in cold water for three hours followed by hot water at 52–57°C for 15 minutes.

Chemical

Various chemical seed treatments have been used e.g. organic mercury, nicotine sulphate, Parathion, Systox, Malathion, mercuric chloride, methyl bromide, Fensulfothian, carbofuran, aldicarb and methomyl. Good control (up to 100%) is often achieved using carbofuran (Martins *et al.*, 1976; Ribeiro, 1977). In India Rao *et al.* (1986*a*) reported 72% control using soil applications of carbofuran and Lee *et al.* (1972) reported effective control by treating water or by root dipping with Diazinon and Nemagon. *A. besseyi* control with phosphomidon and carbosulfore sprays has been reported (Rao *et al.*, 1986*a*) but pre-harvest chemical treatments alone are only partially effective (Aleksandrova, 1981). No economic assessment of the use of chemical control for *A. besseyi* has been made.

Resistance and tolerance

Resistance to *A. besseyi* appears to be widespread. Cralley (1949) and Cralley and Adair (1949) first reported variations in susceptibility of rice to *A. besseyi* and listed the cultivars Arkansas Fortuna, Nira 43 and Bluebonnet as resistant. In the USA, *A. besseyi* has been controlled principally through the use of resistant cultivars.

Resistance to *A. besseyi* has subsequently been reported from Japan (Nishizawa, 1953*b*; Yamada *et al.*, 1953; Goto & Fukatsu, 1956), Korea (Park & Lee, 1976), India (Rao *et al.*, 1986), Brazil (Oliveira & Ribeiro, 1980; Silveira *et al.*, 1982), USSR (Popova *et al.*, 1980) and Italy (Orsenigo, 1954). Resistance to *A. besseyi* is said to be genetically controlled and carried by the Japanese cv Asa-Hi (Nishizawa, 1953).

Screening for resistance, based primarily on symptom expression, has commonly revealed symptomless but susceptible (i.e. tolerant) cultivars (Nishizawa, 1953; Goto & Fukatsu, 1956). Symptom expression in the field was particularly variable (Atkins & Todd, 1959) and variations between plants of a cultivar also occur (Orsenigo, 1954). In Thailand, all local cultivars are considered tolerant of *A. besseyi* (Buangsuwon *et al.*, 1971). These variations in part demonstrate the strong influence of environment on *A. besseyi* development and damage.

Cultural

Irrigating seed beds (Yamada *et al.*, 1953) or direct seeding into water (Cralley, 1956) reduces infection. In these conditions nematodes emerge and lose vigour before seed germination. High seedling rates in the seed bed (Kobayashi & Sugiyama, 1977) and high numbers of seedlings/hill (Yamada *et al.*, 1953) tend to increase infection by increasing the number of infection loci in the field. Such problems are thought to be responsible for the re-occurrence of *A. besseyi* in Japan (Inagaki, 1985). In the USA (Cralley, 1949) and Japan (Yoshi & Yamamoto, 1951; Yamada *et al.*, 1953) early planting presumably in cooler conditions reduced or eliminated *A. besseyi* infection.

Summary of control measures

1. Hot water treatment of seed. Probably the most effective and cheapest control measure.
2. Resistant or tolerant cultivars.
3. Early planting if rice season is preceded by a cooler period.
4. Low seed bed planting densities.

Methods of diagnosis

Different sampling methods are used depending on the stage of crop growth. During early growth and tillering, *A. besseyi* is found in the base of the culm and between leaf sheaths. For immediate inspection plant tissue is carefully teased in water to release nematodes. Plant tissue can be stained before examination which is particularly useful for detecting low numbers. Alternatively, *A. besseyi* can be extracted from chopped tillers placed on a sieve, or directly in water.

During the reproductive phase *A. besseyi* is progressively found on or in developing spikelets and peak numbers are found at flowering. *A. besseyi* is recovered from spikelets and grain by soaking a known number in water for 24–48 h at 25–30°C. Quantitative extraction requires that the glumes are separated from the kernel yet remain in the extract. The percentage of infested seed is a useful parameter, but extracting from individual seeds is time consuming. Better recovery is achieved from hulled grain but extraction from unhulled grain is sufficient for detection of *A. besseyi* (e.g. for quarantine) from a large seed sample.

Ditylenchus angustus

D. angustus the cause of 'ufra' (India) or 'Tiem Dot San' (Vietnam) occurs in Bangladesh, Burma, India, Madagascar, Malaysia, Thailand and Vietnam, mainly in deepwater rice areas in major river deltas on both deep water and lowland rice.

Symptoms of damage

During vegetative growth, symptoms of nematode damage are prominent white patches, or white speckles in a splash pattern at the bases of young leaves (Fig. 3 & Plate 1A). Brown stains may develop on leaves and sheaths and later intensify to a dark brown colour; leaves inside such sheaths may be wrinkled. Young leaf bases are twisted, leaf sheaths distorted, and the lower nodes can become swollen with irregular branching (Fig. 4). After heading, infected panicles are usually crinkled with empty, shrivelled glumes, especially at their bases; the panicle head and flag leaf are twisted and distorted (Fig. 5 & Plate 1B). Panicles often remain completely enclosed within a swollen sheath or only partially emerge (Fig. 6) (Butler, 1913; Hashioka, 1963; Vuong & Rabarijoela, 1968; Cox & Rahman, 1980; Chakrabarti *et al.*, 1985). Dark brown patches of ufra infected plants can be observed in the field normally after panicle initiation (Plate 1D).

Biology and life cycle

D. angustus is an ectoparasite, feeding on young, foliar tissues. Nematodes in water, invade rice within one hour, but invasion varies with plant age – older plants being less easily invaded (Rahman & Evans, 1988). In deep water rice seedlings, nematodes are found around the growing point but in all parts of the plant in lowland rice. Nematodes are carried or migrate upwards to feed on newly forming tissues enclosed in the rolled leaf sheaths. They accumulate and feed on the primordia of the developing panicles and at harvest are coiled in a quiescent state mainly within the dried glumes of the lower spikelets on each panicle, but not within the grains. Activity and infectivity is resumed when water returns for the next rice crop. On deep water rice in Bangladesh, Butler (1913) assumed that multiplication of *D. angustus* takes place between May, June and November with at least three generations. The greatest infection of rice occurs in the temperature range 27 to 30°C (Butler, 1913, 1919; Hashioka, 1963; Vuong & Rabarijoela, 1968; Vuong, 1969).

Survival and means of dissemination

Between crops, *D. angustus* remains active in ratoons, volunteer or wild rice (Rathaiah, 1988) and other hosts. It also survives in a desiccated state in crop residues, mainly panicles enclosed or partially enclosed in leaf sheaths (Cox & Rahman, 1979*b*; Kinh, 1981). Nematodes can be reactivated in water after 7–15 months (Butler, 1913) but may not remain infective. There is an "overwinter

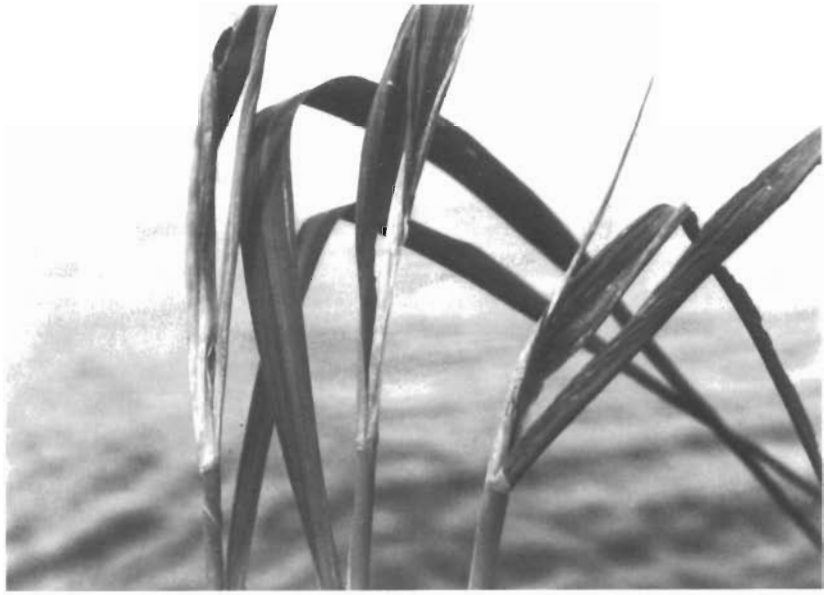

Fig. 3. White patches on rice leaf base caused by *Ditylenchus angustus*.

Fig. 4. Twisting and distortion of leaf bases caused by *Ditylenchus angustus*.

Fig. 5. Twisting and distortion of rice panicles and flag leaf caused by *Ditylenchus angustus*.

Fig. 6. Partial emergence of rice panicle due to *Ditylenchus angustus*.

decay" of *D. angustus* in crop residues between rice crops (Cod & Rahman, 1979*b*) and populations rapidly decline after harvest.

Nematodes in flooded soil are inactive in less than 4 months (Butler, 1913) and probably lose their infectivity in a much shorter period. However, infested soil dried for 6 weeks can produce ufra disease symptoms two months after planting rice (Cuc, 1982*b*). Soil from around diseased plants does not normally appear to produce the disease (Hashioka, 1963) and is a minor component in disease transmission and nematode survival.

Most *D. angustus* die after a few days in water but survival for longer periods has been observed (Butler, 1919). Nematode death appears to occur in water but even a relatively brief survival in water would allow *D. angustus* to spread by water flow to infect new plants (Hashioka, 1963; Sein & Zan, 1977). Long distance transmission in run off water, canals and rivers is possible. Nematodes can migrate from diseased to healthy plants in water, and by stem and leaf contact under high humidity (>75% R.H.) (Rahman & Evans, 1988).

D. angustus can be found inside filled and unfilled spikelets of freshly harvested rice but not in dried seed from infected plants (Butler, 1919; Hashioka, 1963; Sein, 1977*b*; Cuc & Giang, 1982) therefore dissemination in seed seems unlikely.

Environmental conditions affecting parasitism

D. angustus is a parasite of deepwater, irrigated and lowland rice and requires at least 75% humidity to migrate on the foliage. Ufra disease is most severe in the wettest years and in the wettest areas of Bangladesh where the median rainfall exceeds 1.6 m (Cox & Rahman, 1980). In Vietnam, the disease is most severe in months of high rainfall or in fields with high water levels (Cuc & Kinh, 1981).

Hosts of *D. angustus*

Hosts are mainly confined to wild and cultivated species of deepwater and lowland rice (*O. sativa* var. *fatua, O. glaberrima, O. cubensis, O. officinalis, O. meyriana, O. latifolia, O. perennis, O. eichingeri, O. alta, O. minuta*) but *Leersia hexandra* has also been found to support populations of the nematode (Hashioka, 1963; Vuong & Rabarijoela, 1968; Sein & Zan, 1977). Two other weeds, *Echinochloa colona* and *Sacciolepsis interrupta*, have also been found to be infected (Cuc, 1982*a*).

Disease complexes

The ufra nematode can increase the N content of rice plants and thus the plants become more susceptible to the plant pathogen *Pyricularia oryzae* (Mondal *et al.*, 1986). Foliar brown spots associated with the nematode could be secondary invasion sites for *Fusarium* and *Cladosporium* fungi (Vuong, 1969).

Economic importance

Ufra has a restricted distribution because of the unique environmental requirements of the nematode. It is often localized in a rice growing region and does not always occur in the same fields every year. The worldwide and national yield losses caused by *D. angustus* are therefore seemingly low. In Bangladesh, for example, an annual yield loss of 4% (20% yield loss over 20% of the area) has been estimated on deepwater rice (Catling *et al.*, 1979). However, when it does occur, it is one of the most devastating of all diseases affecting rice (Cox & Rahman, 1980).

D. angustus is a serious problem in Vietnam in the Mekong Delta. It can cause 50% to 100% loss of deepwater, irrigated and lowland rice, and during 1974 hundreds of hectares of deepwater rice in one Province were totally lost (Cuc & Kinh, 1981). During 1982 60 000 to 100 000 ha of rice in the Mekong Delta were affected by *D. angustus* (Catling & Puckridge, 1984) and, in Dong Thap Province, 10 000 ha were affected (Puckeridge, 1988). Hashioka (1963) estimated that 500 ha of lowland rice in southern Thailand had yield losses of 20 to 90% caused by ufra. Rice in Assam and West Bengal, India has been found infected with *D. angustus* with losses estimated at 10 to 30% in

some areas (Pal, 1970; Rao *et al.*, 1986*b*). In Bangladesh, 60–70% of low lying areas covering about 200 000 ha are now infested with *D. angustus* (Mondal & Miah, 1987).

Serious yield losses can occur if transplanted rice seedlings are infected with *D. angustus*, even at low initial percentage infection. Yield losses varying from 1.26 to 3.94 t/ha have been recorded with 4 to 10% infected seedlings (Mondal *et al.*, 1988).

Control measures

Many different measures to control *D. angustus* have been suggested, some practical, others less feasible. Those likely to achieve the best results are destruction or removal of infested stubble and straw, crop rotation, control of weeds and volunteer rice, control of water flow, varietal resistance, and escape cropping.

Destruction or removal of infested stubble and straw

Burning of infested crop residues gives very effective control and has long been advocated (Butler, 1919). Thorough burning is essential, although it is not always possible where soil remains water-logged after harvest or when a large proportion of the straw is removed for other purposes, e.g. for cattle fodder, leaving insufficient for effective burning (McGeachie & Rahman, 1983). Ploughing in crop residues can reduce ufra as nematodes decline more rapidly in moist soil than in foliar remains (Butler, 1919). This is not always possible and depends on local circumstances and soil conditions.

Crop rotation

Growing a non-host crop such as jute in rotation with deepwater rice can reduce the incidence of ufra in fields where the rise of floodwater is not excessively fast (McGeachie & Rahman, 1983). Lowland transplanted rice rotated with a non-host, mustard, is less affected by ufra than continuously cultivated rice (Miah & Rahman, 1985).

Eliminating other hosts

Removal of volunteer and ratoon rice plants, wild rice and other host weeds will help prevent the carry over of nematodes from one rice crop to the next (Hashioka, 1963; Sein & Zan, 1977).

Controlling water flow

As nematodes can easily be spread in surface water, preventing river overflow into fields by improved bunding or banks could be beneficial (Sein & Zan, 1977).

Resistance

A large number of deepwater and lowland rice cultivars have been tested against *D. angustus*. In Vietnam, four high-yielding local improved breeding lines (IR9129–393–3–1–2, IR9129–169–3–2–2, IR9224–117–2–3–1, IR2307–247–2–2–3) and three cvs (BKN6986–8, CNL53, Jalaj) are described as slightly infected (Kinh & Phuong, 1981; Kinh & Nghiem, 1982). A Burmese cv (B–69–1) from the Irawaddy Delta was tolerant of ufra disease (Sein, 1977*a*), and a Thailand cv (Khao Tah Ooh) was relatively less susceptible (Hashioka, 1963). Two cvs in West Bengal, India (IR36 and IET4094) were also less susceptible (Chakrabarti *et al.*, 1985). Complete resistance to *D. angustus* has been found in a wild rice, *Oryza subulata*, and a deepwater cv, RD–16–06 (Miah & Bakr, 1977*b*). The Rayada group of deepwater rice lines show the most promise because of their strong resistance. Nine Rayada lines are highly resistant to *D. angustus* in Bangladesh, and others showing moderate resistance are CNL–319, BR306-B–3–2, BR308-B–2–2, Bazail 65 and Dalkatra (Rahman ,1987). Improved cultivars could become available to farmers in the near future (Anon., 1987).

The cvs Padmapani and Digha are not attacked by *D. angustus* in areas of India and Bangladesh. It is suggested that they escape the disease because of their short growth duration (Mondal & Miah, 1987; Rathaiah & Das, 1987).

Escape cropping

D. angustus survives for a limited period and lengthening the overwinter period can reduce primary infection (Cox & Rahman, 1980; McGeachie & Rahman, 1983). This can be achieved with deepwater rice by using short duration cultivars or late sowing and transplanting. Manipulation of rice cropping patterns and cultivation techniques is a promising means of control (McGeachie & Rahman, 1983).

Chemical

Chemicals such as carbofuran, mocap, hexadris monocrotophos, phenazine and benomyl have been used with some success, but their high cost and difficulties of correct application make them uneconomical and they have not been recommended for large scale field use.

The greatest reduction in nematode populations and disease incidence has been achieved with carbofuran and benomyl, alone and in combination (Sein, 1977*c*; Miah & Bakr, 1977*a*; Cox & Rahman, 1979*a*; Rahman *et al.*, 1981; Miah & Rahman, 1985) but at rates which are generally uneconomic.

Summary of control measures

The recommended control measures against *D. angustus* are broadly those put forward by the Deepwater Rice Management Project (Anon., 1987): 1) thorough burning of crop residues to eliminate all infested stem terminals; 2) extending the overwintering period by delayed planting; 3) the use of shorter duration cultivars. The use of resistant cultivars, when they become available, should prove to be the most effective measure.

Methods of diagnosis

D. angustus is found in the foliage of growing plants (and crop residues) mainly near the growing points of leaves and inflorescences and it is these portions of the plants that need to be sampled. Pieces of plant about 5 mm long are cut longitudinally to expose the innermost young leaves.

Nematodes can be extracted from plant pieces placed in a small container on a Baermann funnel or small tray with water and left for 24 hours or overnight before examining the suspension (Chapter 2).

For immediate examination of material, the rolled leaves or young inflorescence can be teased apart in a Petri dish of water and observed directly. Nematodes are active in fresh material but will require some time to resume activity from dried panicles.

Root Parasites

Meloidogyne

Root-knot nematodes, *Meloidogyne* spp., have been found on rice in many countries. *M. graminicola* is mainly distributed in the countries of S.E. Asia, Burma, Bangladesh, Laos, Thailand, Vietnam, India, and is likely to occur in other countries of the region. A *Meloidogyne* sp., probably *M. graminicola*, is reported damaging rice in Hainan Island, China (Guo *et al.*, 1984). *M. graminicola* has recently been found in the Philippines (Plowright, unpubl.) and has also been reported on rice in the USA. It is a damaging parasite on upland, lowland and deepwater rice. *M. oryzae* has only been found in Surinam, S. America (Maas *et al.*, 1978) on irrigated rice. Four species of *Meloidogyne* occur only on upland rice; *M. incognita* (Costa Rica, Cuba, Egypt, Ivory Coast, Nigeria, S. Africa and Japan). *M. javanica* (Brazil, Egypt, Comoro Islands, Nigeria and Ivory Coast), *M. arenaria* (Nigeria, Egypt and S. Africa) and *M. salasi* (Costa Rica and Panama) (Lopez, 1984).

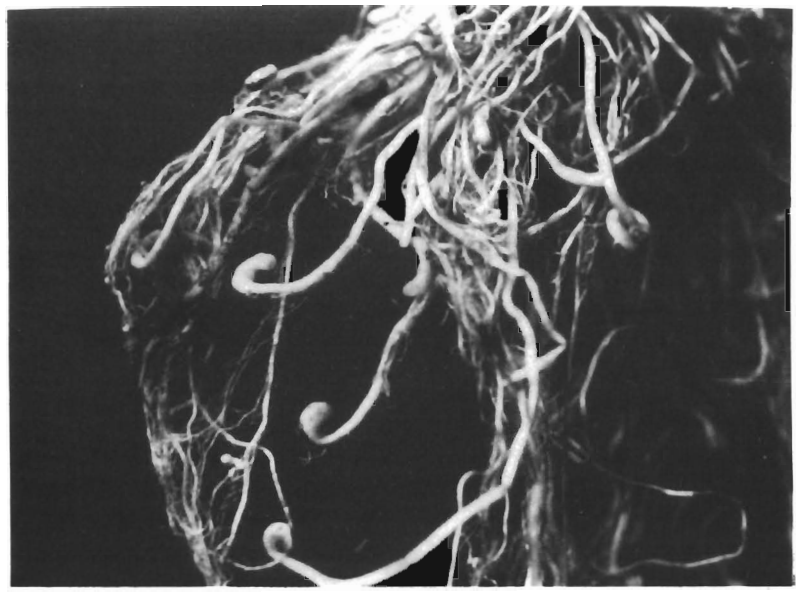

Fig. 7. Characteristic hooked, root tip galls on rice caused by *Meloidogyne graminicola*.

Symptoms

All *Meloidogyne* spp. cause swellings and galls throughout the root system. Infected root tips become swollen and hooked, a symptom which is especially characteristic of *M. graminicola* and *M. oryzae* (Fig. 7).

Above ground symptoms vary according to the type of rice and the species of *Meloidogyne*. In upland conditions and shallow intermittently flooded land all species can cause severe growth reduction, unfilled spikelets, reduced tillering, chlorosis, wilting and poor yield (Babatola, 1984). Symptoms often appear as patches in a field.

M. graminicola is known to cause serious damage to deepwater rice. Prior to flooding, symptoms are the typical stunting and chlorosis of young plants. When flooding occurs, submerged plants with serious root galling are unable to elongate rapidly, and do not emerge above the water level (Bridge & Page, 1982). This causes death or drowning out of the plants leaving patches of open water in the flooded fields (Plate 1E).

Biology and life cycle

The biology and life cycle of *M. incognita* and *M. javanica* on rice is similar to that described for other crops. The life cycle of *M. oryzae* is four weeks at a mean temperature of 27°C (Segeren-V.d. Oever & Sanchit-Bekker, 1984). *M. graminicola* from Bangladesh has a very short life cycle on rice of less than 19 days at temperatures of 22–29°C (Bridge & Page, 1982), and an isolate from the USA completed its cycle in 23–27 days at 26°C (Yik & Birchfield, 1979). In India the life cycle of *M. graminicola* is reported to be 26 to 51 days depending on time of year (Rao & Israel, 1973). Females and egg masses of *M. oryzae* are completely embedded in root tissues and up to 50 females can be present in a single gall (Segeren-V.d. Oever & Sanchit-Bekker, 1984).

Infective, second stage juveniles of *M. graminicola* invade rice roots in upland conditions just behind the root tip (Buangsuwon *et al.*, 1971; Rao & Israel, 1973). Females develop within the root and eggs are mainly laid in the cortex (Roy, 1976*a*). Juveniles can remain in the maternal gall or migrate intercellularly through the aerenchymatous tissues of the cortex to new feeding sites within the same root (Bridge & Page, 1982). This behaviour appears to be an adaptation by *M. graminicola*

to flooded conditions enabling it to continue multiplying within the host tissues even when roots are deeply covered by water. Juveniles that migrate from rice roots in flooded soil cannot reinvade (Bridge & Page, 1982).

Biological races

Rice cultivars are susceptible to race 1 of *M. arenaria* and races 2 and 4 of *M. incognita* (Ibrahim *et al.*, 1983).

Survival and means of dissemination

M. incognita, M. javanica, M. arenaria and *M. salasi* are parasites mainly of upland rice and survive in soil as eggs or juveniles, or on alternative hosts. They do not survive long periods in flooded soil. *M. oryzae* can survive in shallow flooded (<10 cm) rice fields for relatively short periods (Segeren-V.d. Oever & Sanchit-Bekker, 1984) but *M. graminicola* is well adapted to flooded conditions and can survive in waterlogged soil as eggs in eggmasses or as juveniles for long periods. Numbers of *M. graminicola* decline rapidly after 4 months but some egg masses can remain viable for at least 14 months in waterlogged soil (Roy, 1982). *M. graminicola* can survive in soil flooded to a depth of 1 m for at least 5 months (Bridge & Page, 1982), it cannot invade rice in flooded conditions but quickly invades when infested soils are drained (Manser, 1968). All *Meloidogyne* spp. can be spread in soil and on seedlings of other crop hosts planted to a field. Because *M. oryzae* and, especially, *M. graminicola* are found in flooded rice there is the additional danger of dissemination in irrigation and run-off water.

Hosts of *Meloidogyne*

M. incognita, M. javanica and *M. arenaria* have numerous hosts other than rice.

M. graminicola also has a wide host range which includes many of the common weeds of rice fields (Table 2). It is parasitic on both the *indica* and *japonica* races of *Oryza sativa* (Manser, 1971).

TABLE 2. Hosts of *Meloidogyne graminicola*

Alopecurus sp.	*Monochoria vaginalis* (Burm. f.) Presl
Avena sativa L.	*Oryza sativa* L.
Beta vulgaris L.	*Panicum miliaceum* L.
Brachiara mutica (Forsk.) Stapf	*P. repens* L.
Brassica juncea (L.) Czem. & Coss	*Paspalum scrobiculatum* L.
B. oleracea L.	*Pennisetum typhoides* (Burm. f.) Stapf & Hubbard
Colocasia esculenta (D.) Schott	*Phaseolus vulgaris* L.
Cyperus procerus Rottb.	*Poa annua* L.
C. pulcherrimus Willd. ex Kunth	*Ranunculus* sp.
C. rotundus L.	*Saccharum officinarum* L.
Echinochloa colona (L.) Link	*Sorghum bicolor* (L.) Moench
Eleusine indica (L.) Gaertn.	*Sphaeranthus* sp.
Fimbristylis miliacea (L.) Vahl	*Sphenoclea zeylanica* Gaertn.
Fuirena sp.	*Spinacia oleracea* L.
Glycine max (L.) Merr.	*Triticum aestivum* L.
Lactuca sativa L.	*Vicia faba* L.
Lycopersicon esculentum Mill.	

Birchfield (1965); Manser (1971); Buangsuwon *et al.* (1971); Roy (1977); Yik & Birchfield (1979).

A number of weeds and crops are also alternative hosts of *M. oryzae* (Maas *et al.*, 1978; Segeren-V.d. Oever & Sanchit-Bekker, 1984) and *M. salasi* (Lopez, 1984).

Economic importance

M. incognita can cause poor seedling establishment and reduced yields in upland rice. Yields can decrease to 60% when 8000 eggs and juveniles/dm^3 of soil are present at sowing (Babatola, 1984). Significant yield reductions can occur in both upland and irrigated rice with *M. incognita* (Ibrahim *et al.*, 1972) but damage is generally more severe under upland conditions (Fademi, 1984). Damage to irrigated rice will occur where seedlings are raised in well-drained nursery soils. High initial soil populations of both *M. incognita* and *M. javanica* are necessary to cause yield loss in rice, and populations above 1000 eggs/plant are needed to reduce grain yield with *M. javanica* (Sharma, 1980).

M. graminicola can cause economic yield loss in upland, lowland and deepwater rice. In upland rice, there is an estimated reduction of 2.6% in grain yield for every 1000 nematodes present around young seedlings (Rao & Biswas, 1973). The population levels which cause 10% loss in yield of upland rice are 120, 250 and 600 eggs/plant at 10, 30 and 60 days age of plants in direct seeded crops (Rao *et al.*, 1986). In flooded rice, damage by *M. graminicola* is caused in nurseries before transplanting (Fig. 8) – the tolerance limit of seedlings is <1 J2/cm^3 soil (Plowright & Bridge, unpubl.). Damage also occurs prior to flooding where rice is sown directly in well drained soils. Experiments have shown that 4000 juveniles/plant of *M. graminicola* can cause destruction of up to 72% of deepwater rice plants by drowning out. Losses as high as this in the field are unlikely as natural root populations vary considerably (Bridge & Page, 1982).

Control measures

The recommended control of *Meloidogyne* on rice depends on the species. Flooding of soil even for relatively short periods will control *M. incognita, M. javanica* and *M. arenaria* and probably *M. salasi*, but continuous flooding would be necessary for *M. oryzae* and *M. graminicola*. Increasing soil fertility can compensate for some damage by the nematodes (Diomandé, 1984). Resistant cultivars hold out the most promise for effective and economic control, and some resistance to the

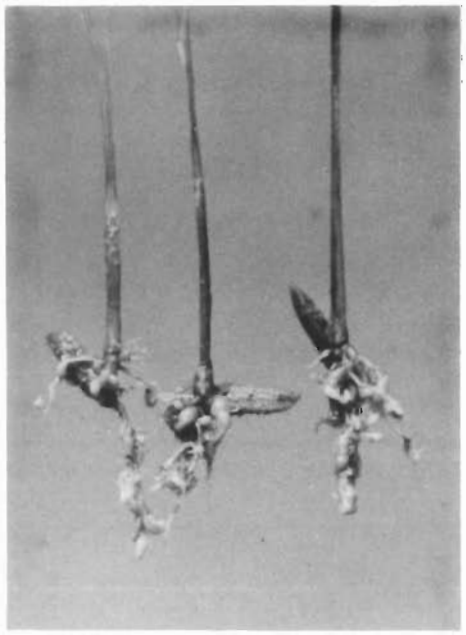

Fig. 8. *Meloidogyne graminicola* root galls on rice seedlings.

different species has been found. Chemical control on the field scale is generally uneconomic particularly with low yielding upland rice, but could be an economic proposition for nursery soils.

Flooding

M. incognita, M. javanica and *M. arenaria* are not important parasites of lowland rice except in nursery seedlings, and can be controlled by flooding where this is possible. Although *M. oryzae* can survive some flooding, it can be controlled at depths greater than 10 cm (Segeren-V.d. Oever & Sanchit-Bekker, 1984). It is mainly a problem in the elevated areas of flooded rice fields where levelling is poor. *M. graminicola* will survive normal flooding but damage to the crop can be avoided by raising rice seedlings in flooded soils thus preventing root invasion by the nematodes (Bridge & Page, 1982). Continuous flooding is highly effective in controlling *M. graminicola* in Vietnam (Kinh *et al.*, 1982).

Resistance

A number of rice cultivars and breeding lines have been recorded as resistant to *Meloidogyne* species although only a small number of these are truly resistant. Diomandé (1984) found that cultivars of *Oryza glaberrima* were resistant to *M. incognita*. Generally cultivars of *O. sativa* were susceptible although some improved cvs IRAT 109, IRAT 112, IRAT 133, IRAT 106 and a traditional cv CG – 18 also showed tolerance. Rice cultivars IR 28, IR 459 and P24 are "resistant" to *M. arenaria, M. javanica* and *M. incognita* (races 2, 3 and 4), and A95, Giza 171 and Giza 172 are "resistant" to *M. incognita* (race 3) and *M. javanica* (Ibrahim *et al.*, 1983). The cultivars IR 20, Ikong Pao Faro 21 and 27 support low populations of *M. incognita* in Nigeria (Babatola, 1980; Fademi, 1987). The majority of rice cultivars are susceptible to *M. graminicola*. For example, all 80 cultivars tested in Laos were found to be susceptible (Manser, 1971). However, there are a number of cultivars from India, Thailand and USA which are reported to be resistant to *M. graminicola* (Table 3).

TABLE 3. Rice cultivars reported to be resistant, or only supporting low populations of *M. graminicola*

Khao Dok Ma Li 105	Farma
Arya 66	Dubaichenga
Rd, 6	K 115
Rd, 7	Jagannath
Rd, 8	Endolia lahi
Rd, 15	Basant Bahar
LA 110	Prosadbhog
Bonnet 73	IR 33
Le Bonnet	IR 20
Bellepatna	Jayanthi
Toride 1	Pankaj
Magnolia	Vijaya
SS Starbonnet	Supriya
Garem	Hamsa
Dumai	Monoharsali
Bahagia	Zenith

Roy (1973); Jena & Rao (1974, 1976); Prasad *et al.* (1979, 1986*b*); Yik & Birchfield (1979); Chunram (1981); Rao *et al.* (1986).

Crop rotation

Certain crops are resistant or poor hosts of *M. graminicola* and could be used in rotation to reduce nematode populations e.g. castor, cowpea, sweet potato, soybean, sunflower, sesame, onion, turnip, *Phaseolus vulgaris*, jute and okra (Rao *et al.*, 1986). Long rotations, greater than 12 months, will be needed to reduce *M. graminicola* soil populations to low levels. Introducing a fallow into the

rotation will also give control of the nematodes but, to be effective, it needs to be a bare fallow free of weed hosts (Roy, 1978) and is therefore impractical in most circumstances. However, one weed, *Eclipta alba*, is toxic to *M. graminicola* and could be grown and incorporated into the field soil to kill the nematodes (Prasad & Rao, 1979*b*).

Soil amendments

The use of decaffeinated tea waste and water hyacinth compost has been suggested to control *M. graminicola* (Roy, 1976*b*).

Chemicals

Seed treatments, root dips, soil drenches and soil incorporation have been tested in experimental trials with varying success in India (Rao *et al.*, 1986) but their practical and economic applicability has not been determined. Carbofuran and diazinon have given effective control of *M. graminicola* in Vietnam when applied to irrigation water (Kinh *et al.*, 1982) but this means of application has many dangers.

Diagnosis

The presence and populations of *Meloidogyne* in rice roots can be determined by standard root staining techniques (Chapter 2). Root extractions will only isolate hatched juveniles and males, and a combination of root maceration and staining of a known weight of roots can be a more efficient and practical way of determining populations of sedentary females within roots. Assessing the severity of root damage by the amount of galling (root-knot index) is a practical and speedy method, but can be difficult with rice. One useful rating system is to rate only the percentage of affected large roots with the root tip galls characteristic of *Meloidogyne* on rice (Diomandé, 1984).

Hirschmanniella

A number of *Hirschmanniella* species, known collectively as rice root nematodes, are parasites of rice. The most commonly recorded species is *H. oryzae* but there was a tendency in the early literature for all *Hirschmanniella* spp. found in rice roots to be grouped under the name *H. oryzae* (Taylor, 1969). Seven species are reported to damage rice (*H. belli, H. gracilis, H. imamuri, H. mexicana* [=*H. caudacrena*], *H. mucronata, H. oryzae* and *H. spinicaudata*) (Table 1), whilst a further six species have been found in rice roots (*H. kaverii, H. magna, H. nghetinhiensis, H. ornata, H. shamimi*, and *H. thornei*). Four species have been recorded from weeds in rice fields (*H. asteromucronata, H. furcata, H. obesa* and *H. truncata*).

Symptoms of damage

There are no easily identifiable above-ground symptoms of nematode damage in the field. Retardation of growth rate occurs especially in early growth, with a decrease in tillering. Yellowing of rice plants is observed occasionally (Plate 1F), and flowering can be delayed by up to 14 days. Roots invaded by *Hirschmanniella* spp. turn yellowish brown and rot (Van der Vecht & Bergman, 1952,; Kawashima & Fujinuma, 1965; Mathur & Prasad, 1972; Muthukrishnan *et al.*, 1977; Fortuner & Merny, 1979; Babatola & Bridge, 1979; Hollis & Keoboonrueng, 1984; Khuong, 1987; Ichinohe, 1988).

Biology

Hirschmanniella species are migratory endoparasites of roots (Fig. 9). The nematodes produce cavities and channels through the cortex which become necrotic for some distance into the root (Van der Vecht & Bergman, 1952; Mathur & Prasad, 1972*b*; Lee & Park, 1975; Babatola & Bridge, 1980; Hollis & Keoboonrueng, 1984).

Fig. 9. *Hirschmanniella oryzae* female and eggs in roots of rice.

Eggs of *H. oryzae* are deposited in the roots a few days after invasion and hatching occurs 4–6 days after deposition (Van der Vecht & Bergman, 1952; Mathur & Prasad, 1972*a*). The life cycle is of variable length. In north India, it is suggested there is only one generation of *H. oryzae* a year (Mathur & Prasad, 1972*a*); in Japan two generations (Kuwahara & Iyatomi, 1970; Ou, 1985); and in Senegal three generations (Fortuner & Merny, 1979). In Java, the minimum duration of development from egg to adult is one month, with a multiplication rate of 13 per generation (Van de Vecht & Bergman, 1952). Maximum root populations occur between tillering and heading of the rice crop (Kuwahara & Iyatomi, 1970; Fortuner & Merny, 1979).

Survival and means of dissemination

H. oryzae survives between crops in weeds and other hosts (Table 4), in ratooning rice roots, and in undecayed roots of rice stubble (Mathur & Prasad, 1973*b*; Feng, 1986; Ichinohe, 1988). *Hirschmanniella* spp. can also survive in soil. They survive longer in roots than in soil but survival of root populations is shorter in flooded soil due to the more rapid decay of roots. Populations of *H. oryzae* decrease slowly in wet rice fields in the absence of a host, surviving for at least 7 months (Park *et al.*, 1970) and are eradicated after 12 months (Fortuner & Merny, 1979). In dry conditions, survival is enhanced by quiescence (Fortuner & Merny, 1979) e.g. *H. oryzae* can survive for longer than 12 months in soils that are not continually wet (Muthukrishnan *et al.*, 1977). *H. oryzae*, *H. imamuri*, and *H. spinicaudata* have also been shown to survive in anaerobic conditions over a wide range of pH (Babatola, 1981). In fallow field soil, populations of *H. oryzae* can survive high temperatures of 35–45°C and low temperatures of 8–12°C (Mathur & Prasad, 1973).

Hirschmanniella is spread in irrigation and flood water, and in soil adhering to implements and field workers. Where there is a long history of rice cultivation, the nematodes are likely to be widespread. In Japan, for example, virtually every rice paddy is infested with either *H. imamuri* or *H. oryzae* (Ichinohe, 1988). The nematodes are also disseminated to the field in roots of rice seedlings from nurseries. *Hirschmanniella* spp. are unusual nematodes being perfectly adapted to constant flooding (Fortuner & Merny, 1979).

Other hosts

Hirschmanniella spp. are parasites of a considerable number of rice field weeds (Van der Vecht & Bergman, 1952) mainly of the families Cyperaceae and Gramineae (Table 4). Few cultivated crops are hosts for *H. oryzae* in India (Mathur & Prasad, 1973*b*) however, some crop plants are hosts of *Hirschmanniella* spp. (Babatola, 1979).

Disease complexes

Necrotic areas develop around nematodes as they migrate and feed on cortical tissues but diminish as nematodes penetrate deeper into the roots. This suggests a phoretic relationship between the rice root nematodes and soil micro-organisms, as necrosis does not occur at all in the absence of these organisms (Babatola & Bridge, 1980). Similarly, "root browning" of rice, caused mainly by soil micro-organisms, is increased in the presence of *H. oryzae* (Lee & Park, 1975).

Economic importance

It is estimated that *Hirschmanniella* spp. infest 58% of the world's rice fields causing 25% yield losses (Hollis & Keoboonrueng, 1984). However, there are discrepancies in yield loss estimates around the world and suggestions that yield reductions occurring in the presence of *Hirschmanniella* are not always solely attributable to the nematodes. In Japan, for example, it has not always been possible to demonstrate high correlations between nematode population levels and yield reductions (Ichinohe, 1988). Similarly in Ivory Coast, where nematicide treatments against *H. spinicaudata* increased rice yields by 20 to 53%, there was no significant correlation between yields and nematode populations. The suggested explanation is that there is a bacteriological factor present which suppresses both nematodes and rice yields (Cadet & Quénéhervé, 1982). Contrasting evidence in Senegal in microplots has established that *H. oryzae* can cause a yield loss of 42% when fertilizers are not applied, with nematode populations at harvest of 3200 to 6000 nematodes/dm^3 of soil, and 5 to 30 nematodes/g root. Even when rice is grown in the best conditions with adequate fertilizers, yield losses are 23%, with nematode populations at harvest of 1500 to 2500/dm^3 of soil and 90 to 410 nematodes/g root (Fortuner, 1974, 1977, 1985).

Experiments with *Hirschmanniella* spp. have established varying degrees of yield loss. Inoculations of one and 10 *H. oryzae*/g soil caused 27% and 39.4% yield loss (Jonathan & Velayuthan, 1987) and the numbers of panicles and grain weight were reduced by 16% and 32% respectively with a population level of 1200 *Hirschmanniella* per plant (Yamsonrat, 1967). *H. imamuri, H. oryzae* and *H. spinicaudata* reduced yields by 31–34.3% at population levels of 1000 nematodes per plant or 500 nematodes/dm^3 of soil (Babatola & Bridge, 1979). The yield of plants inoculated with 5000 *H. mucronata*/plant at one and 40 days was reduced by 50.6% and 45.6% respectively (Panda & Rao, 1971). *H. oryzae* populations of 100 per plant reduced grain yield by 35% (Mathur & Prasad, 1972*b*). In microplots natural populations of 29 to 68 *H. oryzae*/500 cm^3 soil at transplanting reduced grain weight by 13.8–19.2% (Venkitesan *et al.*, 1979).

In Vietnam, economic damage by *Hirschmanniella* spp. occurs when 40 or more nematodes are present in a rice hill one week after transplanting; equivalent after multiplication to 800 nematodes per hill at heading (Khuong, 1987). Yield losses caused by *Hirschmanniella* spp. are influenced by soil fertility (Fortuner & Merny, 1979), age of plant when infected (Panda & Rao, 1971), number of crops and flooding (Khuong, 1987), and seasonal climatic conditions (Mathur & Prasad, 1972*b*).

Control measures

Control of *Hirschmanniella* spp. has been achieved or recommended by various practices, in particular, fallow, weed control, use of "resistant" cultivars, rotation with non-host plants, chemical soil treatment of nurseries and fields, and chemical root dipping and seed coating.

Cultural practices

Yield losses due to *Hirschmanniella* spp. are greater in poor soils. It is, therefore, possible to reduce yield losses by improving the nutritional status of the soil (Mathur & Prasad, 1972*b*).

Nematode populations decline in the absence of host plants but a considerable percentage can survive depending on environmental conditions (Van der Vecht & Bergman, 1952; Mathur & Prasad, 1973; Muthukrishnan *et al.*, 1977). Prolonged fallows might control *Hirschmanniella* but the evidence suggests that fallows would need to be at least 12 months in wet conditions and longer in dry. They would also need to be free of other crop and weed hosts. The management of weeds, which are generally good hosts, will reduce nematode populations both in the absence of rice and during growth of the crop.

Rotation of crops is not possible in continuous rice cropping, but is often normal practice where a single wet season rice crop is followed by dry season crops. In fields with a single rice crop, populations of *Hirschmanniella*, are always low in some localities (Khuong, 1987). This is due to a

TABLE 4. Hosts of *Hirschmanniella* spp. parasitic on rice

Weeds	Crops
Alternanthera sessilis R. Br	* *Oryza sativa* L.
* *Brachiaria ramosa* (L.) Stapf	*Abelmoschus esculentus* (L.) Moench.
* *Crogophora* sp.	*Gossypium hirsutum* L.
* *Cyperus difformis* L.	*Lycopersicon esculentum* Mill.
C. elatus L.	*Pennisetum typhoides* (Burm. f.) Stapf & Hubbard
C. nutans Vahl	*Saccharum officinarum* L.
* *C. iria* L.	*Triticum aestivum* L.
C. procerus Rottb.	*Zea mays* L.
C. pulcherrimus Willd. ex Kunth.	
C. rotundus L.	
* *Echinochloa colona* (L.) Link	
* *E. crus-galli* (L.) Beauv.	
* *Eclipta alba* (L.) Hassk.	
Eichhornia crassipes (Mart.) Solms	
* *Eleocharis spiralis* (Rottb.) Roem & Schult.	
* *Eleusine indica* (L.) Gaertn.	
Eragrostis pilosa (L.) Beauv.)	
* *Fimbristylis ferruginea* (L.) Vahl	
F. globulosa (Retz.) O. Kuntze	
F. miliacea (L.) Vahl	
* *Hydrolea zeylanica* (L.) Vahl	
Ischaeum rugosum Salisb.	
Leptochloa chinensis (L.) Nees	
L. fascicularis (Lam.) A. Gray	
Lindernia antipoda (L.) Alston	
Ludwigia perennis L.	
Mnesithia laevis (Retz.) Kunth	
* *Monochoria hastata* (L.) Solms	
M. vaginalis (Burm. f.) Presl	
Nelumbo nucifera Gaertn.	
Scirpus articulatus L.	
Vallisneria spiralis L.	

* Plants supporting high nematode populations

Van der Vecht & Bergman (1952); Kawashima (1963); Yamsonrat (1967); Mathur & Prasad (1973*b*); Babatola (1979); Mohandas, *et al.* (1979); Venkitesan *et al.* (1979); Razjivin *et al.* (1981); Edward *et al.* (1985); Khuong (1987).

combination of dry soil and non-host dry season crops such as cowpea, pigeon pea, soybean, groundnut, sweet potato, sorghum, tobacco, finger millet, onion against *H. oryzae*, *H. imamuri* and *H. spinicaudata* (Mathur & Prasad, 1973*b*; Babatola, 1979) and millet, cotton and wheat against *H. oryzae* in India (Mathur & Prasad, 1973*b*). Any of these or other non-host crops in rotation with rice should reduce the risk of *Hirschmanniella* damage, but their host status may vary with different nematode species.

Two green manure legume crops, *Sesbania rostrata* and *Sphenoclea zeylanica*, can give good, practical control with the additional benefit of increased soil nitrogen. The yield of rice following *Sesbania* was increased by 214% in micro plots compared to repeated rice cropping. *Sphenoclea* can give 99% control of *Hirschmanniella* spp., *S. rostrata* appears to act as a trap crop (Germani *et al.*, 1983), while *S. zeylanica* produces toxic plant exudates (Mohandas *et al.*, 1981).

Other cultural measures to alleviate damage by *Hirschmanniella* spp. in Japan are (i) early planting and (ii) direct sowing which both reduce initial infection (Sato *et al*, 1970; Nakazato *et al.*, 1964 quoted in Fortuner & Merny, 1979).

Resistance

The majority of rice cultivars tested are good hosts of *Hirschmanniella* spp. These include cultivars from India, Korea, Japan, Nigeria, El Savador, Iraq, Ecuador, Thailand and Vietnam. In Korea, all 270 cultivars tested were susceptible to *H. oryzae*, although six supported only low numbers (Park *et al.*, 1970). Cultivars supporting relatively low nematode numbers have been rated as "resistant" (Table 5). Some of these could be truly resistant, such as cv. TKM9 to *H. oryzae* from India (Ramakrishnan *et al.*, 1984).

TABLE 5. Rice cultivars and breeding lines reported to support low populations of *Hirschmanniella* spp.

Annapurna	Mtu. 28
CR.52	N.136
CR. 320	Ptb.27
CR.44–32	RP.1155–128–1
CR.130–203	Suwon 64
CR.294–548	Tin Pakhia
CR.142–3–2	TMK9
CR.141–6058–1–35	W.113
CR.44–140–2–1051	
Kao Paung Klang	
Kao Paung	
Kao Tah Jue	
Kao Yaun	
Kao Klang Pee	

Park *et al.* (1970); Ramakrishnan *et al.* (1984); Arayaungsarit *et al.* (1986); Rao *et al.* (1986).

Because of their widespread occurrence in rice fields, for example from all locations in Thailand (Yamsonrat, 1967) and virtually every rice paddy in Japan, it is possible that the rice cultivars which now grow best in paddies are those which are relatively resistant to, or tolerant of, *Hirschmanniella* spp. (Ichinohe, 1988).

Chemical

High yield increases have been achieved using chemicals against *Hirschmanniella* but there is little indication that chemical control is economic or practical except in special circumstances (Ichinohe, 1972).

Most of the available chemicals with nematicidal action have been applied with varying success against *Hirschmanniella* especially in India (Edward *et al.*, 1985; Rao *et al.*, 1986), also in Japan

Fig. 10. *Heterodera oryzicola* cyst and white female emerging from roots of rice.

(Ichinohe, 1988), Thailand (Taylor, 1969) and Ivory Coast (Cadet & Quénéhervé, 1982). Chemical control has been attempted by application to field and nursery soil, as root dips for transplanted seedlings, and for soaking seeds. In field soil, various methods of application have been tried including soil incorporation, application in standing water, and "mud ball" application (Prasad *et al.*, 1986).

Heterodera

Four cyst-nematodes infect rice: *H. oryzicola, H. elachista, H. oryzae* and *H. sacchari. H. oryzicola* is found only on upland rice in Kerala State, India (Rao & Jayaprakash, 1978) and *H. elachista* specifically on upland rice in Japan (Okada, 1955). *H. oryzae* occurs on lowland rice in parts of Ivory Coast, Senegal (Fortuner & Merny, 1979) and in Bangladesh (Page & Bridge, 1978). *H. sacchari* occurs on upland and flooded rice throughout western Africa. The Japanese *Heterodera* sp., first referred to by Okada (1955), was attributed to *H. oryzae* until being described as *H. elachista* by Ohshima (1974).

Symptoms

The symptoms of infection by each species are similar. Root growth is suppressed and infected roots turn brown or black. Lemon shaped white females and brown cysts can be observed protruding from infected roots (Fig. 10). Rice responds to *H. sacchari* by the proliferation of secondary roots which have a compensatory function (Babatola, 1983*a*) but generally the reduced size and function of cyst-nematode infected roots leads to leaf chlorosis and slowed plant growth and development, i.e. stunting and reduced tillering. Seedlings are usually more vulnerable and Jayaprakash and Rao (1984) have observed seedling death in patches heavily infested by *H. oryzicola*.

Biology

H. oryzicola and *H. elachista* are parasites of upland rice and *H. sacchari* is damaging only in upland rice (Babatola, 1983*a*) although it is also found in flooded conditions. *H. oryzae* differs by its

adaptation to flooding and second stage juveniles of *H. oryzae* can survive better in anaerobic than in aerobic water (Reversat, 1975).

The biology is as described in Chapter 1. Females of *H. oryzicola, H. elachista* and *H. oryzae* deposit many eggs into a large egg sac attached to the vulval cone. Juveniles in egg sacs hatch freely in water but there is evidence that exudates from actively growing roots are required to stimulate hatch from cysts of *H. oryzicola* (Jayaprakash & Rao, 1982*b*) and *H. oryzae* (Merny, 1966). These differences in hatching behaviour indicate that J2's from later generation egg sacs invade rice during crop growth and that cysts are principally a means of survival. In contrast, *H. sacchari* rarely has an egg sac and eggs hatch freely in water. *H. sacchari* also differs from the other rice cyst-nematodes as it is a parthenogenetic triploid the others being amphimictic. The life cycle of each species is complete in 24–30 days which allows multiple generations depending on the duration of the crop; *H. oryzicola* is said to have twelve generations/year in continuous rice, while *H. oryzae, H. elachista* and *H. sacchari* have 2–3 generations/crop (Berdon-Brizuela, 1969; Merny, 1966, 1972; Netscher, 1969; Netscher *et al.*, 1969; Nishizawa *et al.*, 1972; Shimizu, 1977; Jayaprakash & Rao, 1982*a*; Sharma & Swarup, 1984)

Other hosts

H. oryzicola and *H. oryzae* have a narrow host range with many wild and cultivated Gramineae being non-hosts (Merny & Cadet, 1978; Sharma & Swarup, 1984). *H. oryzicola* has some weed hosts e.g. *Cynodon dactylon* and *Brachiara* sp. (Charles & Venkitesian, 1985), and some Cyperaceae e.g. *Mariscus umbellatus* are hosts of *H. oryzae* (Merny & Cadet, 1978), strangely, banana is a host of both nematodes (Taylor, 1978; Charles & Venkitesian, 1985). In this respect, *H. sacchari* is again quite distinct as it has a wide host range, including many wild Cyperaceae and Gramineae indigenous of W. African savannah and humid lowlands (Odihirin, 1975).

Economic importance

Because of their restricted distribution, cyst nematodes on rice are only of local importance. Watanabe *et al.* (1963) noted that damage by *H. elachista* varied between years and this is likely to be true for the other species as local climatic and edaphic factors, and cultural practises vary. Shimizu (1971) considered that *H. elachista* was important in later growth (presumably grain filling and maturation) and could decrease yield by 7–19%. In India, higher yield losses (17–42%) are attributed to *H. oryzicola* (Kumari & Kuriyan, 1981). *H. oryzae* is a minor problem in Senegal and Ivory Coast and is replaced by *H. sacchari* in mixed populations; its importance on rice crops in Bangladesh requires assessment. Babatola (1983*a*) considered *H. sacchari* to be potentially important on rice in Nigeria.

Control

Exploiting the narrow host range of *H. oryzicola, H. elachista* and *H. oryzae* through rotation with non-host crops is likely to be beneficial, e.g. rotation with soybean or sweet potato to control *H. elachista* has given yield improvements of 2.8 to 3.7 fold (Nishizawa *et al.*, 1972). Fumigation with D-D (300 l/ha) and to a lesser extent EDB, have also given effective control. Rice cvs vary in their susceptibility to *H. oryzae* (Merny & Cadet, 1978), *H. sacchari* (Babatola, 1983*b*) and *H. oryzicola* (Jayaprakash & Rao, 1983), but few have complete resistance. Unfortunately the cvs Lalnakanda, CR143–2–2 & TKM6, although resistant to *H. oryzicola* are susceptible to *Meloidogyne graminicola* (Prasad *et al.*, 1986).

Pratylenchus

Ten species of root lesion nematodes have been reported on rice throughout the world. The most common are *P. zeae*, found in Africa, North and South America, Australia, S. and S.E. Asia and Egypt, and *P. brachyurus*, reported from Africa, South America, Pakistan and the Philippines. They

occur predominantly on upland rice and only *P. zeae* and *P. indicus*, a species found in India and Pakistan, have been reported to cause damage.

Symptoms

There are no specific above-ground symptoms of infection by *P. zeae* (Plowright *et al.*, 1990). However, the leaves of 22 day old rice seedlings infected with *P. indicus* are said to yellow from the tip, wilt and dry up (Rao & Prasad, 1977). *Pratylenchus* spp. cause discrete lesions in the root cortex which become necrotic and coalesce as infection spreads. Root size and function is diminished, growth rate (either tillering or shoot extension) is reduced and plants become stunted.

Biology

Population levels of *P. indicus* decline rapidly during the fallow periods and persist in low numbers (Prasad & Rao, 1978*a*). *P. zeae* can survive in a cultivated clean fallow for up to 6 months (Plowright *et al.*, 1989). Weed hosts of *P. zeae* are *Cynodon dactylon, Amaranthus spinosus, Dactylodenium aegyptium, Digitaria sanguinalis* and *Echinochloa* sp. (Fortuner, 1976).

Invasion by *P. zeae* takes place within one week of emergence, the life cycle being completed in about 30 days. *P. indicus* completes a life cycle in 33–34 days and several overlapping generations occur on a single crop (Prasad & Rao, 1982*a*). The optimum temperature for *P. indicus* reproduction is 23–30°C and peaks of population are always immediately preceded by rainfall (Prasad & Rao, 1979*a*). During crop growth *P. zeae* is found mainly in rice roots and soil populations levels are generally low. Plowright *et al.* (1990) found that the rate of *P. zeae* reproduction was greatest after flowering and numbers increased toward grain maturity. *P. zeae* migrates into soil from heavily infected necrotic roots. *Pratylenchus* spp. are readily disseminated in soil and infected root material.

Economic importance

Despite the prevalence of *P. zeae* in upland rice there is very little information on its pest status. Plowright *et al.* (1990) have shown that rice yield can be increased 13–29% by control of *P. zeae* but some cultivars may be tolerant of infection. The maximum yield reduction in the field was 30% with an infection of 1000 *P. zeae*/g of root at harvest and higher nematode densities at harvest will not necessarily cause further yield loss. Martin (1972) reported that the growth of rice infected with >500 *Pratylenchus* sp. (probably *P. zeae*)/g of root was poor and severely stunted plants had > 3500 nematodes/g of root. Prasad and Rao (1978*b*) found that the yield of rice cv Bala was reduced by 33% at final population densities of *P. indicus* up to 1625/g of root. The data suggest that *P. zeae* and *P. indicus* can cause yield loss in upland rice but further studies are required.

Control

P. zeae can be effectively controlled using chemicals e.g. carbofuran (Plowright *et al.*, 1990). However, chemical control is undesirable in upland rice and requires economic appraisal. Control through crop rotation has been reported using poor or non-host crops such as *Vigna radiata* (L.) Wilczek (Mung bean), *Vigna mungo* (L.) Hepper (black gram), *Vigna unguiculata* (L.) Walp (cowpea), and *Sesamum indicum*, L. (sesame) (Prasad & Rao, 1978*a*). However, *P. zeae* has a wide host range and many of the food crops (mainly cereals) in upland rice cropping systems are good hosts (Table 6). Fallow periods of a practical length will reduce but not eliminate damage by *P. zeae* to susceptible, intolerant cultivars.

Differences in susceptibility of rice cultivars and accessions to *P. zeae* (Plowright & Matias, unpubl.) and *P. indicus* (Prasad & Rao, 1982*b*) have been found but no useful field resistance has yet been identified. Upland rice cultivars appear to differ in their tolerance of *P. zeae* (Plowright *et al.*, 1990) if this is a reliable and hereditable trait then it will be useful for alleviating yield loss.

TABLE 6. Some important hosts of *Pratylenchus zeae*

Oryza sativa L.	*Vigna unguiculata* L. (Walp)
O. glaberrima Steud	*Lycopersicon esculentum* Mill
O. breviligulata A. Chev & Roechr.,	*Ipomoea batatas* (L.)
Eleusine coracana (L.) Gaertn	*Glycine max* (L.) Merr
Sorghum bicolor (L.) Moench	*Arachis hypogaea* L.
Zea mays L.	*Saccharum* spp.
Triticum aestivum	*Solanum tuberosum* L.
Avena sativa L.	*Allium cepa* L.
Hordeum vulgare L.	*Lactuca sativa* L.
Secale cereale L.	*Nicotiana tabacum* L.
Amaranthus sp.	*Gossypium* spp.

Other nematodes

Many nematodes, in addition to those already discussed, are found with rice (Fortuner & Merny, 1979), but few of these are reported to be associated with damage and are probably of limited or local importance.

Criconemella and *Criconema*

Criconemella spp. (*C. curvata, C. obtusicaudata, C. onoensis, C. ornata, C. palustris, C. rustica, C. sphaerocephala*) and *Criconema crassianulatum* occur on upland and flooded rice in various areas of the world (Fortuner & Merny, 1979; Fortuner, 1981; De Waele & van den Berg, 1988), but only *C. onoensis* has been shown to be harmful (Hollis & Keoboonrueng, 1984). *C. onoensis* is known to occur on rice in U.S.A., Guinea, Ivory Coast, Mauritius, Surinam, Belize and India (Luc, 1970; Maas, 1970; Baqri, 1978; Hollis & Keoboonrueng, 1984; Chinappen *et al.*, 1989).

In flooded rice fields, *C. onoensis* causes no obvious symptoms but, in pot tests, the presence of 210 nematodes/dm^3 of soil can cause severe stunting and yellowing of plants (Hollis, 1977). Parasitized main and secondary roots are stunted with lesions near club-shaped root tips. *C. onoensis* is ectoparasitic, feeding on or near root tips of both flooded and upland rice. In West Africa, *C. palustris* is more common than *C. onoensis* in flooded rice (Luc, 1970; Merny, 1970).

Dissemination of *C. onoensis* could result from transportation of infested soil and certainly by irrigation water in flooded rice. Survival is insured by the presence of several permanent weed hosts belonging to the Cyperaceae and Gramineae such as *Cynodon dactylon, Paspalum hydrophilum, Cyperus iria, C. esculentus, C. haspan, C. articulatus, Fimbristylis milacea, Fuirena* sp., *Eleocharis* spp. (Hollis, 1972*a*, *b*; Hollis & Joshi, 1976). Rice supports only low population densities because of root decay caused by early nematode attack (Hollis, 1977).

Aggressive Cyperaceae weeds are very susceptible to *C. onoensis* and may proliferate in the absence of the nematode. Thus chemical control of the nematode is effective only if rice fields are weeded. Hand removal is uneconomic and the combined use of nematicides and herbicides may be harmful to rice. However, the nematicide Furadan can be satisfactorily combined with herbicides containing the active ingredient 3,4 dichloro-propionanilide (Hollis & Keoboonrueng, 1984). The increase of rice yield after weeding and treatment with phenamiphos is about 17% (Hollis, 1977).

In Louisiana, *C. onoensis* decreased rice production in 1967 by 15% (Hollis *et al.*, 1968), and *C. onoensis* may be harmful to flooded rice in Mauritius (Chinappen *et al.*, 1989).

Hoplolaimus indicus

A number of lance nematodes (*Hoplolaimus* spp.) are found on upland rice but only *H. indicus*, a migratory endoparasite, is reported to be damaging. *H. indicus* is a parasite of rice only in India.

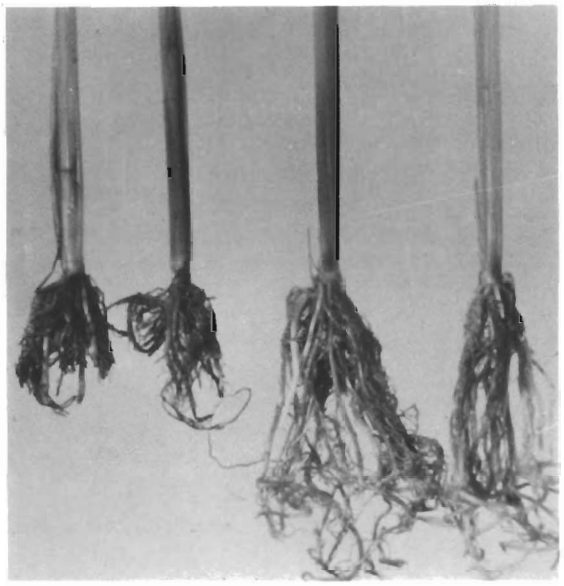

Fig. 11. Roots damaged by *Paralongidorus australis* compared to healthy rice roots (Photo. Graham Stirling).

Damage by *H. indicus* is not always obvious in the field and, in the early seedling stage, is very similar to nitrogen deficiency. Leaves of seedlings infected by *H. indicus* are yellowish before turning brown and brittle with ash coloured tips. Plants are stunted with shortened upper internodes, new leaves can be curled. The symptoms can be less apparent in the latter stage of the crop (Banerji & Banerji, 1966; Das & Rao, 1970). Rice roots have brown lesions at invasion points. Cavities can be found in the cortex, cells lose their rigidity, vascular elements become distorted and roots become flaccid (Das & Rao, 1970; Ramana & Rao, 1975; Alam *et al.*, 1978).

There are few studies of the yield losses caused by *H. indicus* in the field, but, in pot experiments, initial population levels of 100–10 000 nematodes per plant can reduce numbers of tillers by 21.5–36.0% and reduce grain yields by 10.7–19.8% (Ramana & Rao, 1978).

Paralongidorus

Two species of *Paralongidorus* have been recorded on flooded rice: *P. oryzae* occurs in Nepal and India (Verma, 1973) but no data are available concerning its relationship with rice. *P. australis* is locally important along the Burdekin River, N. Queensland, Australia (Stirling & Vawdrey, 1984).

In the field, *P. australis* causes poor growth, mainly in rice planted during the summer. The first symptoms appear 7 to 10 days after flooding and develop into patches of stunted yellow plants of which many may die (Plate 1G). Primary roots show brown necrotic tips, sometimes hooked or curled; secondary roots are shorter than normal, often with a forked appearance. The root system is severely reduced (Fig. 11), attacked roots being 1 to 5 cm long *vs* 15 to 20 cm in healthy plants (Stirling & Channon, 1986). Experimentally inoculating rice seedlings with 250 to 900 nematodes per plant produces symptoms of damage (Stirling, 1984). *P. australis* is an unusually long species, the smallest juveniles being 2–5 mm long and the adults often reaching 10 mm (Stirling & McCulloch, 1985). This inhibits movement in relatively dry or even fine-grained wet soils and restricts full activity to flooded conditions (Stirling, 1986). The nematode is able to survive in micro-aerobic and anaerobic soils. The life cycle is long, lasting three to four rice crops i.e. about two years (Stirling & Shannon,

1986) with most of the active population in the top 25 cm of the soil. Optimal temperature for nematode development is 22–30°C.

After harvest, the nematodes move deeper as the soil dries and become anabiotic. They can survive at least 14 months resuming activity when the soil is flooded (Stirling, 1986). Being limited to flooded rice fields in a relatively narrow area, and with no other known host, the risk of dissemination of this nematode is low.

Control can be achieved by increasing the rate of nitrogenous fertilizer in combination with deep ploughing (> 40 cm) or by changing to moist cultivation rather than flooded in order to inhibit nematode movement (Stirling & Shannon, 1986). Control by dry fallow is effective but not normally appropriate because *P. australis* can remain anabiotic for several years. Crop rotation with maize, sorghum or soybeans may be a preferable substitute to fallow. No resistance has been found.

Xiphinema

X. bergeri is very common in flooded rice fields of Senegal, Ivory Coast and Gambia (Fortuner & Merny, 1973), and appears to be widespread in Western Africa; *X. rotundatum* has occasionally been found in Ivory Coast (Merny, 1970).

Several species of *Xiphinema* have been recorded from the rhizosphere of upland rice: *X. insigne* and *X. orbum* in India, *X. nigeriense* and *X. oryzae* in Nigeria, *X. seredouense* in Guinea, and *X. cavenessi* in Ivory Coast. None of these species are known to be harmful. However, Lamberti *et al.* (1988) claim that *X. ifacolum* is pathogenic on upland rice in Liberia.

Tylenchorhynchus

Tylenchorhynchus spp. are very common in upland, lowland and deepwater rice throughout the world. They have been found infecting rice in central and South America, Africa, the Middle East, India, S. E. Asia, Malaysia and Australia. *Tylenchorhynchus annulatus* (syn. *martini*) has the widest distribution, other less commonly reported species are *T. claytoni, T. mashoodi, T. elegans, T. crassicaudatus, T. clarus, T. nudus* and *T. brassicae. T. annulatus* can be pathogenic to rice in pot culture and damage is accentuated by an aggregation phenomenon known as 'swarming' (Joshi & Hollis, 1976). However, none of the above species have been consistently shown to cause damage to rice in the field.

Helicotylenchus and *Caloosia*

Helicotylenchus spp. are common on upland rice and *H. abunaamai* has been observed feeding ectoparasitically on rice roots (Padhi & Das, 1984). Similarly, *Caloosia heterocephala* feeds ectoparasitically on upland rice roots and can arrest their apical growth (Rao & Mohanadas, 1976).

Conclusions and future prospects

Most rice nematodes are potentially damaging but their economic importance is strongly influenced by the environment. With some widespread nematodes, such as *A. besseyi*, the damage they cause is not proportional to their distribution; for others, such as *Hirschmanniella* spp., yield losses are probably underestimated. The damage caused by *D. angustus* can be devastating, but it has a limited distribution and its occurrence is unpredictable. Furthermore, as new rice cultivars are bred and regional cropping practises change, nematodes may emerge to be even more important. An ominous example of this is the spread of *D. angustus* from its traditional host, deepwater rice, to the more widely grown and globally important irrigated and lowland rice. Other new nematode problems are surfacing, e.g. *Paralongidorus* at present only damaging in Australia. This genus could be more widespread on rice and may have avoided detection as it is difficult to isolate.

Control of rice nematodes poses a number of problems, primarily because measures to control one nematode may increase the damage caused by another. This complicates the recommendation of cultural methods for nematode control on rice and other crops in a rice cropping system, e.g. flooding reduces or eliminates populations of *Pratylenchus, Hoplolaimus, Heterodera*, and most *Meloidogyne* spp., but encourages *Hirschmanniella* spp. Significant reductions in populations of *Hirschmanniella* attacking rice and in soil populations of *Meloidogyne* spp. damaging vegetables, can be achieved where irrigated or lowland rice is rotated with upland vegetable crops. However, this same system would increase damage and yield loss to rice by *M. graminicola*. An accurate knowledge of the species present in a field is thus an important prerequisite for investigating such control methods. Chemical control of rice nematodes will rarely be economic or efficient, and the dangers and difficulties of applying nematicides in flooded rice are self-evident. In flooded soils, sulphur dioxide, produced by anaerobic bacteria, could be used as a form of nematode control and preliminary trials have proven the efficacy of such phenomena (Jacq & Fortuner, 1979). The difficulty is that rice seedlings may also be killed. More research on this and other similar techniques could be beneficial but requires the cooperation of nematologists, agronomists and soil microbiologists. Cultivars with resistance or tolerance to nematodes hold out the most promise for acceptable and economic control of rice nematodes. There is some information on the variations in the susceptibility of rice cultivars to most rice nematodes but essentially very little is known about the mechanisms and inheritance of resistance. Progress is being made with some of the important rice nematodes, but a coordinated international effort is required by nematologists, agronomists and plant breeders to identify and transfer resistance to commercially acceptable rice cultivars.

Acknowledgements

We wish to acknowledge all those who have helped us in preparing this chapter, with particular thanks to Dr. Loothfar Rahman of the Bangladesh Rice Research Institute. Some of the work was done as part of a rice nematode project (R3804) funded by the U.K. Overseas Development Administration.

References

Addoh, P. G. (1971). The distribution and economic importance of plant parasitic nematodes in Ghana, *Ghana Journal of Agricultural Science*, 4: 21–32.

Alam, M. M., Saxena, S. K. & Khan, A. M. (1978). Suitability of crops to certain ectoparasitic nematodes. *Acta Botanica Indica*, 6 (Suppl.): 205–208.

Aleksandrova, I. V. (1981). [Decontamination of seed rice from *Aphelenchoides besseyi* Christie by combined treatment with chemical and irradiation.] *Byulleten Vsesoyuznogo Instituta Gel'mintologii im. K. I. Skryabina*, 31: 105.

Anon. (1972). Report of the Secretary for agriculture for the period 1st October 1970 to 30 September 1971. Salisbury Rhodesia: 26.

Anon. (1987). Deep Water Rice Pest Management Project. Recognition of Ufra Disease. *International Rice Research Institute, Government of India and West Bengal.*

Arayaungsarit, L., Panpitpat, R. & Puttirut, N. (1986). Reaction of rice varieties to root nematode *Hirschmanniella* spp. in the field. *International Rice Research Newsletter*, 11: 14–15.

Atkins, J. G. & Todd. E. H. (1959). White tip disease of rice. III. Yield tests and varietal resistance. *Phytopathology*, 49: 189–191.

Babatola, J. O. (1979). Varietal reaction of rice and other food crops to the rice-root nematodes, *Hirschmanniella oryzae, H. spinicaudata* and *H. imamuri. Nematropica*, 9: 123–128.

Babatola, J. O. (1980). Reactions of some rice cultivars to the root-knot nematode, *Meloidogyne incognita. Nematropica*, 10: 5–9.

Babatola, J. O. (1981). Effect of pH, oxygen and temperature on the activity and survival of *Hirschmanniella* spp. *Nematologica*, 27: 285–291.

Babatola, J. O. (1983*a*). Pathogenicity of *Heterodera sacchari* on rice. *Nematologia mediterranea*, 11: 21–25.

Babatola, J. O. (1983*b*). Rice cultivars and *Heterodera sacchari*. *Nematologia mediterranea*, 11: 103–105.

Babatola, J. O. (1984). Rice nematode problems in Nigeria; their occurrence, distribution and pathogenesis. *Tropical Pest Management*, 30: 256–265.

Babatola, J. O. & Bridge, J. (1979). Pathogenicity of *Hirschmaniella oryzae, H. spinicaudata* and *H. imamuri* on rice. *Journal of Nematology*, 11: 128–132.

Babatola, J. O. & Bridge, J. (1980). Feeding behaviour and histopathology of *Hirschmanniella oryzae, H. imamuri* and *H. spinicaudata* on rice. *Journal of Nematology*, 12: 48–53.

Banerji, S. N. & Banerji, D. K. (1966). Occurrence of the nematode *Hoplolaimus indicus* in West Bengal. *Current Science*, 35: 597–598.

Baqri, Q. H. (1978). Nematodes from West Bengal (India). VI. Species of Criconematoidea (Tylenchida). *Indian Journal of Nematology*, 8: 116–121.

Barat, H., Delassus, M. & Huu-Hai-Vuong. (1969). The geographical distribution of white tip disease of rice in tropical Africa and Madagascar. In: Peachey, J. E. (Ed.) *Nematodes of Tropical Crops. Technical Communication Commonwealth Bureau of Helminthology*, No. 40: 269–273.

Berdon, B. R. & Merny, G. (1964). Biologie d'*Heterodera oryzae* Luc & Berdon, 1961. I. Cycle du parasite et réactions histologiques de l'hôte. *Revue de Pathologie végétale et d'Entomologie agricole de France*, 43: 43–53.

Birchfield, W. (1965). Host parasite relations and host range studies of a new *Meloidogyne* species in Southern USA. *Phytopathology*, 55: 1359–1361.

Biswas, H. & Rao, Y. S. (1971). Toxicological assays of nematicides with rice nematodes. *Indian Phytopathology*, 24: 159–165.

Borovkova, A. M. (1967). [*Aphelenchoides besseyi* in the USSR and its control.] In: Sveshnikova, N. M. (Ed.) [*Nematode diseases of crops.*] Moscow: Izdatelstvo "Kolos": 153–157.

Bridge, J. & Page, S. L. J. (1982). The rice root-knot nematode, *Meloidogyne graminicola*, on deep water rice (*Oryza sativa* subsp. *indica*.). *Revue de Nématologie*, 5: 225–232.

Buangsuwon, D., Tonboon-ek, P., Rujirachoon, G., Braun, A. J. & Taylor, A. L. (1971). Nematodes. In: *Rice Diseases and Pests of Thailand*, English edition: 61–67.

Butler, E. J. (1913). Diseases of rice. *Agricultural Research Institute, Pusa, Bulletin* 34, 37 p.

Butler, E. J. (1919). The rice worm (*Tylenchus angustus*) and its control. *Memoirs of the Department of Agriculture in India*. Botanical Series, 10: 1–37.

Cadet, P. & Queneherve, P. (1982). Action des nématicides en rizière inondée contre *Hirschmanniella spinicaudata. Revue de Nématologie*, 5: 93–102.

Catling, H. D. & Puckridge, D. W. (1984). Report on a visit to Vietnam, October, 1983. *Deepwater Rice*,: 3–4.

Catling, H. D., Cox, P. G., Islam, Z. & Rahman, L. (1979). Two destructive pests of deep water rice – yellow stem borer and ufra. *ADAB News*, 6: 16–21.

Chakrabarti, H. S., Nayak, D. K. & Pal, A. (1985). Ufra incidence in summer rice in West Bengal. *International Rice Research Newsletter*, 10 (1): 15–16.

Charles, J. S. & Venkitesan, T. S. (1985). New hosts of *Heterodera oryzicola* Rao & Jayaprakash, 1978, in Kerala, India. *Indian Journal of Nematology*, 14: 181–182.

Chinappen, M., Lamberti, F., Ciancio, A. & Jokhun, P. (1989). Losses caused by concomitant infestation of *Criconemella onoensis* and *Helicotylenchus dihystera* on upland rice in Mauritius. *Nematologia mediterranea*, 16 (1988): 175–177.

Chunram, C. (1981). Progress report on the root-knot nematode studies in Thailand. *Proceedings of the 3rd Research Planning Conference on Root-knot nematodes*, Meloidogyne *spp., Region VI, July 20–24, 1981, Jakarta*, pp. 97–103.

Cox, P. G. & Rahman, L. (1979*a*). Synergy between benomyl and carbofuran in the control of ufra. *International Rice Research Newsletter*, 4 (4): 11.

Cox, P. G. & Rahman, L. (1979*b*). The overwinter decay of *Ditylenchus angustus*. *International Rice Research Newsletter*, 4 (5): 14.
Cox, P. G. & Rahman, L. (1980). Effects of ufra disease on yield loss of deep water rice in Bangladesh. *Tropical Pest Management*, 26: 410–415.
Cralley, E. M. (1949). White tip of rice. *Phytopathology*, 39: 5.
Cralley, E. M. (1952). Control of white tip of rice. *Arkansas Farm Research*, 1: 6.
Cralley, E. M. (1954). Controlling white tip of rice. *Arkansas Farm Research*, 3: 8.
Cralley, E. M. (1956). A new control measure for white tip. *Arkansas Farm Research*, 5: 5.
Cralley, E. M. & Adair, C. R. (1949). Rice diseases in Arkansas in 1948. *Plant Disease Reporter*, 33: 257–259.
Cralley, E. M. & French, R. G. (1952). Studies on the control of white tip of rice. *Phytopathology*, 42: 6.
Cuc, N-t. T. (1982*a*). New weed host of rice stem nematode identified in Vietnam. *International Rice Research Newsletter*, 7 (3): 15.
Cuc, N-t. T. (1982*b*). Field soil as a source of rice stem nematodes. *International Rice Research Newsletter*, 7 (4): 15.
Cuc, N-t. T. & Giang, L. T. (1982). Relative humidity and nematode number and survival in rice seeds. *International Rice Research Newsletter*, 7 (4): 14.
Cuc, N-t. T. & Kinh, D. N. (1981). Rice stem nematode disease in Vietnam. *International Rice Research Newsletter*, 6 (6): 14–15.
Das, P. K. & Rao, Y. S. (1970). Life history and pathogenesis of *Hoplolaimus indicus* in rice. *Indian Phytopathology*, 23: 459–464.
Dastur, J. F. (1936). A nematode disease of rice in the Central Provinces. *Proceedings of the Indian Academy of Sciences*, Section B. 4: 108–121.
De Waele, D. & van den Berg, E. (1988). Nematodes associated with upland rice in South Africa, with a description of *Hemicycliophora oryzae* sp.n. (Nemata: Criconematoidea). *Revue de Nématologie*, 11: 45–51.
Diomandé, M. (1984). Response of upland rice cultivars to *Meloidogyne* species. *Revue de Nématologie*, 7: 57–63.
Edward, J. C., Sharma, N. N. & Agnihothrudu, V. (1985). Rice root nematode (*Hirschmanniella* spp.) – A review of the work done in India. *Current Science*, 54: 179–182.
Fademi, O. A. (1984). Influence of rate and time of carbofuran application to control root-knot nematodes in upland rice. *International Rice Research Newsletter*, 9 (6): 22–23.
Fademi, O. A. (1987). Resistance of some rice varieties to the root-knot nematode (RKN) *Meloidogyne incognita*. *International Rice Research Newsletter*, 12 (1): 11.
Fend, R. Z. (1986). [A preliminary study on the distribution, occurrence and fluctuation of rice root nematodes.] *Journal of Guangxi Agricultural College*, 2: 57–62.
Fomba, S. N. (1984). Rice disease situation in mangrove and associated swamps in Sierra Leone. *Tropical Pest Management*, 30: 73–81.
Fortuner, R. (1974). Evaluation de dégats causés par *Hirschmanniella oryzae* (Van Breda de Haan, 1902) Luc & Goodey, 1963, nématode endoparasite des racines du riz irrigué. *L'Agronomie tropicale, Nogent*, 29: 708–714.
Fortuner, R. (1976). *Pratylenchus zeae. C. I. H. Descriptions of Plant-parasitic Nematodes*. Set 6, No. 77.
Fortuner, R. (1977). Fertilization du riz et dégats causés par le nématode *Hirschmanniella oryzae* (Van Breda de Haan) Luc & Goodey. *Procès-verbal de la Séance du ler Juin, 1977, Académie d'Agriculture de France*, 58: 624–630.
Fortuner, R. (1981). Les nématodes associés au riz pluvial en Côte d'Ivoire. *L'Agronomie tropicale, Nogent*, 36: 70–77.
Fortuner, R, (1985). Nematode damage assessment problems and solutions for a rice nematode: *Hirschmanniella oryzae*. *California Plant Pest and Disease Report*, 4: 2–7.
Fortuner, R. & Merny, G. (1973). Les nématodes parasites des racines associés au riz en Basse-Casamance et en Gambie. *Cahiers de l'ORSTOM, Série Biologie*, 21: 3–20.
Fortuner, T. & Merny, G. (1979). Root-parasitic nematodes of rice. *Revue de Nématologie*, 2: 79–102.
Fortuner, R & Orton Williams, K. J. (1975). Review of the literature on *Aphelenchoides besseyi* Christie, 1942,

the nematode causing "white tip" disease in rice. *Helminthological Abstracts. Series B. Plant Nematology*, 44: 1–40.

Fukano, H. (1962). [Control method against rice white tip disease] *Nogyo oyobi Engei*, 37: 689–692.

Germani, G., Reversat, G. & Luc, M. (1983). Effect of *Sesbania rostrata* on *Hirschmanniella oryzae* in flooded rice. *Journal of Nematology*, 15: 269–271.

Goto, K. & Fukatsu, R. (1952). [Studies on white tip of rice plant caused by *Aphelenchoides oryzae* Yokoo. II. Number and distribution of the nematode on the affected plants.] *Annals of the Phytopathological Society of Japan*, 16: 57–60.

Goto, K. & Fukatsu, R. (1956). [Studies on the white tip of rice plant. III. Analysis of varietal resistance and its nature.] *Bulletin of the National Institute of Agricultural Sciences, Tokyo. Series C. Plant Pathology and Entomology*, No. 6: 123–149.

Guo, Y. Y., Zhou, N. S., Wu, T. T. & Qiu, H. L. (1984). [An investigation and study on rice root-knot nematode on Hainan Island.] *Guangdong Agricultural Science (Guangdong Nongye Kexue)*, No. 4: 32–34.

Hashioka, Y. (1963). The rice stem nematode *Ditylenchus angustus* in Thailand. *F. A. O. Plant Protection Bulletin*, 11: 97–102.

Hollis, J. P. (1969). Genesis of a soil nematode problem in Louisiana rice. *International Rice Commission Newsletter*, 18: 19–28.

Hollis, J. P. (1972*a*). Nematicide-weeds interaction in rice fields. *Plant Disease Reporter*, 56: 420–424.

Hollis, J. P. (1972*b*). Competition between rice and weeds in nematode control tests. *Phytopathology*, 62: 764.

Hollis, J. P. (1977). Loss in yield of rice caused by the ring nematode *Criconemoides onoensis* revealed by the elimination of the yellow nutsedge, *Cyperus esculentus*. *Nematologica*, 23: 71–78.

Hollis, J. P. & Joshi, M. M. (1976). Weed effect on chemical control of ring nematodes in rice. *Annual Proceedings of the American phytopathological Society*, 1975: 44–45.

Hollis, J. P. & Keoboonrueng, S. (1984). Nematode Parasites of Rice. In: Nickle, W. R. (Ed.) *Plant and Insect Nematodes*. New York & Basel, Marcel Dekker: 95–146.

Hollis, J. P., Embabi, M. S. & Alhassan, S. A. (1968). Ring nematode disease of rice in Louisiana. *Phytopathology*, 58: 728–729.

Huang, C. S. & Huang, S. P. (1972). Bionomics of white-tip nematode, *Aphelenchoides besseyi* in rice florets and developing grains. *Botanical Bulletin of Academia Sinica*, 13: 1–10.

Huang, C. S. & Huang, S. P. (1974). Dehydration and the survival of rice White Tip nematode *Aphelenchoides besseyi*. *Nematologica*, 20: 9–18.

Huang, C. S., Cupertino, F. P. & Marinelli, N. M. (1977). Incidence of white-tip nematode, *Aphelenchoides besseyi*, in stored rice seed from Central-West Brazil. *PANS*, 23: 65–67.

Huang, C. S., Huang, S. P. & Chiang, Y. C. (1979). Mode of reproduction and sex ratio of rice white-tip nematode, *Aphelenchoides besseyi*. *Nematologica*, 25: 244–260.

Huang, C. S., Huang, S. P. & Lin, L. H. (1972). The effect of temperature on development and generation period of *Aphelenchoides besseyi*. *Nematologica*, 18: 432–438.

Ibrahim, I. K. A., Ibrahim, I. A. & Rezk, M. A. (1972). Pathogenicity of certain parasitic nematodes on rice. *Alexandria Journal of Agricultural Research*, 20: 175–181.

Ibrahim, I. K. A., Rezk, M. A. & Khalil, H. A. A. (1983). Resistance of some plant cultivars to root-knot nematodes, *Meloidogyne* spp. *Nematologia mediterranea*, 11: 189–192.

Ichinohe, M. (1972). Nematode diseases of rice. In: Webster, J. M. (Ed.) *Economic Nematology*, London, U. K., Academic Press: 127–143.

Ichinohe, M. (1988). Current research on the major nematode problems in Japan. *Journal of Nematology*, 20: 184–190.

Inagaki, H. (1985). The plant parasitic nematodes important in Japan and the related researches. *JARQ*, 18: 194–201.

Iyatomi, K. & Nishizawa, T. (1954). [Artificial culture of the strawberry nematode, *Aphelenchoides fragariae*, and the rice white-tip nematode *Aphelenchoides besseyi*.] *Japanese Journal of Applied Zoology*, 19: 8–15.

Jacq, V. & Fortuner, R. (1979). Biological control of rice nematodes using sulphate reducing bacteria. *Revue de Nématologie*, 2: 41–50.

Jayaprakash, A. & Rao, Y. S. (1982*a*). Life history and behaviour of the cyst nematode, *Heterodera oryzicola* Rao and Jayaprakash, 1978 in rice (*Oryza sativa* L.). *Proceedings of the Indian Academy of Sciences, Animal Sciences*, 91: 283–295.

Jayaprakash, A. & Rao, Y. S. (1982*b*). Hatching behaviour of the cyst-nematode *Heterodera oryzicola*. *Indian Journal of Nematology*, 12: 400–402.

Jayaprakash, A. & Rao, Y. S. (1983). Reaction of rice cultivars against the cyst nematode, *Heterodera oryzicola*. *Indian Journal of Nematology*, 13: 117–118.

Jayaprakash, A. & Rao, Y. S. (1984). Cyst nematode, *Heterodera oryzicola* and seedling blight fungus *Sclerotium rolfsii* disease complex in rice. *Indian Journal of Nematology*, 14: 58–59.

Jena, R. N. & Rao, Y. S. (1974). Root-knot nematode resistance in rice. *Indian Journal of Genetics and Plant Breeding*, 34: 443–449.

Jonathon, E. I. & Velayutham, B. (1987). Evaluation of yield loss due to rice root nematode *Hirschmanniella oryzae*. *International Nematology Network Newsletter*, 4: 8–9.

Joshi, M. M. & Hollis, J. P. (1976). Pathogenicity of *Tylenchorchynchus martini* swarmers to rice. *Nematologica*, 22: 123–124.

Kakuta, T. (1915). [On black grain disease of rice.] *Journal of Plant Protection, Tokyo*, 2: 214–218.

Kawashima, K. (1963). [Investigations on *Hirschmannia oryzae*. I. Varietal susceptibility to the nematode. II. Susceptibilities of weeds to the nematode. III. Durable effect of fungicides.] *Annual Report of Society Plant Protection, North Japan*, 14: 111, 112–113, 158–159.

Khuong, N. B. (1987). *Hirschmanniella* spp. in rice fields of Vietnam. *Journal of Nematology*, 19: 82–84.

Khush, G. S. (1984). Terminology for rice growing environments. In: *Terminology for rice growing environments*. International Rice Research Institute, Los Banos, Philippines: 5–10.

Kinh, D-n. (1981). Survival of *Ditylenchus angustus* in diseased stubble. *International Rice Research Newsletter*, 6 (6): 13.

Kinh, D-n. & Nghiem, N-t. (1982). Reaction of rice varieties to stem nematodes in Vietnam. *International Rice Research Newsletter*, 7 (3): 6–7.

Kinh, D-n. & Phuong, C-d (1981). Reaction of some deepwater rice varieties to *Ditylenchus angustus*. *International Rice Research Newsletter*. 6 (6): 6–7.

Kinh, D-n, Huong, N. M. & Ut, N. U. (1982). Root-knot disease of rice in the Mekong Delta, Vietnam. *International Rice Research Newsletter*, 7 (4): 15.

Kobayashi, Y. & Sugiyama, T. (1977). [Dissemination and reproduction of white tip nematodes *Aphelenchoides besseyi* in mechanical transplantation rice culture.] *Japanese Journal of Nematology*, 7: 74–77.

Kumari, U. & Kuriyan, K. J. (1981). Cyst nematode, *Heterodera oryzicola*, on rice in Kerala. I. Estimation of loss in rice due to *H. oryzicola* infestation, in field conditions. *Indian Journal of Nematology*, 11: 106.

Kuwahara, M. & Iyatomi, K. (1970). Studies on the bionomics of the rice root nematode *Hirschmanniella imamuri* Sher and *Hirschmanniella oryzae* (Soltwedel) Luc and Goodey, with special reference to its mode of life and population dynamics. *Japanese Journal of applied Entomology and Zoology*, 14: 117–121.

Lamberti, F. & Robini, K. E. (1980). Importance of plant parasitic nematodes in Sri Lanka and recommendations for control measures and future work. *The second Asian symposium on plant diseases in the tropics, Bangkok*: 144.

Lamberti, F., Bleve-Zacheo, T., Tuopay, D. K., Ciancio, A. & Boibi, J. B. (1988). Relationships between *Xiphinema ifacolum* and rice in Liberia. *Nematologia mediterranea*, 15 (1987): 303–314.

Lee, Y. B. & Park, J. S. (1975). [Influence of rice root nematode (*Hirschmanniella oryzae*) on the root browning of rice. *Korean Journal of Plant Protection*, 14: 35–36.

Lee, Y. B., Park, J. S. & Han, S. C. (1972). [Studies on the chemical control of white tip nematode, *Aphelenchoides besseyi* Christie, before transplanting.] *Korean Journal of Plant Protection*, 11: 37–40.

Lopez, R. (1984). *Meloidogyne salasi* sp.n. (Nematoda: Meloidogynidae), a new parasite of rice (*Oryza sativa* L.) from Costa Rica and Panama. *Turrialba*, 34: 275–286.

Luc, M. (1970). Contribution à l'étude du genre *Criconomoides*. *Cahiers de l'ORSTOM, Série Biologie*, 11: 69–131.

Maas, P. W. (1970). Tentative list of plant parasitic nematodes in Surinam, with description of two new species of Hemicycliophorinae. *Bulletin van het Landbouwproefstation Suriname*, No. 87, 9p.

Maas, P. W. T., Sanders, H. & Dede, J. (1978). *Meloidogyne oryzae* n.sp. (Nematoda: Meloidogynidae) infesting irrigated rice in Surinam (South America). *Nematologica*, 24: 305–311.

Madamba, C. P., Sukit, V. & Adamo, J. A. (1974). Incidence of plant parasitic nematodes associated with rice grown in the Philippines. *Proceedings. International Rice Research Conference, 1974, International Rice Research Institute, Los Banos, Philippines*,: 4.

Madamba, C. P., Sukit, V., Ong. E. T. & Sevilla, N. C. (1981). Incidence of plant parasitic nematodes associated with rice grown in the Philippines. *The Philippine Agriculturist*, 64: 231–236.

McGrawley, E. C., Rush, M. C. & Hollis, J. P. (1984). Occurrence of *Aphelenchoides besseyi* in Louisiana rice seed and its interaction with *Sclerotium oryzae* in selected cultivars. *Journal of Nematology*, 16: 65–68.

Manser, P. D. (1968). *Meloidogyne graminicola* a cause of root knot of rice. *FAO Plant Protection Bulletin*, 16: 11.

Manser, P. D. (1971). Notes on the rice root knot nematode in Laos. *FAO Plant Protection Bulletin*, 19: 138–139.

Martin, G. C. (1972). Rhodesia. A nematode affecting rice. *FAO Plant Protection Bulletin*, 20: 40–41.

da Martins, J. F., Goncalo, J. F. P. & Lordello, L. G. E. (1976). Tratamento quimico de sementes de arroz visando a erradicacao do nematoide *Aphelenchoides besseyi*. *O Solo*, 68: 58–61.

Mathur, V. K. & Prasad, S. K. (1972*a*). Embryonic development and morphology of larval stages of the rice root nematode, *Hirschmanniella oryzae*. *Indian Journal of Nematology*, 2: 146–157.

Mathur, V. K. & Prasad, S. K. (1972*b*). Role of the rice root nematode, *Hirschmanniella oryzae* in rice culture. *Indian Journal of Nematology*, 2: 158–168.

Mathur, V. K. & Prasad, S. K. (1973*a*). Control of *Hirschmanniella oryzae* associated with paddy. *Indian Journal of Nematology*, 3: 54–60.

Mathur, V. K. & Prasad, S. K. (1973*b*). Survival and host range of the rice root nematode, *Hirschmanniella oryzae*. *Indian Journal of Nematology*, 3: 88–93.

McGeachie, I. & Rahman, L. (1983). Ufra Disease: A review and a new approach to control. *Tropical Pest Management*, 29: 325–332.

Merny, G. (1966). Biologie d'*Heterodera oryzae* Luc & Berdon, 1961. II. Rôle des masses d'oeufs dans la dynamique des populations et la conservation de l'espèe. *Annales des Epiphyties*, 17: 445–449.

Merny, G. (1970). Les nématodes phytoparasites des rizières inondees en Côte d'Ivoire. I. Les espèces observées. *Cahiers de l'ORSTOM, Serie Biologie*, 11: 3–43.

Merny, G. (1972). Les nématodes phytoparasites des rizières inondées de Côte d'Ivoire. III. Etude sur la dynamique des populations de deux endoparasites: *Hirschmanniella spinicaudata* et *Heterodera oryzae*. *Cahiers de l'ORSTOM, Série Biologie*, 16: 31–87.

Merny, G. & Cadet, P. (1978). Penetration of juveniles and development of adults of *Heterodera oryzae* on different plants. *Revue de Nématologie*, 1: 251–255.

Miah, S. A. & Bakr, M. A. (1977*a*). Chemical control of ufra disease of rice. *PANS*, 23: 412–413.

Miah, S. A. & Bakr, M. A. (1977*b*). Sources of resistance to ufra disease of rice in Bangladesh. *International Rice Research Newsletter*, 2 (5): 8.

Miah, S. A. & Rahman, M. L. (1985). Severe ufra outbreak in transplanted rice in Bangladesh. *International Rice Research Newsletter*, 10 (3): 24.

Mohandes, C., Rao, Y. S. & Sahu, S. C. (1981). Cultural control of rice root nematodes (*Hirschmanniella* spp.) with *Sphenoclea zeylandica*. *Proceedings of the Indian Academy of Sciences (Animal Sciences)*, 90: 373–376.

Mondal, A. H. & Miah, S. A. (1987). Ufra problem in low lying areas of Bangladesh. *International Rice Research* Newsletter, 12 (4): 29–30.

Mondal, A. H., Rahman, L., Ahmed, H. J. & Miah, S. A. (1986). The causes of increasing blast susceptibility of ufra infected rice plants. *Bangladesh Journal of Agriculture*, 11: 77–79.

Mondal, A. H., Rahman, M. L. & Miah, S. A. (1988). Yield loss due to transplanting of ufra infected seedlings. *Bangladesh Journal of Botany*, 18 (in press).

Muthukrishnan, T. S., Rajendran, G. & Chandrasekara, J. (1974). Studies on the white tip nematode of rice *Aphelenchoides besseyi* in Tamil Nadu. *Indian Journal of Nematology*, 4: 188–193.

Muthukrishnan, T. S., Rajendran, G., Ramamurthy, V. V. & Chandrasekaran, J. (1977). Pathogenicity and control of *Hirschmanniella oryzae*. *Indian Journal of Nematology*, 7: 8–16.

Netscher, C. (1969). L'ovogenèse et la reproduction chez *Heterodera oryzae* et *H. sacchari* (Nematoda: Heteroderidae). *Nematologica*, 15: 10–14.

Netscher, C., Luc, M. & Merny, G. (1969). Description du mâle d'*Heterodera sacchari* Luc & Merny, 1963. *Nematologica*, 15: 156–157.

Nishizawa, T. (1953*a*). [On the relation between the rice nematode disease 'white tip' and the stem-rot of rice plants.] *Annals of the Phytopathological Society of Japan*, 17: 137–140.

Nishizawa, T. (1953*b*). [Studies on the varietal resistance of rice plants to the rice nematode disease "Senchu shingare byo" (VI).] *Bulletin of the Kyushu Agricultural Experimental Station*, 1: 339–349.

Nishizawa, T. (1976). [Occurrence of abnormal rice kernels associated with the infestation of white tip nematode, *Aphelenchoides besseyi*.] *Japanese Journal of Nematology*, 6: 73–79.

Nishizawa, T., Shimizu, K. & Nagashima, T. (1972). Chemical and cultural control of the rice nematode, *Heterodera oryzae* Luc et Berdon Brizuela, and hatching responses of the larvae to some root extracts. *Japanese Journal of Nematology*, 2: 27–32.

Noegel, K. A. & Perry, V. G. (1963). A foliar disease of Chrysanthemum incited by the strawberry summer crimp nematode. *Proceedings of the soil crop science Society of Florida, 22nd Annual Meeting* (1962); 162–166.

Odihirin, R. A. (1975). Occurrence of *Heterodera* cyst nematode (Nematoda: Heteroderidae) on wild grasses in southern Nigeria. *Occasional Publication, Nigerian Society for Plant Protection*, 1: 24–25.

Ohshima, Y. (1974). *Heterodera elachista* n.sp., an upland rice cyst nematode from Japan. *Japanese Journal of Nematology*, 4: 51–56.

Okada, T. (1955). On morphological characters of the upland rice nematode, *Heterodera* sp. *Annual Meeting of the Japanese Society of applied Entomology and Zoology*, 1955: 11.

Oliveira, J. V. & Ribeiro, A. S. (1980). Estudo do nematoide *Aphelenchoides besseyi* Christie, em arroz irrigado. *Lavoura Arrozeira*, 33: 40–43.

Orsenigo, M. (1954). Suscettibilita di varieta Italiane di riso alla malattia della "white-tip". *Annali della Facolta di Agraria Universita Cattolica del S. Cuore, Milano*, 51: 1–7.

Ou, S. H. (1985). *Rice Diseases* (2nd Edition). Kew, England, Commonwealth Mycological Institute, 380 p.

Padhi, N. N. & Das, S. N. (1984). Some aspects of the ecological behaviour of *Helicotylenchus abunaamai* Siddiqi, 1972. *Indian Journal of Nematology*, 14: 25–29.

Page, S. L. J. & Bridge, J. (1978). Plant nematodes on deep water rice in Bangladesh. *Ministry of Overseas Development, U. K. Report on visit to Bangladesh*, 48p.

Pal, A. K. (1970). Survey on nematode infection of paddy and successful treatment with hexadrin. *Proceedings of the Indian Science Congress Association*, 57: 496.

Panda, M. & Rao, Y. S. (1971). Evaluation of losses caused by the root-nematodes (*Hirschmanniella mucronata* Das) in rice (*Oryza sativa* L.) *Indian Journal of Agricultural Science*, 41: 611–614.

Park, J. S. & Lee, J. O. (1976). Varietal resistance of rice to the white-tipped nematode *Aphelenchoides besseyi*. *International Rice Research Newsletter*, 1: 15.

Park, J. S., Han, S. C. & Lee, Y. B. (1970). [Studies on the ecology and feeding preference of *Hirschmanniella oryzae*.] *Research Reports of the Office of Rural Development, Korea, Plant Environment*, 13: 93–98.

Plowright, R. A. (1986). The interaction of *Aphelenchoides besseyi* and *Meloidogyne graminicola* on rice cv. IR36. *18th International Symposium of European Society of Nematologists*, Antibes: 24.

Plowright, R. A., Matias, D., Aung, T. & Mew, T. W. (1990). The effect of *Pratylenchus zeae* on upland rice. *Revue de Nématologie* (in press).

Popova, M. B. (1984). [Principal factors determining the intensity and pathogenicity of *Aphelenchoides besseyi* infestation on rice.] *Byulleten' Vsesoyuznogo Instituta Gel'mintologii im. K. I. Skryabina*, No. 36: 39–41.

Popova, M. B. & Chizhov, V. N. (1984). [Method for inoculating *Aphelenchoides besseyi* Christie, 1942.] *Byulleten Vsesoyuznogo Instituta Gel'mintologii im. K. I. Skryabina*, No. 36: 42–44.

Popova, M. B., Andrusenko, V. V. & Korsakova, L. A. (1980). [Degree of resistance of rice varieties to *Aphelenchoides besseyi* Christie, 1942.] *Byulleten Vsesoyuznogo Instituta Gel'mintologii im. K. I. Skryabina (Fitogel'mintologiya)*, No. 26: 43–49.

Prasad, J. S. & Rao, S. Y. (1978*a*). Influence of crop rotations on the population densities of the root lesion nematode *Pratylenchus indicus* in rice and rice soils. *Annales de Zoologie et Ecologie animale*, 10: 627–634.

Prasad, J. S. & Rao, S. Y. (1978*b*). Potentiality of *Pratylenchus indicus* the root lesion nematode as a new pest of upland rice. *Annales de Zoologie et Ecologie animale*, 10: 635–640.

Prasad, J. S. & Rao, Y. S. (1979*a*). Factors influencing the prevalence of the root-lesion nematode, *Pratylenchus indicus*, Das 1960 in rice. *Revue d'Ecologie et de Biologie du Sol*, 16: 517–523.

Prasad, J. S. & Rao, Y. S. (1979*b*). Nematicidal properties of the weed *Eclipta alba* Hask (Compositae). *Revista di Parasitologia*, 50: 87–90.

Prasad, J. S. & Rao, Y. S. (1982*a*). Studies on the life cycle of *Pratylenchus indicus*, the root lesion nematode in rice. *Oryza*, 19: 209–211.

Prasad, J. S. & Rao, Y. S. (1982*b*). Screening of some rice cultivars against the root lesion nematode, *Pratylenchus indicus*. *Nematologia mediterranea*, 10: 215–216.

Prasad, K. S. K., Krishnappa, K. & Rao, Y. S. (1979). Response of some improved rice varieties to the development and reproduction of *Meloidogyne graminicola* Golden and Birchfield, 1965. *Mysore Journal of Agricultural Sciences*, 13: 60–62.

Prasad, J. S., Panwar, M. S. & Rao, Y. S. (1986*a*). Chemical control of the root nematode (*Hirschmanniella mucronata*) in rice. *Beitrage zur Tropischen Landwirtschaft und Veterinarmedizin*, 24: 65–69.

Prasad, J. S., Panwar, M. S. & Rao, Y. S. (1986*b*). Screening of some rice cultivars against the root knot nematode *Meloidogyne graminicola*. *Indian Journal of Nematology*, 16: 112–113.

Prasad, J. S., Panwar, M. S. & Rao, Y. S. (1986*c*). Reaction of some rice cultures to root-knot and cyst nematodes. *Oryza* 23: 59–61.

Puckeridge, D. W. (1988). DWR in S. Vietnam, July, 1988. *Deepwater Rice*, 14: 6–7.

Rahman, M. L. (1987). Source of ufra-resistant deep water rice. *International Rice Research Newsletter*, 12 (1): 8.

Rahman, M. L. & Evans, A. A. F. (1988). Studies on host-parasite relationships of rice stem nematode, *Ditylenchus angustus* (Nematoda: Tylenchida) on rice, *Oryza sativa*, L. *Nematologica* (in press).

Rahman, M. L. & McGeachie, I. (1982). Occurrence of white tip disease in deepwater rice in Bangladesh. *International Rice Research Newsletter*, 7 (5): 15.

Rahman, M. L. & Taylor, B. (1983). Nematode pests associated with deepwater rice in Bangladesh. *International Rice Research Newsletter*, 8 (5): 20–21.

Rahman, M., Sharma, B. R. & Miah, S. A. (1981). Incidence and chemical control of ufra in boro fields. *International Rice Research Newsletter* 6 (2): 12.

Rajendran, G., Muthukrishnan, T. S. & Balasubramanian, M. (1977). Rice varieties of the white tip nematode. *International Rice Research Newsletter*, 2 (2): 3.

Ramakrishnan, S., Varadharajan, G. & Sutharsan, P. D. (1984). TKM9 is resistant to rice-root nematode. *International Rice Research Newsletter*, 9 (5): 20.

Ramana, K. V. & Rao, Y. S. (1975). Histopathogenesis in rice roots infested by *Hoplolaimus indicus*. *Indian Journal of Nematology*, 5: 232–234.

Ramana, K. V. & Rao, U. S. (1978). Evaluation of yield losses due to lance nematode, *Hoplolaimus indicus* Sher in rice. *Andhra Agriculture Journal*, 24: 124–125.

Rao, J. (1985). Population build-up of white tip nematode (*Aphelenchoides besseyi* Christie, 1942) in different monoxenic cultures. *Oryza*, 22: 45–49.

Rao, Y. S. (1976). Abnormal development of earheads in rice (*Oryza sativa* L.) due to the white tip nematode (*Aphelenchoides besseyi* Christie, 1942). *Current Science*, 45: 560–561.

Rao, Y. S. & Biswas, H. (1973). Evaluation of yield losses in rice due to the root-knot nematode *Meloidogyne incognita*. *Indian Journal of Nematology*, 3: 74.

Rao, Y. S. & Israel, P. (1973). Life history and bionomics of *Meloidogyne graminicola*, the rice root-knot nematode. *Indian Phytopathology*, 26: 333–340.

Rao, Y. S. & Jayaprakash, A. (1977). Leaf chlorosis in rice due to a new cyst nematode. *International Rice Research Newsletter*, 2(4): 5.

Rao, Y. S. & Jayaprakash, A. (1978). *Heterodera oryzicola* n.sp. (Nematoda: Heteroderidae) a cyst nematode on rice (*Oryza sativa* L.) from Kerala State, India. *Nematologica*, 24: 241–346.

Rao, Y. S. & Mohanadas, C. (1976). Occurrence of *Caloosia heterocephala* n.sp. (Nematoda: Hemicycliophoridae) on roots of rice (*Oryza sativa*). *Nematologica*, 22: 227–234.

Rao, Y. S. & Prasad, J. S. (1977). Root-lesion nematode damage in upland rice. *International Rice Research Newsletter*, 2 (1): 6–7.

Rao, Y. S., Prasad, J. S. & Panwar, M. S. (1986*a*). Nematode problems in rice: crop losses, symptomatology and management. In: Swarup, G. & Dasgupta, D. R. (Eds.) *Plant Parasitic Nematodes of India. Problems and Progress*, Indian Agricultural Research Institute, New Delhi: 279–299.

Rao, Y. S., Prasad, J. S. & Panwar, M. S. (1986*b*). Stem nematode (*Ditylenchus angustus*) a potential pest of rice in Assam and West Bengal, India. *International Nematology Network Newsletter*, 3 (4): 24–26.

Rathaiah, Y. (1988). Volunteer rice, host for diseases in DWR. *Deepwater Rice*, 14: 1–2.

Rathaiah, Y. & Das, G. R. (1987). Ufra threatens deepwater rice in Majuli, Assam. *International Rice Research Newsletter*, 12 (4): 29.

Ray, S., Das, S. N. & Catling, H. D. (1987). Plant parasitic nematodes associated with deepwater rice in Orissa, India. *International Rice Research Newsletter*, 12 (5): 20–21.

Razjivin, A., Fernandez, M., Ortega, J. & Quincosa, A. (1981). Nuevas especies de *Hirschmanniella* (Nematoda: Pratylenchidae), parasitas de plantas indeseables en plantaciones de arroz. *Poeyana*, 216: 1–11.

Reversat, G. (1975). Etude préliminaire de la survie en anaérobiose des juvéniles du nématode *Heterodera oryzae (Tylenchida: Heteroderidae)*. *Comptes-rendus de l'Académie des Sciences, Paris*, 280, Série D: 2865–2868.

Ribeiro, A. S. (1977). Tratamento de sementes de arroz irrigado para controle da disseminacao do nematoide *Aphelenchoides besseyi*. In: *Anais, VIII Reuniano da cultura do Arroz, Rio Grande do Sul, Embressa Brasileria de Pesquisa Agropecuaria*,: 138–142.

Roy, A. K. 91973). Reaction of some rice cultivars to the attack of *Meloidogyne graminicola*. *Indian Journal of Nematology*, 3: 72–73.

Roy, A. K. (1976*a*). Pathological effects of *Meloidogyne graminicola* on rice and histopathological studies on rice and maize. *Indian Phytopathology*, 29: 359–362.

Roy, A. K. (1976*b*). Effect of decaffeinated tea waste and water hyacinth compost on the control of *Meloidogyne graminicola* on rice. *Indian Journal of Nematology*, 6: 73–77.

Roy, A. K. (1977). Weed hosts of *Meloidogyne graminicola*. *Indian Journal of Nematology*, 7: 160–163.

Roy, A. K. (1978). Effectiveness of rotation with non-host or fallow on reducing infestation of *Meloidogyne graminicola*. *Indian Journal of Nematology*, 8: 156–158.

Roy, A. K. 91982). Survivial of *Meloidogyne graminicola* eggs under different moisture conditions *in vitro*. *Nematologia mediterranea*, 10: 221–222.

Sato, T., Koyama, T. & Koshihara, T. (1970). [Relation between the occurrence of rice root nematodes (*Hirschmanniella oryzae* Luc & Goodey and *Hirschmanniella imamuri* Sher) and the cultivating practices of paddy rice plant.] *Bulletin of the Tohoku National Agricultural Experiment Station*, No. 39:207–219.

Segeren-V.d.Oever. H. & Sanchit-Bekker, M. L. (1984). Observations on *Meloidogyne oryzae* Maas, Sanders and Dede 1978 in irrigated rice in Suriname. *Surinaamse Landbouw*, 32: 51–59.

Sein, T. (1977*a*). Varietal resistance to ufra disease in Burma. *International Rice Research Newsletter*, 2 (2): 3.

Sein, T. (1977*b*). Seed-borne infection and ufra disease. *International Rice Research Newsletter*, 2 (2): 6.

Sein, T. (1977*c*). Testing some pesticides against ufra disease. *International Rice Research Newsletter*, 2 (2): 6.

Sein, T. & Zan, K. (1977). Ufra disease spread by water flow. *International Rice Research Newsletter*, 2 (2): 5.

Sharma, R. D. (1980). Patogenicidade de um nematoide *Meloidogyne javanica* (Treub, 1885) Chitwood, 1949 ao arroz (*Oryza sativia* L.). *Sociedade Brasileira de Nematologia*, No. 5: 91–98.

Sharma, S. B. & Swarup, G. (1985). *Cyst forming nematodes of India*. New Delhi, Cosmo Publications, XV + 152p.

Shimizu, K. (1971). [Influence of the rice cyst nematode on the yield of paddy rice.] *Annual Meeting to the Japanese Society of applied Entomology and Zoology, Fuchu, Tokyo, April 7–9, 1971*: 32.

Shimizu, K. (1977). [Seasonal fluctuation and rhizospherical distribution of population of the upland rice cyst nematode, *Heterodera elachista*.] *Japanese Journal of Nematology*, 7: 49–57.

da Silveira, S. G. P., Curi, S. M., Fernandes, C. D. & Bona, A.de. (1977). Occurrencia do nematoide *Aphelenchoides besseyi* Christie, 1942, em areas produtoras de sementes de arroz, no estado de Sao Paulo. *Reunias de Nematologia*, 2: 81–91.

da Silveira, S. G. P., Curi, S. M., Souza, D. M.de & Arruda, H. V.de (1982). Comportamento de algumas cultivares de arroz em relacao ao nematoide *Aphelenchoides besseyi* Christie, 1943. *Biologico, 48: 213–216.*

Sivakumar, C. V. (1987*a*). Post-embryonic development *Aphelenchoides besseyi in vitro* and its longevity in stored rice seeds. *Indian Journal of Nematology*, 17: 147–148.

Sivakumar, C. V. (1987*b*). The rice white tip nematode in Kanyakumari district Tamil Nadu, India. *Indian Journal of Nematology*, 17: 72–75.

Stirling, G. R. (1984). A needle nematode (*Paralongidorus* sp.) causing poor growth of rice in North Queensland. *Australasian Plant Pathology*, 13: 22–23.

Stirling, G. R. (1985). Observations on the biology and ecology of *Paralongidorus australis* in rice in North Queensland. *Nematologica*, 31 (1986): 218–228.

Stirling, G. R. & McCulloch, J. S. (1985). *Paralongidorus australis* n.sp. (Nematoda, Longidoridae), causing poor growth of rice in Australia. *Nematologica*, 30 (1984): 387–394.

Stirling, G. R. & Shannon, E. (1986). Needle nematodes. A potential problem for the Burdekin rice industry. *Queensland Agricultural Journal*, 112: 258–261.

Stirling, G. R. & Vawdrey, L. L. (1985). Distribution of a needle nematode, *Paralongidorus australis*, in rice fields and areas of natural vegetation in North Queensland. *Australasian Plant Pathology*, 14: 71–72.

Sudakova, M. I. (1968). [Effect of temperature on the life cycle of *Aphelenchoides besseyi*.] *Parazitologiya*, 2: 71–74.

Sudakova, M. I. & Stoyakov, A. V. (1967). [Reproduction and duration of life of *Aphelenchoides besseyi* Christie, 1942.] *Zoologicheski Zhurnal*, 46: 1079–1099.

Tamura, I. & Kegasawa, K. (1958). [Studies on the ecology of the rice nematode, *Aphelenchoides besseyi* Christie. II. On the parasitic ability of rice nematodes and their movement into hills.] *Japanese Journal of Ecology*, 8: 37–42.

Tamura, I. & Kegaswa, K. (1959*a*). [Studies on the ecology of the rice nematode, *Aphelenchoides besseyi* Christie. IV. The injurious feature and population dynamics of nematodes in unhilled rice grain with special reference to the cultural environment of rice plant.] *Japanese Journal of Ecology*, 9: 65–68.

Tamura, I. & Kegasawa, K. (1959*b*). [Studies on the ecology of the rice nematode, *Aphelenchoides besseyi* Christie, V. On the abnormal growth of rice plant and decrease in yield caused by rice nematode.] *Japanese Journal of Ecology*, 9: 120–124.

Taylor, A. L. (1969). Nematode parasites of rice. In: Peachey, J. E.. (Ed.) *Nematodes of Tropical Crops*.

Technical Communication, No. 40, Commonwealth Bureau of Helminthology, St. Albans, England: 264–268.

Taylor, D. P. (1978). Parasitism of banana by *Heterodera oryzae*. *Revue de Nématologie*, 1: 165–169.

Taylor, D. P., Ngundo, B. N. & Othieno, S. M. (1972). Tanzania. Rice white tip nematode. *FAO Plant Protection Bulletin*, 20: 41–42.

Tikhonova, L. V. (1966). [*Aphelenchoides besseyi* Christie, 1942 (Nematoda; Aphelenchoididae) of rice and its control.] *Zoologicheski Zhurbnal*, 45: 1759–1766.

Tikhanova, L. V. & Ivanchenko, Yu.N. (1968). [The combined infection of rice with a fungus, *Piricularia* and a nematode, *Aphelenchus*.] *Trudy Vsesoyuznogo Instituta Gel'mintologii im. K. I. Skryabina*, 14: 287–290.

Timm, R. W. (1955). The occurrence of *Aphelenchoides besseyi* Christie, 1942 in deep water paddy of East Pakistan. *Pakistan Journal of Science*, 7: 47–49.

Todd, E. H. (1952). Further studies on the white tip disease of rice. *Proceedings. Association of Southern Agricultural Workers. 49th Annual Convention*: 141.

Todd, E. H. & Atkins, J. G. (1958). White tip disease of rice. I. Symptoms, laboratory culture of nematodes, and pathogenicity tests. *Phytopathology*, 48: 632–637.

Uebayashi, Y., Amano, T. & Nakanishi, I. (1976). [Studies on the abnormal rice kernel "Kokutenmai". Mechanisms of the symptoms development.] *Japanese Journal of Nematology*, 6: 67–72.

Van der Vecht, J. & Bergman, B. H. H. (1952). Studies on the nematode *Radopholus oryzae* (Van Breda de Haan) Thorne and its influence on the growth of the rice plant. *Pemberitaan Balai Besar Penjelidikan Pertanian Bogor*, No. 131: 82p.

Venkitesan, T. S. Nalinakumari, T. & Satykumar, J. (1979). Distribution of rice root nematode in Kerala. *Indian Journal of Nematology*, 9: 55.

Verma, R. S. (1973). Two new species in the subfamily Longidorinae (Nematoda) from Uttar Pradesh, India, with a key to species of *Paralongidorus* Siddiqi *et al.*, 1963. *Zoologischer Anzeiger*, 190: 170–174.

Vuong, H. H. (1969). The occurrence in Madagascar of the rice nematodes. *Aphelenchoides besseyi* and *Ditylenchus angustus*. In: Peachey, J. E. (Ed.) *Nematodes of Tropical Crops*. Technical Communication No. 40 Commonwealth Bureau of Helminthology, St. Albans, England: 274–288.

Vuong, H. H. & Rabarijoela, P. (1968). Note préliminaire sur la présence des nématodes parasites du riz à Madagascar: *Aphelenchoides besseyi* Christie 1942, *Ditylenchus angustus* (Butler, 1913) Filipjev, 1936. *L'Agronomie tropicale, Nogent*, 23: 1025–1048.

Watanabe, T., Yasuo, M., Ishii, K., Nagai, M. & Ichibki, K. (1963). *Journal of the central agricultural Experiment Station*, 5: 1–44.

Winslow, R. D. (1960). Some aspects of the ecology of free-living and plant-parasitic nematodes. In: Sasser, J. N. & Jenkins, W. R. (Eds.) *Nematology, Fundamentals and Recent Advances with Emphasis on Plant Parasitic and Soil Forms*. University of North Carolina Press, Chapel Hill: 341–415.

Yamada, W. & Shiomi, T. (1950). [Studies on the rice white tip diseae. II. Disease control with special reference to rice seed disinfection.] *Special Bulletin. Okayama Prefecture Agricultural Experiment Station*, No. 47: 1–8.

Yamada, W., Shiomi, T. & Yamamoto, H. (1953). [Studies on the white tip disease of rice plants. III. Hibernation of the causal nematode, varietal resistance of rice plants to the disease, and effect of rice culture upon the disease occurrence.] *Special Bulletin. Okayama Prefecture Agricultural Experiment Station*, No. 48: 27–36.

Yamsonrat, S. (1967). Studies on rice-root nematodes (*Hirschmanniella* spp.) in Thailand. *Plant Disease Reporter*, 51: 960–963.

Yik, C. P. & Birchfield, W. (1979). Host studies and reactions of cultivars to *Meloidogyne graminicola*. *Phytopathology*, 69: 497–499.

Yokoo, T. 91948). [*Aphelenchoides oryzae* Yokoo n.sp., a nematode parasitic to rice plant.] *Annals of the Phytopathological Society of Japan* 13: 40–43.

Yoshii, H. (1951). [On the growth habit and yield of rice plants affected with *Aphelenchoides oryzae*.] *Science Bulletin of the Faculty of Agriculture, Kyushu University*, 12: 133–141.

Yoshii, H. & Yamamoto, S. (1950*a*). A rice nematode disease "Senchu Shingare Byo". I. Symptom and pathogenic nematode. *Journal of the Faculty of Agriculture, Kyushu University*, 9: 209–222.

Yoshii, H. & Yamamoto, S. (1950*b*). A rice nematode disease 'Senchu Shingare Byo'. II. Hibernation of *Aphelenchoides oryzae*. *Journal of the Faculty of Agriculture, Kyushu University*, 9: 223–233.

Yoshii, H. & Yamamoto, S. (1950*c*). A rice nematode disease "Senchu Shingare Byo". IV. Prevention of the present disease. *Journal of the Faculty of Agriculture, Kyushu University*, 9: 293–310.

Yoshii, H. & Yamamoto, S. (1951). [On some methods for the control of the rice nematode disease.] *Science Bulletin of the Faculty of Agriculture, Kyushu University*, 12: 123–131.

Chapter 4

Nematode Parasites of Cereals

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Cereals constitute the world's most important source of food. Amongst cereals, wheat and rice occupy the most eminent position in terms of production, acreage and source of nutrition, particularly in the developing countries. Maize, sorghum, barley, and millet and the other edible grains, conversely, are restricted to specific growing regions and are limited in area under cultivation. It has been estimated that about 70% of the land cultivated for food crops is devoted to cereal crops. The contribution of the individual cereal crops to total world food production can be seen in Table 1. Cereals as source of human nutrition and animal feed provide both calories and proteins. It has been estimated that wheat will produce more calories, proteins and essential amino-acids from an acre of arable land than the livestock that can be supported by that land (Johnson, 1984).

TABLE 1. Contribution of cereals in world food production.

Countries	Total production (1000 mt)							
	Wheat	Barley	Rice	Maize	Oats	Sorghum	Millet	Total
World	536457	182739	473131	480894	48556	70221	29731	1866494
Africa	11550	6291	9840	30807	261	14336	11844	86442
North America	93468	28733	8259	231263	9588	30417	–	404626
South America	16771	784	15278	38184	856	6151	107	78354
Asia	189558	18708	434147	99723	1056	17356	15336	780237
Europe	115756	70255	2234	67954	13143	430	39	288848

Adapted from FAO Bulletin Statistics Vol. 10, 9–17, 1987.

Although the introduction of new cultivars of wheat, rice and other cereals has boosted agricultural output, the yield potential of the new cultivars has not been fully expressed and is often far below theoretical maximum yields. The disparity between actual and theoretical yield expression can be attributed to "production constraints". Attention has, therefore, been focused on minimizing these constraints to increased production. Although insect pests and diseases have long been recognized as important constraints affecting crop production, extensive research on the "weak linkages" in the plant-pest-system are lacking. When compared to insect, fungal, bacterial and virus diseases, plant parasitic nematodes have only recently been subjected to detailed study.

It is now well accepted that apart from diseases and insect pests, nematodes cause sizable annual

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

losses to many crops. Paddocks (1967) estimated that nematodes were responsible for a 3–4% loss in yield of various crops including cereals. More than two million hectares in Victoria and South Australia are infested with *Heterodera avenae* and annual losses in wheat yields are estimated to be 70 million U.S. dollars (Brown, 1984).

In this chapter, an attempt is made to identify known and potential problems affecting cereal crops other than rice which is covered separately in Chapter 3.

Wheat and Barley

In terms of production, wheat, *Triticum aestivum*, occupies the prime position among the food crops in the world, and is the staple food for abut 35% of the global population. High quality wheats are produced in areas favoured with cool and moist weather for a fairly long growing period, followed by dry and warm weather.

Barley, *Hordeum vulgare*, is adapted to a broader spectrum of ecological niches than wheat and is grown under more extreme environmental conditions. Barley, for example, grows well under low fertility and moisture stress situations common in the semi-arid subtropics of North Africa and West Asia (Sikora, 1988).

The availability of fertilizer and water are the two abiotic factors regulating yield levels in present day wheat and barley cultivars. Crop yields are also profoundly influenced by pesticide use and other agronomic practices. These, in turn, affect nematode population fluctuations and the degree of economic loss.

Nematodes of Wheat and Barley

Although quite a sizeable number of plant parasitic nematodes have been recorded associated with wheat and barley, only a few species can be regarded as economically important. The most important nematodes of these crops are: 1) cereal cyst nematode, *Heterodera avenae*, 2) the ear-cockle nematode, *Anguina tritici*, 3) root-knot nematodes, *Meloidogyne* species, and 4) the lesion nematodes, *Pratylenchus* species.

Heterodera avenae

The cereal cyst nematode, *H. avenae* has been detected in a large number of countries. Initial research on the nematode was confined to Europe, Canada, Australia and India. Meagher (1977) has listed 31 countries as being infested including Italy, Spain, Portugal, Israel, Peru, Yugoslavia, Australia and India. More recently, cysts of *H. avenae* were detected in soil, but not from roots of cereal crops, in Pakistan (Maqbool, 1988). There are also a number of reports of this nematode in the semi-arid regions of North Africa (Saxena *et al.*, 1988). The distribution of *H. avenae* in the tropical and subtropical areas is listed in Table 2.

It is almost certain that the origin of the species was in Europe, where it was first recorded on oats, then later on wheat and barley (Meagher, 1977) and maize (Swarup *et al.*, 1964*a*). From Europe, the species may have been distributed to other parts of the world in soil particles adhering to seed or through other forms of planting material. Within a country, irrigation water, rivulets flowing through infested areas, sand/dust storms, farm machinery, etc. appear to be the main sources of spread (Swarup & Singh, 1961; Brown, 1987).

Biology and life cycle

The life cycle is typical of many *Heterodera* species and similar to that of the type species, *H. schachtii* (Raski, 1950). There is only one generation during the cropping season irrespective of geographical region. Juvenile emergence from eggs in brown cysts requires a period of "dormancy" of two or more months and is strongly regulated by temperature. In the subtropics, this period may be prolonged from April to October, although a few juveniles may emerge as early as August. Often the periods of mass emergence from cysts coincides with the cropping season. In the "white" stage

TABLE 2. Distribution of *Heterodera avenae* in tropical and subtropical regions along with climate types (adapted after Holdeman & Watson, 1977).

Country	Climate type
India	Humid subtropical
Pakistan	Dry subtropical
Israel	Steppe
Japan	Humid subtropical
USSR	Humid continental
Australia (New South Wales, South Australia, West Australia, Victoria)	Steppe
New Zealand (South Island)	Marine West Coast
Morocco	Mediterranean
Tunisia	Steppe

of cyst nematode development, when suitable temperature conditions are available, emergence of juveniles may take place spontaneously (Rajan, 1984). The moment such cysts turn brown, emergence stops completely. The induction of dormancy appears to be correlated with the change in cyst colour and as well as with increases in temperature (Banyer & Fisher, 1971, 1976).

Temperature, availability of moisture and root diffusate are important determinants in juvenile emergence. Emergence can take place at temperatures between 10–25°C, with the optimum between 20–22°C (Winslow, 1955; Swarup & Gill, 1972). The optimum for the Australian population is 10°C (Brown, 1987). Fluctuating temperatures or alternate exposure of cysts to low and high temperatures stimulates maximum emergence of juveniles (Williams & Beane, 1972; Swarup & Gill, 1972), the relationship differing with the geographical locality (Williams, 1978). Although *H. avenae* does not require host root diffusates to initiate emergence, release of juveniles at low temperatures of 10–15°C can be obtained with wheat and barley root diffusates. Root diffusate from one-week old barley seedlings stimulates emergence of juveniles from the cysts (Gill, 1967; Williams & Beane, 1972).

Survival

The eggs in cysts are quite susceptible to drying, with prolonged exposures markedly reducing juvenile emergence. However, populations present in the tropics that are exposed to prolonged dry summer conditions do not completely lose their viability. Even in the hot dry summers existing in Israel and India, juveniles in the cyst remain viable until suitable temperatures for emergence are reached (Minz, 1956).

Economic threshold levels

The relationship between initial nematode density and crop yield is important in determining the economic impact on the cereal crop. Environmental conditions also affect crop loss at a specific population density, which means similar nematode densities may not cause equal levels of crop damage in the spring and autumn cropping seasons.

Twenty eggs and juveniles/g soil is considered the damage threshold level for wheat and barley (Stone, 1968; Gill & Swarup, 1971). Germershausen *et al.* (1976) have recorded decreased wheat yields with increasing population levels from 0–3000 eggs/100 cm^3 soil. In general, damage can be expected at population levels ranging between 10–40 eggs and juveniles/g soil.

The number of juveniles penetrating the host roots also has a direct bearing on the expression of damage. With increasing inoculum density, more juveniles penetrate the roots, but the percentage penetration decreases (O'Brien & Fisher, 1978). Gokte and Swarup (1984*a*) reported that an inocu-

Fig. 1. Uneven patchy growth of wheat crop in field infested with *Heterodera avenae*.

lum increase of 100 to 1000 eggs and juveniles/g soil resulted in a four-fold increase in penetration, whereas the next ten-fold increase caused only a two-fold increase, affecting cyst production. The number of juveniles penetrating wheat roots increase linearly with increasing inoculum densities until a maximum is reached (O'Brien & Fisher, 1978).

Environmental factors

Many abiotic factors, for example, fertility, pH, soil type, and organic matter content influence nematode population development and damage severity (Duggan, 1963). Moderate nematode population levels, under favourable environmental conditions for plant growth, may not cause as much damage as when plant growth is restricted by moisture stress or low fertility levels (Kornobis *et al.*, 1980). Increased nitrogen application is known to reduce the intensity of nematode damage to the crop. At high nematode population levels, however, this may no longer hold true (Germershausen, *et al.*, 1976).

Loose and friable sandy loam soils are best for nematode development, although the nematode thrives well in the slightly heavier soils of the western area of Rajastan, India.

Symptoms of damage

The symptoms associated with *H. avenae* damage are characterized by uneven patches of poor growing plants randomly distributed throughout the field (Fig. 1; Plate 2 A), the damage to the plants and the size and number of patches being directly related to nematode population levels as well as nematode distribution in the field. Under monoculture, the patches coalesce and damage can uniformly cover the entire field within 3–4 years. Severely infected plants remain stunted, one to two feet high. The leaves become pale yellowish green in colour with thin and narrow leaf blades. Ears, if formed, have very few grains. In heavily infested fields, severe inhibition of grain formation may make harvesting uneconomical.

The root system exhibits a characteristic elongation of the main root. The tips of some rootlets

may appear bunchy and slight swellings may form at the point of cyst attachment. Such diseased plants lack anchorage and can be easily pulled out of the soil.

Such symptoms are recognizable within 45 days after sowing. Under European conditions, root division takes place at the points of juvenile invasion, giving an appearance of a knotted root system. Moisture stress may produce a similar effect, therefore, the presence of cysts on the roots is the only means of confirming the presence of a nematode infestation (Kort, 1972).

In Australia, a much branched root system is characteristic of infested wheat and barley and to a lesser extent oat. Tufting of roots may not be noticeable during field examination due to adhering soil (Holdeman & Watson, 1977). Wheat and barley in India are sown in the last fortnight of November or early December. The above-ground symptoms of damage can be seen within a month after sowing, becoming quite marked by the end of January. During this period second stage juveniles are abundant in the soil. By mid-February, white females can be seen attached to the roots.

Pathotypes

The existence of pathotypes in *H. avenae* populations was noticed on barley cultivars as early as 1920 in Sweden. Results obtained with the International Test Assortment in 1972–1973 demonstrated the existence of more pathotypes than originally recognized, especially in subtropical regions. For instance, Barley 191 which is reported to be resistant to the known populations of *H. avenae* in Europe is susceptible to *H. avenae* populations in Australia, Norway and India (Brown, 1972; Stoen, 1971; Mathur *et al.*, 1974) (Table 3). In these tests, it is quite difficult to make clear-cut distinctions between resistance and susceptibility based on the number of cysts alone. Pathotypes may also occur in mixtures, further complicating delineation of the pathotype in a particular sample. This and the inclusion of additional hosts, other than those recommended in the International Test Assortment, may be responsible for conflicting observations on pathotype numbers from India (Mathur *et al.*, 1974; Swarup *et al.*, 1979). The pathotypes present in India are, however, distinctly different from those in Australia. At present ten pathotypes are recognized in Europe (Andersen & Andersen, 1982).

TABLE 3. Reaction of differential cultivars of barley and wheat to five populations of *Heterodera avenae* in India (after Dhawan & Sethi, 1986).

	Barley															Wheat		
Populations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Jaipur	S	R	R	R	R	R	R	R	R	R	R	R	S	S	S	S	S	RS
Udaipur	S	R	R	R	R	R	R	R	R	R	R	R	S	S	S	S	S	RS
Narnaul	S	R	R	R	R	R	R	R	R	R	R	R	S	S	S	S	S	RS
Hoshiarpur	S	R	R	R	R	R	R	RS	S	S	S	S	R	S	S	S	S	S
Ludhiana	S	R	R	R	R	R	R	RS	S	S	S	S	R	S	S	S	S	RS

R = Resistant; S = Susceptible; RS – Mixed reaction.

1 – Varde; 2 – Herta; 3 – Ortolan; 4 – Morocco CI. 3902; 5 – Osira; 6 – Drost; 7- Rabat; 8 – Martin 403–1; 9 – Siri; 10 – P 31322–1; 11 – Pabjerg; 12 – 191; 13 – La Estanzuela; 14 – Emir; 15 – LG_2; 16 – Clapa; 17 – Iskamish K–2 Dark; 18 – Iskamish K–2 Light.

In India, there are also two distinct populations recognized by cyst form. Although there are no major morphological differences between the two nematodes, the cysts of one population are distinctly smaller in size and lighter in colour than the other. The population containing the small sized cysts is also restricted in distribution (Swarup, unpubl.).

Economic importance

H. avenae in the north-western part of India and in southern Australia is considered a major limiting factor of wheat and barley. Figures have been computed that suggest that for every 10 eggs/g soil,

there is a loss of 188 kg/ha in wheat and 75 kg/ha in barley (Duggan, 1961; Dixon, 1969). In the north-western part of India, four and sixteen fold increases in yields of wheat and barley have been obtained after nematicidal treatments, respectively (Swarup *et al.*, 1976). Losses have been calculated to range between 45–48% on light soils even at densities of 6 eggs/g soil. According to Sabova *et al.* (1981) grain yields are reduced by 17–44% in wheat and 32–44% in barley. Grosse *et al.* (1982) tested the impact of heavy infestations of the nematode on resistant and susceptible cultivars of barley and oats. They observed that 3900 eggs and juveniles/100 cm^3 soil caused damage to the resistant oat comparable to that on the susceptible cultivar. Staggering monetary losses of 3 000 000 pounds sterling in Europe and approximately 9 million dollars in India have been calculated as being caused by the nematode (Wallace, 1965; Van Berkum & Seshadri, 1970).

Control

In areas where *H. avenae* is responsible for economic losses, the best approaches have been adoption of crop rotation and the use of resistant cultivars, whenever the latter are available.

Chemical

Although low rates of non-fumigant nematicides have been shown to be effective in nematode control programmes in Australia (Gurner *et al.*, 1980), the costs still remain prohibitive to the average subsistence farmer in most tropical and subtropical countries. However, under severe infestation conditions, where more than ten juveniles/g soil occur in light soils, application of aldicarb or carbofuran at the rate of 1.5 kg a.i./ha has been demonstrated by Swarup (1986) to be economical in India (Table 4).

TABLE 4. Performance of aldicarb and carbofuran against *Heterodera avenae* on wheat (Swarup, 1986).

Treatments with dose (a.i./ha)	Yield (q/ha) Grain + Fodder	Benefit: Cost ratio
Aldicarb 1.5	33.0 + 53.0	3.2 : 1
Carbofuran 1.5	32.0 + 50.0	2.0 : 1
Untreated Control	19.0 + 33.0	–

C.D.: Grain – 3.3; Fodder – 5.3.

Rotation

Whereas in Europe a four year rotation can be practiced for nematode control, economic factors do not permit such long rotations in most subtropical and tropical countries.

Crop rotation with non-host crops for two years gives some control in areas where crop diversity is acceptable to the farmers. One or two year rotations with crops like cumin or fenugreek have been shown to be beneficial to the farmers.

One to five deep ploughings during the hot summer months can cause reductions in nematode populations between 9.3 and 42.4% with a corresponding yield increase of 4.4 to 97.5% (Mathur *et al.*, 1987). The decrease in population is attributable to killing of the cyst contents by intense solar heat and to desiccation of the eggs and juveniles by hot winds.

Resistance

Resistant cultivars should be considered the most economical component of a nematode management system. Intensive screening of wheat, barley and oat germplasm in Denmark resulted in identification of the highly resistant barley cultivar "Drost" (Nilsson-Ehle, 1920) and the spring wheat cultivar "Loros" was also identified as resistant. In Australia the wheat cultivar Katyl has been bred for resistance (Brown & Young, 1982). However, Katyl is susceptible to Indian populations. In barley, the Indian lines and cultivars BP 263, BP 264, C 164, DL 350, DL 375, DL 376 and Rajkiran have

been reported resistant (Dhawan & Sethi, 1983; Gokte & Swarup, 1984*b*). Three wheat selections were also considered highly resistant to an Indian population (Sikora *et al.*, 1972). According to O'Brien *et al.* (1980) resistance appears to be governed by a single dominant gene. The use of resistant cultivars has to be viewed with some caution, because of the presence of pathotypes that can breakdown resistance. Pathotype determination and preliminary tests with local populations are necessary for breeding programmes and before making recommendations to the farmer.

Biological control

Natural enemies of *H. avenae*, mainly fungi, have been recognized for quite some time but not as yet exploited as biological control agents for field application. Recent observations (Kerry, 1981; Kerry & Crump, 1977; Kerry *et al.*, 1982*a, b, c;* Crump *et al.*, 1983) have demonstrated that, despite cereal monoculture, the nematode density does not increase appreciably, indicating natural suppression of the population. Fungal parasites of eggs and females were demonstrated to act as agents in population regulation. According to these workers, damage to cereal crops in monoculture systems occurs sporadically and not in accordance with fluctuations in nematode density related to ecological or population stress conditions, but is regulated by natural agents. Sharma and Swarup (1988) detected *Pasteuria penetrans*, a bacterial parasite of juveniles, which may prove to be a promising agent for *H. avenae* control.

A summary of the different measures available for *H. avenae* control in tropical and subtropical cereal production along with their advantages and disadvantages is given in Table 5.

Other cyst nematodes

Heterodera latipons has been recorded on roots of stunted barley in Israel, Tunisia, Cyprus and Libya (Saxena *et al.*, 1988). According to Sikora (1988), the nematode could be an important constraint to barley production in the temperate semi-arid regions of North Africa and West Asia. Symptoms of damage in the semi-arid regions consists of heterogeneous plant growth patterns similar to that produced by *H. avenae* (Plate 2 A).

Anguina tritici

The seed gall nematode, *A. tritici*, cause of the "ear-cockle" disease of wheat and barley, is of historical importance since it is the first plant parasitic nematode recorded in the literature. Although it has been eradicated from the western hemisphere through successful adoption of seed cleaning techniques, it is a problem on the Indian sub-continent, West Asia and to some extent in China.

A nematode vectored bacterial disease (yellow ear-rot), vernacularly known as "tundu" or "tannan" in India is also commonly found associated with the ear-cockle nematode problem. The disease was first recorded from India by Hutchinson (1917). It has only been recently detected on barley in northern Iraq where infestations reached 90% (Al-Talib *et al.*, 1986; Stephan, 1988).

Symptoms of damage

In both ear-cockle and yellow ear-rot, the first observable symptom is an enlargement of the basal stem portion near the soil base, observable in 20–25 day old wheat seedlings. The emerging leaves are twisted (Fig. 2) and crinkled. Frequently, some leaves remain folded with their tips held near the growing point. These leaves, after about 30–45 days, straighten out and many appear normal with faint ridges on the surface (Fig. 3). In comparison to healthy seedlings, the affected plants are dwarfed with a spreading habit. These symptoms are more clearly discernible on young seedlings and decrease with plant age. Under very low infestation levels, the plants may not exhibit any observable symptoms even though a few seed galls are produced in the ears; whereas severely infested plants may die without heading. Infested seedlings produce more tillers and grow faster than normal plants.

The increased number of tillers does not necessarily result in an increase in the number of ears.

TABLE 5. Merits and demerits of different control measures used against *Heterodera avenae* in tropical and subtropical regions.

	Merits	Demerits	Countries where evaluated/recommended
Fallowing	Check in population build up by starvation as well as death of emerged juveniles with exposure to solar heat	Weeds need to be thoroughly controlled; loss of cropping period to farmers; usually difficult to adopt in a multicropping scheme	Wheat/barley – Fallow India (Swarup, 1986); Australia (Meagher, 1972; Brown, 1987).
Summer ploughing	Viability of cysts exposed to solar heat is reduced; other pests and weeds are also reduced	May cause wind erosion and cyst dispersal especially in light soils	2–5 deep summer ploughing during May-June; India (Mathur *et al.*, 1987).
Time of planting	No additional cost required	Cultivar selection for time of sowing essential. Also detailed information on population dynamics necessary. Difficult to follow in multicropping system	Early sowing (May-June); Australia (Meagher, 1977; Brown, 1987).
Nitrogenous fertilizers	Improvement in host tolerance and yield	Moderate additional cost involved. May leave high final nematode population.	Urea at the rate of 25 kg N/ha. Small increases in grain yield with increasing levels of nitrogen. India & Australia (Swarup, 1986; Brown, 1987).
Crop rotation	Cropping period is not lost and there is no soil erosion	Difficulty in finding alternative remunerative crop acceptable to farmers	Rotation with cumin/carrot India (Swarup, 1986); 3 years under fallow or non-host crops; Australia (Brown, 1987).
Resistant/Tolerant cultivars	Most economical and durable. Nematode population is decreased	Evolution of resistant breaking biotypes	Katyl – resistant wheat to Australian population (Brown, 1987); Rajkiran, BP 264, C 164, DL 350, DL 375 resistant barley to Indian population (Dhawan & Sethi, 1983; Gokte & Swarup, 1984 *b*).
Chemicals	Quick and effective. Used for demonstration of crop losses	High cost; may harm natural enemies and non-target organisms; residue and toxicity problems; health hazard	DD, DBCP, Temik, Furadan (Australia and India); Counter (Australia); Oxamyl as seed treatment (Australia).

Furthermore, the ears emerge 30–40 days earlier in diseased plants. Such ears are short and broad with very small or no awns on the glumes (Fig. 4). Either all or some of the grains are replaced by nematode galls (Plate 2 E). The number of galls produced on one spikelet may vary from one to five. Galls are sometimes formed at the base of awns and on the glumes.

In the yellow ear-rot disease (Fig. 4), the characteristic feature is the production of bright yellow slime or gum-like substance on the abortive ears as well as the leaves, which remains in contact with such ears while still in the boot leaf. Under humid conditions, the bacterial slime trickles down the

Fig. 2. Twisted leaves of wheat caused by *Anguina tritici* at right and healthy ear-head at extreme left.

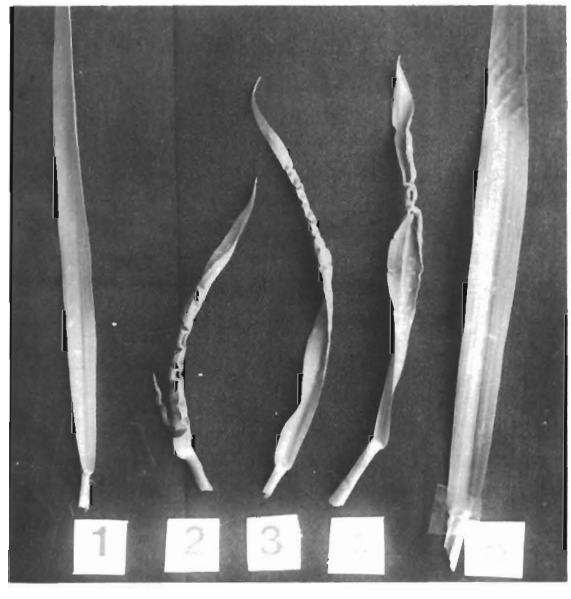

Fig. 3. Stages in the recovery of twisted wheat leaves caused by *Anguina tritici*. 1. Healthy leaf; 2–4. Twisted leaves exhibiting gradual recovery; 5. Almost straightened leaf with faint ridges.

Fig. 4. *Anguina tritici* infested ear-heads with ear-cockle and yellow ear-rot disease (extreme right).

tissues and upon drying it appears brown in colour (Plate 2 F). The infected spike is narrow and short with the wheat grains partially or completely replaced by slime. In the latter event, the emerging spike remains sterile. The stalk of the infected spike is always distorted.

Biology and life cycle

Nematode galls, which may be present already in the soil, or sown into the soil at planting with contaminated seed, become moist and soft, with soil moisture facilitating the release of juveniles. Nine days elapse from the time nematode galls are placed in the soil until the juveniles can be traced in the growing point of the germinating plant. These juveniles move upward passively on the growing point as the plant grows. They do not exhibit any morphological change until the 67th day. Nematode morphological changes take place only when the juveniles penetrate the flower primordia. The juveniles then develop to adults between the 68th and 102nd day after germination. The total life cycle is completed in 113 days. Temperature, humidity, planting depth and the source of galls are the major determinants in symptom expression.

Temperature, humidity and the source of galls are particularly important for development of yellow ear-rot. The bacterium, *Corynebacterium michiganense* pv. *tritici*, is invariably present along with the juveniles in the galls and is responsible for the expression of the disease. On its own, the

bacterium is only capable of producing yellow streaks on leaves that run parallel to the veins. The nematode carries the bacterium to the growing point as an external body contaminant (Gupta & Swarup, 1972). Atmospheric temperatures between 5–10°C and a relative humidity of 95–100% favour multiplication of the bacterium in the plants.

The bacterium multiplies very quickly under favourable environmental conditions, increasing its concentration in the plant and forming a thick viscous fluid in which the nematode juveniles are not able to survive. Under such conditions, the emerging ears are totally sterile and are covered with yellow slime. However, under less favourable conditions for the bacterium, the juveniles survive to produce partial ear-cockle and partial yellow ear-rot symptoms.

Economic threshold levels

A minimum population of 10 000 juveniles/kg soil is essential for development of ear-cockle. Disease intensity is greatest when nematode galls are placed in soil at a depth of 2–6 cm than when placed deeper.

Yellow ear-rot requires a combination of 0.4 optical density of the bacterium and 10 000 juveniles for maximum expression of the bacterial phase of the disease.

Control

Sanitation

Since the ear-cockles are the only source for perpetuation of both diseases, their removal from the contaminated seed lot can completely eliminate both diseases. The galls are lighter in weight than the wheat seed and can be easily discarded through a winnowing process or by flotation of contaminated seeds in 20% brine solution. It is important, however, to wash the wheat seed after brine treatment two or three times in plain water to remove the adhering salt particles, otherwise seed germination is impaired.

Hot water treatment

To dispense with salt treatment, Byars (1920) suggested presoaking contaminated seeds in plain water then soaking them at either 50 °C for 30 min, 52 °C for 20 min, 54 °C for 10 min or at 56°C for 5 min. The principle being to reactivate the quiescent juveniles before killing them with hot water. Leukel (1957) suggested presoaking the galls for 4–6 h in water and then exposure to hot water at 54 °C for 10 min.

Resistance

There have not been any recent efforts at resistant breeding against this nematode. The earliest record of a resistance source is the cultivar Kanred (Leukel, 1924) used in the breeding programme initiated by Shen *et al.* (1934). Crosses between Kanred and a highly susceptible wheat cultivar resulted in a few lines in the F_2 and F_3 free from nematode attack. Unfortunately, this work was not continued.

Meloidogyne

The root-knot nematodes *M. incognita, M. javanica* and *M. arenaria* are all known to attack cereal crops. *M. incognita* is encountered frequently on wheat in tropical and subtropical areas, whereas only isolated cases of damage by *M. javanica* and *M. arenaria* have been recorded. In all these cases, typical small sized root-knot galls are produced on roots. The egg masses attached to the posterior end of the protruding females are normally transparent, but darken on exposure to air and can resemble cysts of *H. avenae*.

Experimentally, *M. incognita* and *M. javanica* have been shown to reduce plant growth of wheat.

The crop is more susceptible to *M. incognita* than to *M. javanica* (Roberto *et al.*, 1981; Sharma, 1981; Abdel Ahmed *et al.*, 1981). *M. incognita* is recognized as a field problem in the northwestern part of India where it produces symptoms similar to *H. avenae*.

Pratylenchus

The lesion nematodes, *P. thornei, P. fallax* and *P. minyus*, are considered important pests although their true economic importance has not been adequately assessed. *P. thornei* parasitizes cereals in North America and Australia. Infested wheat roots are markedly darkened and stunted, with lysis of cells and formation of cavities which eventually destroy the cortex (Baxter & Blake, 1968). A long fallow disorder of wheat in some soils in Australia is considered to be due to heavy infestation with *P. thornei*, which also reduces beneficial mycorrhizal colonization of the root (Anon., 1982; O'Brien, 1983). *P. thornei* causes significant losses in wheat in Mexico (Van Gundy *et al.*, 1974).

Other nematodes

Longidorus elongatus, Merlinius brevidens, Ditylenchus dipsaci, and species of *Tylenchorhynchus* and *Paratrichodorus* have been reported to cause poor growth and sometimes economic losses in specific wheat growing regions. These nematodes appear to be potentially important.

Tylenchorhynchus nudus, T. vulgaris and *M. brevidens* are responsible for poor growth in limited areas of U.S.A. and India (Smolik, 1972; Upadhyaya & Swarup, 1981). The stem nematode, *Ditylenchus dipsaci* is an important factor in poor wheat yields in Italy, where nematode damage was associated with the presence of *Fusarium* (Belloni, 1954).

Paratrichodorus anemones and *P. minor* are two species reported to cause damage to cereal crops in Australia and U.S.A. In the U.S.A., wheat seeded early in autumn in sandy soils is highly suceptible to *P. minor*.

Maize

Zea mays is one of the important cereal crops used in the human diet and an important feed component for livestock. In terms of total world production, maize ranks third behind rice and wheat. Global production exceeds 480 million t with about 60% produced in the developed countries; 20% by China, and the rest by countries of Latin America, Africa and Southern Asia (CIMMYT, 1987; FAO, 1987).

The most important abiotic limiting factor affecting maize production is drought. However, many plant pathogens and pests, including plant parasitic nematodes cause considerable loss during crop development and aggravate plant damage under moisture stress conditions. Information on the importance of plant parasitic nematodes, however, is very limited.

Nematodes of maize

Over 60 nematode species have been found associated with maize in different parts of the world. Most of them have been recorded from soil around maize roots with little information on their biology or pathogenicity. Some groups of plant parasitic nematodes in particular lesion, cyst and root-knot nematodes have been demonstrated in some regions to be important limiting factors.

Pratylenchus

Lesion nematodes are cosmopolitan in maize fields and are often associated with poor growth. *Pratylenchus brachyurus, P. zeae* and *P. penetrans* are the most commonly encountered species in subtropical and tropical regions followed by: *P. coffeae, P. delattrei, P. goodeyi, P. hexincisus, P.*

minyus, P. pratensis, P. sefaensis and *P. thornei*. Lesion nematodes are consistently found associated with maize wherever it is grown.

Symptoms of damage

Nematode species, population density, as well as environmental conditions affect symptom expression. Above-ground symptoms are not highly specific. Stunting, reduced root and shoot weight, and leaf chlorosis are usually associated with lesion nematode damage. Stunting occurs in patches when high populations of *Pratylenchus* are present in a specific area in a field. Leaf chlorosis is also more common under severe infestations. Nematode damage to the fibrous root system can result in destruction of cortical parenchyma which may cause sloughing-off of the tissue and severe necrosis (Plate 2 G). In addition, severe root pruning as well as proliferation of lateral roots may occur (Ogiga & Estey, 1975; Zirakparvar, 1980). *P. zeae* causes a mechanical breakdown of cells, and necrosis of stelar and cortical tissues resulting in formation of cavities (Olowe, 1977; Olowe & Corbett, 1976). In contrast, *P. brachyurus* causes more necrosis than mechanical damage. Occasionally, slight cell hypertrophy may be observed. Damage by lesion nematodes can often be diagnosed by the presence of small blackish lesions on the root surface.

Biology and life cycle

Temperature, in addition to plant species, greatly affects the development and reproduction of *Pratylenchus. P. zeae, P. brachyurus* and *P. hexincisus* reproduce well at 30°C, whereas *P. penetrans* prefers lower temperatures of 20–24 °C (Olowe & Corbett, 1976; Zirakparvar *et al.*, 1980). Frequently optimum temperature for nematode development is correlated with the optimum temperature required for good plant growth (Olowe & Corbett, 1976). For example, 20 °C which is considered the optimum temperature for good root development is simultaneously the optimum temperature for maximum root penetration and development of *P. brachyurus*. A similar effect was recorded by Dickerson *et al.* (1964) who found differences in the top weight of plants inoculated with *P. penetrans* over the uninoculated controls at 20 °C, but not at 24 °C.

Soil type and tillage operations have also been recorded to affect lesion nematode population dynamics. Most *Pratylenchus* species thrive well in a wide range of soil types, but for others a particular soil may be more suitable. Naganathan and Sivakumar (1975, 1976) reported higher population densities of *P. delattrei* in sandy clay loam soil than in any other soil type. Conversely, *P. hexincisus* is found in a wide range of soil types, but reproduces best in sandy soils (Swarup, unpubl.).

Moisture is an important factor affecting the development of species of *Pratylenchus*. In Nigeria, Egunjobi (1974) demonstrated pathogenicity of *P. brachyurus* on maize and found increased nematode development during the rainy season. Damage to the maize plant, on the other hand, increases with decreasing moisture levels.

Other hosts

Lesion nematodes have wide host ranges which can affect the selection of crop used to control the nematode in rotations. In addition, the presence of weed hosts in a field can strongly influence lesion nematode densities in maize fields (Egunjobi, 1974; Stradioto *et al.*, 1983).

Economic importance

Nematode populations may increase considerably under continuous maize cropping ultimately resulting in significant yield losses (Maqbool & Hashmi, 1986; Reversat & Germani, 1985). Indirect evidence has been obtained with nematicides where the detected yield increases suggested that lesion nematodes are important limiting factors in maize cultivation.

Yield increases of 33 to 128% have been obtained following the application of nematicides (Walters, 1979). Bergeson (1978) and Norton *et al.* (1978) reported that treatment with nematicides

increased yields 10–54%. Similarly, Lordello *et al.* (1983) observed increases of more than two-fold after nematicide treatment.

In Nigeria, *P. brachyurus* has been reported to be responsible for 28.5% yield reduction. The reduction in yield was correlated with a 50% increase in nematode density (Egunjobi, 1974). Zirakparvar (1980) reported that *P. hexincisus* causes reductions in root and top weights of plants.

Disease complexes

Precise evaluations of losses in maize caused by lesion nematodes are hampered by secondary infections of nematode lesions by fungi and bacteria (Egunjobi, 1974). The importance of complex diseases in crop loss of maize caused by lesion nematodes has not been studied.

Punctodera and *Heterodera*

Although nine species of cyst nematodes have been recorded associated with maize in subtropical and tropical countries, only three, *Punctodera chalcoensis, Heterodera zeae* and *H. avenae* are considered economically important (Luc, 1986).

Heterodera cajani, H. delvii, H. gambiensis, H. graminis, H. oryzae and *H. sorghi* have been recorded sporadically, but their role as parasites of maize remains uncertain (Koshy & Swarup, 1972; Merny & Cadet, 1978; Prasad *et al.*, 1980; Sharma & Swarup, 1984; Reversat & Germani, 1985).

Punctodera chalcoensis

Vázques (1976) surveyed maize fields in Mexico State during 1960 and recorded a cyst nematode, identified then as *Heterodera punctata* on maize roots. Sosa-Moss (1965) demonstrated distinct morphological differences between the Mexican population and the original description of *Heterodera punctata* (Thorne, 1928). He also reported that the Mexican population attacks maize instead of wheat and grasses, common hosts of *H. punctata*. The species was later redescribed as *Punctodera chalcoensis* (Stone *et al.*, 1976).

Distribution

P. chalcoensis is limited in distribution to Mexico where it is considered of extreme importance. The nematode has been given the common name of "Mexican corn cyst nematode".

Symptoms of damage

Maize fields infested with the cyst nematode exhibit patches of stunted and chlorotic plants (Plate 2B). Damage can be severe and is dependent on cultivar susceptibility, nematode density and adequate soil moisture levels in the latter part of the growing season.

In heavily infested sandy soils, plants are markedly stunted with chlorotic leaves exhibiting pale colour stripes. It is important to distinguish these symptoms from those caused by the virus disease "Rayado Fino" where the pale striped lines are in green leaves rather than in yellowish leaves in the case of nematode infestation.

The root system is generally poorly developed. Two months after planting, corresponding with the initiation of the rainy season, large numbers of white females can be observed on the root surface.

Biology

The nematode has one generation per year and survives the winter in diapause (Sosa-Moss, 1987). The nematode survives and reproduces well in all soil types with the exception of loamy soils and causes severe damage on volcanic sandy soils.

Control

Early sowing reduces damage by allowing the plant to escape early root infection. The plants develop a strong root system before sufficient moisture (provided by delayed onset of the rainy season) is available for juvenile hatch and root penetration (Sosa-Moss, 1987).

Other hosts

Out of 300 graminaceus plants tested only *Zea mays* and *Z. mexicana* (Teosinte) were considered hosts (Stone *et al.*, 1976).

Economic importance

Under glasshouse conditions, Sosa-Moss and Gonzales (1973) obtained a reduction of about 60% in yield in heavily infested soils. Although yield loss in the field is considered to be high, experimental data is lacking.

Heterodera zeae

Distribution

This nematode was first described from India by Koshy *et al.* (1970) where it is widely distributed (Sharma & Swarup, 1984). The nematode has been also reported from Pakistan (Maqbool, 1980), Egypt (Ibrahim *et al.*, 1976) and the U.S.A. (Golden & Mulvey, 1983).

Symptoms of damage

H. zeae infested plants exhibit poor and unthrifty growth and are stunted and pale green in colour (Koshy & Swarup, 1971).

Biology and life cycle

Temperature plays an important role in the biology of *H. zeae*. The most favourable temperature for emergence of juveniles from cysts is 25°C, with 91% emergence. At temperatures of 10 or 15°C, only 10 to 20% of the juveniles emerge (Srivastava, 1980).

The life cycle is short, taking only 15–17 days at 27–39°C (Srivastava & Sethi, 1985*b*). It has been speculated that the nematode may complete six to seven generations during one crop season (Srivastava & Sethi, 1985*a*, 1986).

Generally, the nematode reproduces well in moderately light soils. The addition of clay to soil mixtures resulted in proportional decline in nematode reproduction levels (Srivastava & Sehi, 1984*a*).

Other hosts

Koshy *et al.* (1970) originally reported barley, *Hordeum vulgare*, as a host for *H. zeae*. Srivastava and Swarup (1975) recorded *Setaria indica* as an additional host and *Zea mexicana* has been added to the host list (Sharma & Swarup, 1984).

Economic importance

Though the pathogenicity of the nematode has been demonstrated on maize, data on economic damage to the crop is lacking. However, Srivastava and Sethi (1984*b*) showed that plant growth reductions are directly correlated with initial nematode population density.

Heterodera avenae

Swarup *et al.* (1964*a*) from India first recorded *H. avenae* on maize in the subtropics. The nematode has also been reported in maize fields in Egypt (Ibrahim *et al.*, 1986). The worldwide distribution on cereals as well as information on nematode biology has been discussed in the section under

wheat. It has been suggested that there are virulent and less-virulent pathotypes in *H. avenae* populations with regard to their ability to parasitize maize (Saefkow & Lucke, 1979; Saefkow, 1983).

Meloidogyne

Distribution

Meloidogyne incognita and *M. javanica* have been detected damaging maize in almost all maize growing regions of the world. Conversely *M. africana* and *M. arenaria* have been recorded on maize only in India (Krishnamurthy & Elias, 1967) and Pakistan (Maqbool, 1980; 1981).

Symptoms of damage

Above-ground symptoms include stunting, leaf chlorosis and patchy growth. Root galls may be small or large, terminal or sub-terminal or further back along the root. Typical gall symptoms may be totally absent (Becerra & Sosa-Moss, 1977; Idowu, 1981) and, therefore, maize has been often mistakenly considered a poor host or even immune.

Biology and life cycle

The nematode completes its life cycle in about 30 days. Under poor growing conditions, *M. javanica* juveniles may enter young roots, but fail to mature (Shepherd, 1981).

Pathotypes

The four races of *M. incognita* (see Chapter 7) reproduce well on maize with some cultivars exhibiting specificity to a specific race (Oteifa & Elgindi, 1982; Lopez, 1981).

Diagnosis

Since root galls are often small or even lacking, the root system should be stained and examined for nematode penetration if root-knot nematodes are suspected of being important or if juveniles are detected in the soil.

Disease complex

Goswami and Raychaudhuri (1978) studied the interaction between mosaic virus and *Meloidogyne incognita* in pot trials. They found that the mosaic symptoms appeared earlier and nematode reproduction was greater when both pathogens were together than when alone.

Economic importance

Although root-knot nematodes occur frequently in maize fields, information on economic losses is lacking. However, indirect observations, when nematicides are applied in root-knot infected soils, suggest that these nematodes are economically important in maize. Under experimental conditions 2000 juveniles of *Meloidogyne* spp. per kg of soil reduces the growth and yield of maize (Ahmad, pers. comm.). In Jamaica (Hutton, 1976, 1981), greater damage occurs when maize is sown after sugar cane.

Other nematodes associated with maize

Many other plant parasitic nematodes have been found associated with maize. In most of these cases their importance to maize production has not been determined. Of limited or local importance are: species of *Belonolaimus, Hoplolaimus, Helicotylenchus, Rotylenchulus, Longidorus* and *Paratrichodorus*. *Longidorus* and *Xiphinema* can cause severe root tip damage on sandy soils and yield loss, especially in moisture stress situations. *Belonolaimus longicaudatus* can cause severe losses to sweet corn on sandy soils in Florida (Rhoades, 1977). The nematode causes severe stunting with patches often having well defined borders (Fig. 5). Feeding of the ectoparasite along the root surface causes

stubby-root symptoms and a reduced root system that reduces the plants ability to deal with moisture stress (Fig. 6.).

Control

Chemical

The utilization of nematicides is limited in most instances for economic reasons, in spite of the fact that their application reduces nematode populations and increases yield more than two-fold. The cost factor is augmented further by the low expected yield levels in Latin America, Africa, and Southern Asia. Seed treatment with nematicides is another technique which could prove to be effective (Santiago *et al.*, 1984; Sethi & Srivastava, 1986).

Resistance

Maize cultivars, Seneca 110 and Seneca Explorer, are reported to be resistant to *Meloidogyne, Helicotylenchus*, and *Paratrichodorus* (Johnson, 1975). Other cultivars are also reported as resistant to *M. incognita* and *M. javanica* (Nishizawa, 1981). According to Hutton (1981), sweet maize cultivars generally are tolerant to nematode attack. Oteifa and Elgindi (1982) have reported the cultivars Alexandria, American Early, Asheira 17, Asheira 186, Composite 108, Chedwan, and Giza numbers 1, 4, 69, 102, 213, and 303 as moderately or highly resistant to *M. incognita* and/or *M. javanica*.

According to Sasser and Kirby (1979), the following cultivars are resistant to *M. incognita, M. javanica*, and *M arenaria:* Camel Cross, Golden Beauty, Golden Cross, Indian Chief. Mc Nair 340, Mc Nair 440, Pioneer 309B and Span Cross.

Lordello *et al.*, (1985) have identified several maize genotypes as resistant to *Pratylenchus zeae*, and *P. brachyurus*. Two wild species, *Zea diploperennis* and *Z. mexicana*, have been reported to be resistant against *Pratylenchus scribneri* and *Helicotylenchus pseudorobustus* (Norton *et al.*, 1985). Some resistance to *Punctodera chalcoensis* was found in the maize line H32 (Gonzalez de Salceda, pers. comm.).

Cultural

Practices such as crop rotation, sowing time, application of organic amendments, sanitation and tillage operations have been tested and in many cases were demonstrated to be effective in reducing nematode populations. In most cases maize was tested for its activity as a non-host crop against root-knot nematodes affecting other crops in the rotation. Therefore, little is actually known concerning their effects on root-knot population density in the maize crop. It should be stressed again that in some countries maize is damaged by root-knot and nematode reproduction occurs even though typical root galls are not visible (Becerra & Sosa-Moss, 1977; Idowu, 1981).

In Mexico it has been observed that early sowing dates, as well as adequate fertilization reduces damage caused to maize by *P. chalcoensis* (Sosa-Moss & Gonzalez, 1973; Sosa-Moss, 1987). Organic soil amendments were also shown to be effective in reducing nematode densities in maize (Egunjobi & Larinde, 1975).

Sorghum

Sorghum bicolor is an important food and fodder crop of dry land agriculture. Sorghum is used in various forms of unleavened bread in India and Central America; as fermented bread in Sudan, Ethiopia and India or as porridge in Africa and India. It is also boiled like rice and is used to produce alcoholic as well as non-alcoholic beverages in some African countries. In some parts of Africa, sorghum is also eaten as a vegetable. Green and dried fodder is an important roughage for cattle. Sorghum is also used for ethanol production in Brazil.

Fig. 5. Patches of stunted sweet corn caused by *Belonolaimus longicaudatus* in Florida, USA (Photo: H. Rhoades).

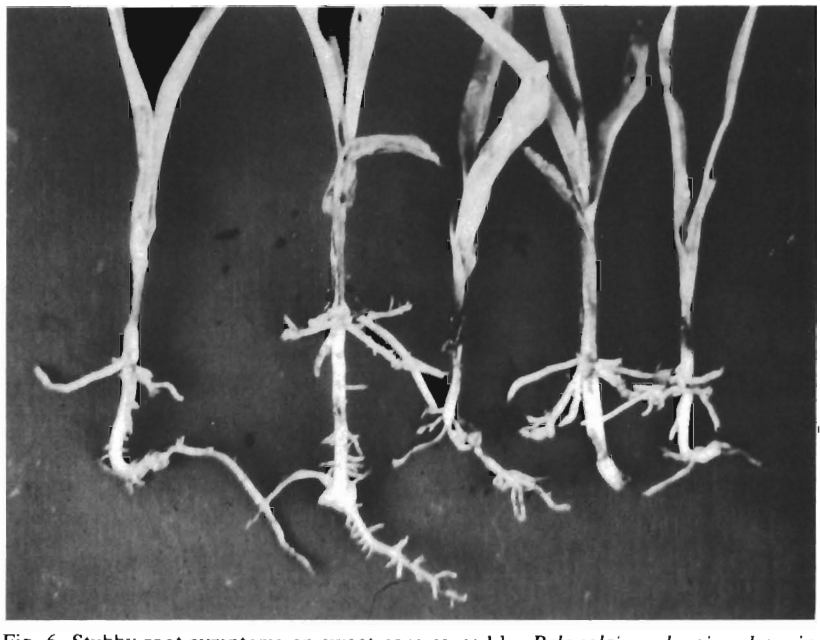

Fig. 6. Stubby-root symptoms on sweet corn caused by *Belonolaimus longicaudatus* in Florida, USA (Photo: H. Rhoades).

Nematodes of sorghum

Although a number of nematodes have been recorded associated with this crop, little information is available on specific nematode problems. Increased yields, after chemical treatment of soil where high population densities of specific nematode species were recorded, provides indirect evidence of significant economic damage. Species in three genera are considered important: *Tylenchorhynchus*, the stunt nematode, *Meloidogyne*, the root-knot nematode and *Pratylenchus*, the lesion nematode.

Tylenchorhynchus

The stunt nematodes *Tylenchorhynchus martini, T. nudus* and *T. acutus* have been recorded as associated with unthrifty growth of plants. Both *T. martini* and *T. nudus* increased in numbers under sorghum monoculture and caused damage at levels of 2000–5000 nematodes/250 cm^3 soil. Yield increased 55% after nematicide treatment where *T. martini* was the dominant population (Hafez & Claflin, 1982). Similarly, *T. nudus* was reported to reduce plant growth by 10 and 56% in fertilized and unfertilized plots, respectively (Smolik, 1977).

Nematode feeding results in poorly developed root systems with few feeder roots. The tissue near some of the root tips may become swollen. Stunted growth and chlorosis may be observed in severely infested fields.

Pratylenchus

The most important lesion nematodes affecting sorghum are *P. zeae* and *P. hexincisus*. As a result of infestation by the lesion nematodes, the roots exhibit necrotic lesions. In heavily infested fields the plants appear stunted and chlorotic. *P. zeae* is reported to reduce uptake of nutrients and water from soil (Chevres-Roman *et al.*, 1971). The species also suppresses top and root growth of sorghum. In combination with the fungus *Curvularia*, it causes severe root necrosis (Bee-Rodriguez & Ayala, 1977). The species is considered of moderate importance to sorghum in tropical areas of the world.

Meloidogyne

The root-knot nematodes *M. incognita, M. naasi* and *M. acronea* are reported associated with sorghum. *M. acronea* has been detected on sorghum in South Africa (Coetzee, 1956) and Malawi (Bridge *et al.*, 1976). In Malawi three cultivars were shown to support high to moderate root populations of the local isolate. The nematode was responsible for delayed flowering and yield losses of 56% in sorghum cv Lindse 555 in pot experiments (Page & Bridge, unpubl.) with delayed flowering also observed in the field (Page, 1985). The nematode causes stunting and chlorosis of infested plants.

M. incognita infestation results in production of elongated swellings or discrete knots and proliferation of roots. Galls produced by *M. naasi* are similar but smaller than *M. incognita* galls. *M. naasi* infested roots may exhibit curving of the roots in the shape of a hook or horseshoe. In comparison to *M. incognita*, it does not cause excessive production of secondary roots. *M. acronea* induce extensive root proliferation but inconspicuous root galls (Page, 1985). Only race 5 of *M. incognita* is able to parasitize sorghum. The optimum soil temperature for development is 26°C and it completes it's life cycle in 34 days (Ediz & Dickerson, 1976).

Other nematodes associated with sorghum

Longidorus africanus and *Heterodera zeae* (Lamberti, 1969; Singh *et al.*, 1979) are associated with sorghum and have been shown to be pathogenic in pot experiments. *Heterodera gambiensis* has been found associated with the crop only in Gambia (Merny & Netscher, 1976). Damage although expected, was not observed in the field in subsequent survey work (Bridge *et al.*, 1978). High

populations of *Longidorus* can cause severe losses (Plate 2 D) when their presence coincides with drought stress (J. Starr, pers. comm.).

Millets

Millets are warm weather cereals with small grains. The millets are found in the following six genera: *Panicum, Setaria, Echinochloa, Pennisetum, Paspalum* and *Eleusine*. These crops form an important staple food in India and several countries of Africa, the near East and South Asia. With the few exceptions listed below, there is practically no information on nematodes of most millet crops.

Millet in the USSR is affected by *Longidorus elongatus*. The infested plants are stunted and chlorotic with shortened, thick and deformed roots. The nematode caused yields reductions of 41% (Semkin, 1975).

Pearl millet

Pearl or bulrush millet, (*Pennisetum typhoides*) is cultivated for grain and fodder in the arid regions of Africa and Asia and as a pasture in the U.S.A. A number of plant parasitic nematode species have been recorded in the rhizosphere of the crop. Pearl millet is a host of both *Meloidogyne incognita* and *M. javanica* (Handa *et al.*, 1971). In the north-western sector of India, *M. incognita* has been reported to be a field problem where it occurs in a combined infection with *Sclerospora graminicola*. The appearance of symptoms of the green ear disease, caused by the fungus, were advanced by about a fortnight when root-knot nematodes were present (Vaishnav & Sethi, 1978). Depending on cultivar, the crop is a poor/non-host for *Meloidogyne acronea* (Bridge *et al.*, 1976; Page, 1983).

In glasshouse tests, pearl millet proved to be the most favourable host for *Tylenchorhynchus vulgaris* multiplication (Upadhyaya & Swarup, 1972). A report from the southern part of India also suggests that the reniform nematode, *Rotylenchulus reniformis*, may be a problem on pearl millet (Seshadri, 1970). Severe stunting and chlorosis of pearl millet (Plate 2 C) were also associated with the presence of *Pratylenchus zeae* and *Tylenchorhynchus obtusus* in southern USA (J. Starr, pers. comm.).

Finger millet

The only nematodes of importance on finger or African millet, *Eleusine coracana*, are *Heterodera gambiensis* and *H. delvii*, both recorded on this crop in the southern part of India and Gambia (Bridge *et al.*, 1978). From the same area, *Rotylenchulus reniformis* is also reported to be a problem in the field (Seshadri, 1970; Krishna Prasad & Krishnappa, 1982).

Conclusions

Despite sustaining research activities during the past four decades, wheat is the only crop, with the exception of rice, identified as having major nematode problems. Barley, sorghum and other millets have not received the same attention, though in some areas, nematodes may be responsible for economic damage to the crops. The cyst, root-knot, lesion and stunt nematodes on cereal crops in general and ear-cockle on wheat and barley are problems which need serious attention. Previously, cereals were considered to be poor hosts of the root-knot nematodes but, it is now becoming quite apparent that *Meloidogyne* species are also important.

Management of nematode problems has so far been dependent largely on the use of rotation and a limited number of resistant cultivars. The cost of chemicals is prohibitive and in some cases environmentally unacceptable to the average cereal farmer. Although resistant/tolerant lines have been identified, their use is dependent on the pathotypes of local populations. While it is most

desirable to concentrate efforts on the development of resistant/tolerant cultivars, the formulation of integrated management programmes must be exploited as well as the development of biological control technology.

References

Abdel Hamid, M. E., Ramadan, H. H., Salem, F. M. & Osman, G. Y. (1981). The susceptibility of different field crops to infestation by *Meloidogyne javanica* and *M. incognita acrita*. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, 54:81–82.

Al-Talib, N. Y., Al-Taae, A. K. M., Neiner, S. M., Stephan, Z. A. & Al-Baldawi, A. S. (1986). New record of *Anguina tritici* on barley from Iraq,. *International Nematology Network Newsletter*, 3:25–27.

Andersen, S. & Andersen, K. (1982). Suggestions for determination and terminology of pathotypes and genes for resistance in cyst-forming nematodes, especially *Heterodera avenae*, *EPPO Bulletin*, 12:379.

Anonymous (1982). Australia, Queensland Department of Primary Industries. Annual Report, 1981–1982, Brisbane, Australia, 160 pp.

Banyer, R. J. & Fisher, J. M. (1971). Effect of temperature on hatching of eggs of *Heterodera avenae*. *Nematologica*, 17:519–534.

Banyer, R. J. & Fisher, J. M. (1976). Effect of host and environment on some aspects of biology of *Heterodera avenae*. *Nematologica*, 22:298–305.

Baxter, R. I. & Blake, C. D. (1968). *Pratylenchus thornei* – a cause of root necroses in wheat. *Nematologica*, 14:351–361.

Becerra, L. E. N. & C. Sosa-Moss. (1977). *Meloidogyne incognita* (Kofoid and White 1919) Chitwood 1949, atacando *Zea mays* (L), en México sin causar agallas radiculares. Memorias IX Reunión de Nematólogos de los Trópicos Americanos. OTAN-ONTA. Lima, Peru.

Bee-Rodriguez, D. & Ayala, A. (1977). Interaction of *Pratylenchus zeae* with four soil fungi on sorghum. *Journal of Agriculture, University of Puerto Rico*, 61:501–506.

Belloni, V. (1954). Comparsa in thalia di und anguillulosi del frumento e prove de lotta. *Notiziario sulle Malattie delle Piante* No. 27, 3–6.

Bergeson, G. N. (1978). Control of the lesion nematode (*Pratylenchus spp.*) in corn with carbofuran. *Plant Disease Reporter*, 62:295–297.

Bridge, J., Jones, E. & Page, L. J. (1976). *Meloidogyne acronea* associated with reduced growth of cotton in Malawi. *Plant Disease Reporter*, 60:5–7.

Bridge, J., Terry, P. J., Tunstall, J. P. & Wàller, J. M. (1978). A survey of crop pests, diseases and weeds of the Gambia. *Report U.K. Ministry of Overseas Development*, 35 pp.

Brown, R. H. (1972). Chemical control on cereal cyst nematode in Victoria – A comparison of systemic and contact nematicides. *Australian Journal of Experimental Agriculture and Animal Husbandary*, 12:662–667.

Brown, R. H. (1984). Ecology and control of cereal cyst nematode (*Heterodera avenae*) in southern Australia. *Journal of Nematology*, 16:216–222.

Brown, R. H. (1987). Control strategies of low value crops. In Brown, R. H. and Kerry, B. R. (Eds.) *Principles and Practice of Nematode Control in Crops*. Academic Press, 351–387.

Brown, R. H. & Young, R. M. (1982). Katyl, a new wheat resistant to cereal cyst nematode. *Agnote Department of Agriculture*, Victoria, Agdex. 112/38.

Byars, L. P. (1920). The nematode disease of wheat caused by *Tylenchus tritici*. *United States Department of Agriculture Bulletin*, 842.

Chevres-Roman, R., Gross, H. D. & Sasser, J. N. (1971). The influence of selected nematode species and number of consecutive plantings of corn and sorghum on forage production, chemical composition of plants and water use efficiency. *Nematropica*, 1:40–41.

CIMMYT (1987). CIMMYT-Hechos y tendencias mundiales relacionados con el maíz 1986: Aspectos económicos de la produccióon de se milla de variedades comerciales de maíz en los países en desarrollo. México, D. F., México 50 p.

Coetzee, V. (1956). *Meloidogyne acroena*, a new species of root-knot nematode. *Nature*, 177:899–900.

Crump, D. H., Sayre, R. M. & Young, L. D. (1983). Occurrence of nematophagous fungi in cysts. *Plant Disease*, 67:63–64.

Dhawan, S. C. & Sethi, C. L. (1983). Resistance in barley to the cereal cyst nematode (*Heterodera avenae*). *Indian Journal of Nematology*, 13:235–237.

Dickerson, O. J., Darling, H. M. and Griffin, C. D. (1964). Pathogenicity and population trends of *Pratylenchus penetrans* on potato and corn. *Phytopathology*, 54: 317–322.

Dixon, G. M. (1969). The effect of cereal cyst eelworm on spring sown cereals. *Plant Pathology*, 18: 109–112.

Duggan, J. J. (1961). The effect of cereal root eelworm on its hosts. *Irish Journal of Agriculture Research*, 1: 7–16.

Duggan, J. J. (1963). Relationship between cereal root eelworm (*Heterodera avenae*) infestation and pH value of soil. *Irish Journal of Agriculture Research*, 2: 105–110.

Ediz, S. A. & Dickerson, O. J. (1976). Life cycle, pathogenicity, histopathology and host range of race 5 of the barley root-knot nematode. *Journal of Nematology*, 8: 228–232.

Egunjobi, O. A. (1974). Nematodes and maize growth in Nigeria. I. Population dynamics of *Pratylenchus brachyurus* in and about the roots of maize in Ibadan. *Nematologica*, 20: 181–196.

Egunjobi, O. A., & Larinde, M. A. (1975). Nematodes and maize growth in Nigeria. II. Effects of some amendments on populations of *Pratylenchus brachyurus* and on the growth and production of maize (*Zea mays*) in Nigeria. *Nematologia Mediterranea*, 3: 5–73.

FAO (1987). *FAO production yearbook*. Vol. 41. Rome, Italy.

Germershausen, K., Kastner, A. & Schmidt, W. (1976). Observations on the threshold of damage by *Heterodera avenae* on cereals under different rates of nitrogen fertilization. In: Vortragstagung zu Aktuellen Problemen der Phytonematologie: 11–30.

Gill, J. S. (1967). Studies on *Heterodera avenae*, the causal organism of 'molya' disease of wheat and barley. Ph.D. Thesis, Punjab University, India.

Gill, J. S. & Swarup, G. (1971). On the host range of cereal cyst nematode, *Heterodera avenae*, the causal organism of 'molya' disease of wheat and barley in Rajasthan, India. *Indian Journal of Nematology*, 1:63–67.

Gokte, N. & Swarup, G. (1984*a*). Relationship between initial inoculum levels of *Heterodera avenae* and penetration of juveniles in the roots of susceptible and resistant barley cultivars. *Indian Journal of Nematology*, 14:95–96.

Gokte, N. & Swarup, G. (1984*b*). Development of *Heterodera avenae* in susceptible and resistant barley cultivars in relation to larval inoculum and penetration. *Indian Journal of Nematology*, 14: 128–134.

Golden, A. M. & Mulvey, R. H. (1983). Redescription of *Heterodera zeae*, the corn cyst nematode, with SEM observations. *Journal of Nematology*, 15: 60–70.

Goswami, B. K. & Raychaudhuri, S. P. (1978). Interaction of rootknot nematodes and viruses in maize and tobacco in India. *International Congress of Plant Pathology* (3rd.) GFR. 16–23 August.

Grosse, E., Decker, H. & Focke, L. (1982). Investigations into the injurious effects of *Heterodera avenae* in cereals. *Nachrichtenblatt für den Pflanzenschutz in der DDR*, 36:33–37.

Gupta, P. & Swarup, G. (1972). Ear-cockle and yellow rot disease of wheat. II. Nematode-bacterial association. *Nematologica*, 18: 320–324.

Gurner, P.S., Dube, A. J. & Fisher, J. M. (1980). Chemical control of cereal cyst-nematodes (*Heterodera avenae*). on wheat by a new low-volume applicator. *Nematologica*, 26: 448–454.

Handa, D. K., Mathur, B. N. & Bhargava, L. P. (1971). Occurrence of root-knot on pearl millet. *Indian Journal of Nematology*, 1: 244.

Hefez, S. L. & Claflin, L. E. (1982). Control of plant parasitic nematodes on grain sorghum and yield response. *Fungicide-Nematicide Tests*, 37: 198.

Holdeman, Q. L. & Watson, T. R. (1977). The oat cyst nematode, *Heterodera avenae*, a root parasite of cereal crops and other grasses. *Department of Food and Agriculture*, California, USA, 1–82.

Hutchinson, C. M. (1917). A bacterial disease of wheat in Punjab. *Memoirs of Department of Agriculture, India, Bacteriological* Series 1: 169 pp.

Hutton, D. G. (1976). Informe sobre el status de los Problemas e Investigaciones con *Meloidogyne* spp en Jamaica. Memorias de la Conferencia Regional de Planeamiento del Proyecto Internacional *Meloidogyne*. Panamá 11–22p.

Hutton, G. D. (1981). Informe sobre el trabajo desarrollado en Jamaica para el Proyecto Internacional desde Mayo de 1976 a Julio de 1978. *Memorias de la Segunda Conferencia de Planeamiento del Proyecto Internacional Meloidogyne Region I.* Panamé: 62–78.

Ibrahim, I. K. A., Rezk, M. A. & Ibrahim, A. A. M. (1986). Occurrence of the cyst nematodes *Heterodera avenae, H. daverti* and *H. rosii* in northern Egypt. *Journal of Nematology*, 18: 614 (Abstract).

Idowu, A. A. (1981) A review of Root-Knot nematode work on Maize at National Cereals Research Institute Abadan, and Prospects for future studies. *Proceeding of the Third Research Planning Conference on Root-Knot Nematodes, Meloidogyne spp. Ibadan, Nigeria*: 122–127.

Johnson, A. W. (1975). Resistance of sweet corn cultivars to plant-parasitic nematodes. *Plant Disease Reporter*, 59:373–376.

Johnson, V. A. (1984). New horizons in cereal production. In Gallagher, E. J. (Ed.) *Cereal Production*. Butterworths. Lond., 1–13.

Kerry, B. R. & Crump, D. H. (1977). Observations on fungal parasites of females and eggs of the cereal cyst nematode, *Heterodera avenae* and other cyst nematodes. *Nematologica*, 23: 193–201.

Kerry, B. R. (1981). Fungal parasites, a weapon against cyst nematodes. *Plant Disease*, 65: 390–393.

Kerry, B. R., Crump, D. H. & Mullen, L. A. (1982*a*). Studies on the cereal cyst nematode, *Heterodera avenae* under continuous cereals, 1974–1978. 1. Plant growth and nematode multiplication. *Annals of Applied Biology*, 100: 477–487.

Kerry, B. R., Crump, D. H. & Mullen, L. A. (1982 *b*). Studies on the cereal cyst nematode, *Heterodera avenae* under continuous cereals, 1975–1978. II. Fungal parasitism of nematode females and eggs. *Annals of Applied Biology*, 100: 489–499.

Kerry, B. R., Crump, D. H. & Mullen, L. A. (1982 *c*). Natural control of the cereal cyst nematode, *Heterodera avenae*, by soil fungi at three sites. *Crop Protection*, 1: 99–109.

Kort, J. (1972). Nematode diseases of cereals of temperate climates. In: Webster, J. M. (Ed.) *Economic Nematology*. Acad. Press, 97–126.

Koshy, P. K., Swarup, G. & Sethi, C. L. (1970). *Heterodera zeae* n. sp. (Nematoda: Heteroderidae). a cyst-forming nematode on *Zea mays*. *Nematologica*, 16: 511–516.

Koshy, P. K., & Swarup, G. (1971). Distribution of *Heterodera avenae, H. zeae, H. cajani*, and *Anguina tritici* in India. *Indian Journal of Nematology*, 1: 106–111.

Koshy, P. K. & Swarup, G. (1972). Susceptibility of plants to pigeon-pea cyst nematode, *Indian Journal of Nematology*, 2: 1.

Kornobis, S., Wolny, S. & Wilski, A. (1980). The effect of *Heterodera avenae* population density in the soil on the yield and plant weight of oats. *Zeszyty. Problemowe Postetow Nauk Rolniczych*, 232: 9–17.

Krishnamurthy, G. V. G, & Elias, N. A. (1967). Host range of *Meloidogyne incognita* causing root-knot on tobacco in Hunsur, Mysore State., *Indian Phytopathology* 20: 274–277.

Krishna Prasad, K. S. & Krishnappa, K. (1982). Occurrence of *Heterodera gambiensis* from India. *Indian Journal of Nematology*, 12: 405.

Lamberti, F. (1969). Pathogenicity of *Longidorus africanus* on selected field crops. *Plant Disease Reporter*, 53: 421–424.

Leukel, R. W. (1924). Investigations on the nematode disease of cereals caused by *Tylenchus tritici. Journal of Agricultural Research*, 27: 928–956.

Leukel, R. W. (1957). Nematode disease of wheat and rye. *Farmers' Bulletin*, USDA No. 1607.

López, R. (1981). Informe sobre las investigaciones realizadas en la Universidad de Costa Rica como parte del "Proyecto Internacional Meloidogyne". *Memorias de la Segunda Conferencia Regional de Planeamiento del Proyecto Internacional Meloidogyne Región I. Panamé:* 16–22.

Lordello, R. R. N., Lordello, A. I. L., Sawasaki, E. & Aloisi. Sobinho, J. (1985). Reaco de genotipus de miltho a *Pratylenchus* spp. en campo *Nematologia Brasileira*, 9: 163–173.

Lordello, R. R. A., Sawazaki, E., Lordello, A. I. L. & J.Aloisi Sobrinho, (1982). Controle de *Pratylenchus* spp. em milho. *Reuniao Brasileira de Nematologia Fortaleza*, Resumos, 6 p.

Lordello, R. R. A., Sawazaki, E., Lordello, A. I. L., & Sobrinho, J. A. (1983). Controle de *Pratylenchus* spp. em milho, com nematicidas sistemicos e con torta de mamona. Soc. Brasil. Nemat. Pulic.

Luc, M. (1986). Cyst nematodes in equatorial and hot tropical regions. In: *Cyst Nematodes* edited by F. Lamberti & C. E. Taylor. Plenum Publishing Corporation. 355–372.

Maqbool, M. A. (1980). Occurrence of eight cyst nematodes on some agricultural crops in Pakistan. Karachi University. *Journal of Science*, 8 (1 & 20): 103–108.

Maqbool, M. A. (1981). Occurrence of root-knot and cyst nematodes in Pakistan. *Nematologia mediterranea*, 9: 211–212.

Maqbool, M. A. (1988). Present status of research on plant parasitic nematodes in cereals and food and forage legumes in Pakistan. In: Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (Eds.). *Nematodes Parasitic to Cereals and Legumes in Temperate Semi-arid Regions*. ICARDA, Aleppo, Syria, 173–180.

Maqbool, M. A. & Hashmi, S. (1986). Population trends of parasitic nematodes in different cropping sequences and the effect on yield of corn cv. AZAM. *International Nematology Network Newsletter*, 3 (3): 34–38.

Mathur, B. N., Arya, H. C., Mathur, R. L. & Handa, D. K. (1974). The occurrence of biotypes of the cereal cyst nematode (*Heterodera avenae*) in the light soils of Rajasthan and Haryana, India. *Nematologica*, 20: 19–26.

Mathur, B. N., Handa, D. K. & Swarup, G. (1987). Effect of deep summer ploughings on the cereal cyst nematode, *Heterodera avenae* and yield of wheat in Rajasthan, India. *Indian Journal of Nematology*, 17: 292–295.

Meagher, J. W. (1977). World dissemination of the cereal cyst nematode (*Heterodera avenae*) and its potential as a pathogen of wheat. *Journal of Nematology*, 9: 9–15.

Merny, G. & Netscher, C. (1976). *Heterodera gambiensis* n. sp. (Nematode: Tylenchida) parasiet du mil et du sorgho en Gambie. Cah. ORSTOM, ser. Biol., Vol. XI, No. 3, 209–218.

Merny, G. & Cadet, P. (1978). Penetration of juveniles and development of adults of *Heterodera oryzae* on different plants. *Revue de Nématologie*, 1 (2): 251–255.

Minz, G. (1956). Cyst forming nematodes in Israel. *Plant Disease Reporter*, 40: 971–973.

Naganathan, T. G. & Sivakumar, C. V. (1975). Host parasite relationships and influence of soil types on the lesion nematode *Pratylenchus delattrei* Luc, 1958 on maize. *Indian Journal of Nematology*, 5: 162–169.

Naganathan, T. G. & Sivakumar, C. V. (1976). Control of the lesion nematode *Pratylenchus delattrei* Luc, 1958 on maize. *Indian Journal of Nematology*, 6: 32–38.

Nilsson-Ehle, H. (1920). Über Resistenz gegen *Heterodera schachtii* bei gewissen Gerstensorten, ihre Vererbungweise und Bedeutung fur die Paxis. *Hereditas*, 1: 1–34.

Nishizawa. J. (1981). Preliminary experiment on varietal reaction of corn to three *Meloidogyne* species. *Proc. 3rd. Res. Planning Conf. on root-knot nematodes, Meloidogyne spp. Region VI*, 20–24, July. 1981. North Carolina State University: 55–58.

Norton, D. C., Tollefson, J., Hinz, P., & Thomas, S. H. (1978). Corn yield increases relative to non-fumigant chemical control of nematodes, *Journal of Nematology*, 10: 160–166.

Norton, D. C., Edwards, J. and Hinz, P. N. (1985). Nematode populations in maize and related species. *Maydica*, 30: 67–74.

O'Brien, P. C. (1983). A further study on host range of *Pratylenchus thornei*. *Australian Plant Pathology*, 12: 1–3.

O'Brien, P. C. & Fisher, J. M. (1978). Factors influencing the number of larvae of *Heterodera avenae* within susceptible wheat and barley seedlings. *Nematologica*, 24: 295–304.

O'Brien, P. C., Fisher, J. M. & Rathjen, A. J. (1980). Inheritance of resistance in two wheat cultivars to an Australian population of *Heterodera avenae*. *Nematologica*, 26: 69–74.

Ogiga, I. R. & Estey, R. H. (1975). Penetration and colonization of *Brassica rapa* and *Zea mays* root lesions by *Pratylenchus* penetrans. *Phytoprotection*, 56: 23–30.

Olowe, T. O. (1969). *Pratylenchus species* associated with maize in western Nigeria. *Programme Report Federal Department Agricultural Research*. Ibadan, Nigeria.

Olowe, T. & Corbett, D. C. M. (1976). Aspects of the biology of *Pratylenchus brachyurus* and *P. zeae, Nematologica*, 22: 202–211.

Olowe, T. (1977). Histological changes in mays root induced by *Pratylenchus brachyurus* and *P. zeae* in the absence of other micro-organisms, *Nigerian Journal of Plant Protection*, 3: 41–51.

Oteifa, B. A. (1963). Species of root-lesion nematodes commonly associated with economic crops in the Delta of U.A.R. *Plant Dis. Reptr.*, 46: 572–575.

Oteifa, B. A. & Elgindi, D. M. (1982). Relative susceptibility of certain commercially important cultivars to existing Biotypes of *Meloidogyne incognita* and *M. javanica* in Nile-Delta, Egypt. *Proceedings of the Third Research & Planning Conference on Root-Knot nematodes Meloidogyne spp. Region VII*. Coimbra, Portugal: 157–169.

Paddock, W. C. (1967). Phytopathology in a hungry world. *Annual Review of Phytopathology*, 5: 375–390.

Page, S. L. J. (1983). *Biological studies of the African cotton root nematode, Meloidogyne acronea*. Ph. D. Thesis, University of London. 294 pp.

Page, S. L. J. (1985). *Meloidogyne acronea* C.I.H. Description of Plant-Parasitic Nematodes Set 8, No. 114, 3 pp.

Prasad, K. S. K., Krishnappa, K., Setty, K. G. H., Reddy, B. M. R. & Reddy, H. R. (1980). Susceptibility of some cereals to *ragi* cyst nematode, *Heterodera delvii. Current Research*, 9: 114.

Rajan (1984). *Evaluation of cyst extraction techniques and their effect on biology of* Heterodera cajani, H. zeae *and* H. avenae. Ph.D. Thesis, IARI, New Delhi.

Raski, D. J. (1950). The life history and morphology of the sugarbeet nematode, *Heterodera schachtii. Phytopathology*, 40: 135–152.

Reversat, G. & Germani G. (1985). Recherches sur la pathogenie des nématodes associes auf mais fourrager au Sénegal. *Revue de Nématologie*, 8 (1): 27–30.

Rhoades, H. L. (1977). Effect of nonfumigant nematicides on the sting nematode, *Belonolaimus longicaudatus*, and yield of sweet corn. *Soil and Crop Science Society of Florida Proceedings*, 37: 218–220.

Roberto, P. A., Van Gundy, S. D. & McKinney, H. E. (1981). Effects of soil temperature and planting date of wheat on *Meloidogyne incognita*, reproduction, soil populations and grain yield. *Journal of Nematology*, 13: 338–345.

Sabova, M., Valocka, B. & Liskova, M. (1981). Effect of *Heterodera avenae* on some cereal cultivars under experimental conditions. *Ochrana Rostlin*, 17: 191–197.

Saefkow, M. (1983). Pathotypenuntersuchungen mit Populationen von *Heterodera avenae* an Mais. *Zeitarchiv für Pflanzenkrankheiten und Pflanzenschutz*, 90: 337–344.

Saefkow, M. & Lucke, E. (1979). Die Entwicklung von *Heterodera avenae* in Maiswurzeln. *Nematologica* 25: 309–313.

Santiago de, S. A., Sosa-Moss C. & García-Gómez, F. A. (1984). Control de Nematodos del Maiz (*Zea mays*) criollo chalqueño, mediante immersión de semillas en nematicidas sistémicos. *Revista Chapingo*, 43–44: 93–96.

Sasser, J. N. & Kirby, M. F. (1979). Crop Cultivars Resistant to Root-Knot Nematodes, *Meloidogyne* species. A Cooperative Publication of the Department of Plant Pathol. North Carolina State University and the U.S. Agency for Internation Development, 24 p.

Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (1988). *Nematodes Parasitic to Cereals and Legumes in Temperate Semi-arid Regions*. ICARDA, Aleppo, Syria, 69–84.

Semkin, A. I. (1975). The effect of *Longidorus elongatus* on the crop of millet. *Chelyabinsku Gosudarstvennyi Pedagogichesku Institut Voprosy Zooloqu*, USSR, No. 4, 3–8.

Seshadri, A. R. (1970). Nematology. In; *Agricultural Year Book – Vistas in Crop Yields*. Published by Indian Council of Agricultural Research, New Delhi: 370–411

Sethi, C. L. & Srivastava, A. N. (1986). Management of *Heterodera zeae* on maize through practical seed dressing. *Indian Journal of Nematology*, 16: 82–86.

Sharma, R. D. (1981). Pathogenicity of *Meloidogyne javanica* to wheat. In: *Trabalhes Apresentados V Reunas, Brasileira de Nematologia*, 9 B. Publicao No. 5.

Sharma, S. B. & Swarup G. (1984). *Cyst forming nematodes of India*. New Delhi. India Cosmo Publication. 1, 150 pp.

Sharma, Renu & Swarup, G. (1988). *Pathology of Cyst Nematodes*. Malhotra Publishing House, New Delhi, 88 pp.

Shen, T. H., Tai, S. E. & Chia, W. L. (1934). A preliminary report on the inheritance of nematode resistance and length of beak in a certain wheat cross. *Bulletin College of Agriculture and Forestry*, University of Nanking No. 19.

Shepherd, J. A. (1981). Report to the third regional conference on root-knot nematode research held at the International Institute of Tropical Agriculture, Ibadan, Nigeria. *Proceedings of the Third Research Planning Conference on Root-knot Nematodes,* Meloidogyne *spp. Region IV & Region V*. Ibadan, Nigeria 21–27 p.

Sikora, R. A. (1988). Plant parasitic nematodes of wheat and barley in temperate and temperate semi-arid regions – a comparative analysis. In: Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (Eds.) *Nematodes Parasitic to Cereals and Legumes in Temperate Semi-arid Regions*. International Centre for Agricultural Research in the Dry Areas (ICARDA), Syria, 46–68.

Sikora, R.A., Koshy, P. K. & Malek, R. B. (1972). Evaluation of wheat selections for resistance to the cereal nematode, *Indian Journal of Nematology*, 2: 81–82.

Singh, K. P., Bino, B. N. & Edward, J. C. (1979). Effect of *Heterodera zeae* on growth of *Sorghum vulgare* and on the rhizosphere microflora. *Indian Phytopathology*, 32: 167.

Smolik, J. D. (1972). Reproduction of *Tylenchorhynchus nudus* and *Helicotylenchus leiocephalus* on spring wheat and effect of *T. nudus* on growth of spring wheat. *Proceedings South Dakota Academy of Science*, 51: 153–159.

Smolik, J. D. (1977). Effects of *Trichodorus allius* and *Tylenchorhynchus nudus* on growth of sorghum. *Plant Disease Reporter*, 61: 855–858.

Sosa-Moss, C. (1965). Recherches sur *Heterodera puctata* Thorne, Parasite du mais au Mexique. Comptes Rendus du Huitieme Symposium International de Nematologie, Antibes, France. Publie par. E. J. Brill, Leiden 54 p.

Sosa-Moss, C. (1987). Cyst nematodes in Mexico, Central and South America, *Nematologia Mediterranea*, 15: 1–2.

Sosa-Moss, C., & González, C. (1973). Respuesta de maíz chalpueno fertilizado y no fertilizado a cuatro diferentes niveles de *Heterodera punctata* raza mexicana (Nematoda: Heteroderidae). *Nematrópica*, 3: (1) 13–14.

Srivastava, A. N. (1980). *Studies on the maize cyst nematode. Heterodera zeae*. Ph.D. Thesis. IARI, New Delhi.

Srivastava, A. N. & Sethi, C. L. (1984 *a*) Effect of soil type on reproduction of *Heterodera zeae. Indian Journal of Nematology*, 14:72.

Srivastava, A. N. & Sethi, C. L. (1984 *b*) Relationships of initial populations of *Heterodera zeae* with plant growth of maize and nematode reproduction. *Indian Journal of Nematology*, 14: 110–114.

Srivastava, A. N. & Sethi, C.L. (1985*a*). On the larval penetration and biology of *Heterodera zeae* on maize *Indian Journal of Nematology*, 15: 18–20.

Srivastava, A.N. & Sethi, C. L. (1985 *b*). Effect of temperature on larval emergence of *Heterodera zeae. Indian Journal of Nematology*, 14: 242–243.

Srivastava, A. N. & Sethi, C. L. (1986). Seasonal population fluctuations of *Heterodera zeae, Rotylenchulus reniformis* and *Tylenchorhynchus vulgaris* in maize-cowpea-wheat rotation. *Indian Journal of Nematology*, 16: 16–18.

Srivastava, A. N., & Swarup, G. (1975). Preliminary studies on some graminaceous plants for their susceptibility to the maize cyst nematode *Heterodera zeae* Koshy *et al.*, 1970. *Indian Journal of Nematology*, 5: 257–259.

Stephan, Z. A. (1988). Plant parasitic nematodes on cereals and legumes in Iraq. In: Saxena. M. C., Sikora, R. A. & Srivastava, J. P. (Eds.). *Nematodes Parasitic to Cereals and Legumes in temperate semi-arid Regions*. ICARDA, Aleppo, Syria, 155–159.

Stoen, M. (1971). *Heterodera avenae* rase – Og resistenundes-desokelser. *N.J.F. Kongressen Uppsala, Seksion IV*, 101–102.

Stone, A. R., Sosa-Moss, C. & Mulvey, R. H. (1976). *Punctodera chalcoensis n.* sp. (Nematoda: Heteroderidae) a cyst nematode from Mexico parasitizing *Zea mays. Nematologica*, 22: 381–389.

Stone, L. E. W. (1968). Cereal cyst nematode in spring barley damage assessments 1963–64. *Plant Pathology*, 17: 145–150.

Stradioto, M. F., Barbosa Ferraz, L. C. G. & Pitelli, R.A. (1983). Dinamica Populacional de *Pratylenchus brachyurus* em cultura de Milho (*Zea mays* L.) infestada por plantas daninhas. Soc. Brasil. Nemat. Public. 7: 99–115.

Swarup, G. (1986). Investigations on wheat nematodes. In Tandon J. P. & Sethi A. P. (Eds.). *Twentyfive years of Coordinated Wheat Research 1961–86*. Wheat Project Directorate, Indian Council of Agricultural Research, New Delhi, 189–206.

Swarup, G. & Gill, J. S. (1972). Factors influencing emergence of larvae from cysts of *Heterodera avenae. Indian Journal of Experimental Biology*, 10: 219–225.

Swarup, G., Mathur, R. L.,Seshadri,A. R., Raski, D. J. & Mathur, B. N. (1976). Response of wheat and barley to soil fumigation by DD and DBCP against "molya" disease caused by *Heterodera avenae. Indian Journal of Nematology*, 6: 150–155.

Swarup, G., Prasad, S. K. & Raski, D. J. (1964*a*). Some *Heterodera* species from India. *Plant Disease Reporter*, 48: 235.

Swarup, G., Sethi, C. L. & Gill, J. S. (1964*b*). Some records of plant parasitic nematodes in India. *Current Science*, 33: 593.

Swarup, G., Sethi, C. L., Seshadri, A. R. & Kaushal, K. K. (1979). On the biotypes of *Heterodera avenae*, the causal organism of "molya" disease of wheat and barley in India. *Indian Journal of Nematology*, 9: 164–168.

Swarup, G. & Singh, K. (1961). Molya disease of wheat and barley in Rajasthan. *Indian Phytopathology*, 14: 127–133.

Thorne, G. (1928). *Heterodera punctata* n. sp., a nematode parasitic on wheat roots from Saskatchewan. *Scientific Agriculture*, 8 (11): 707–710.

Upadhyaya, K. D. & Swarup, G. (1972). Culturing, host range and factors affecting multiplication of *Tylenchorhynchus vulgaris* on maize. *Indian Journal of Nematology*, 2: 139–145.

Upadhyaya, K. D. & Swarup, G. (1981). Growth of wheat in the presence of *Merlinius brevidens* singly and in combination with *Tylenchorhynchus vulgaris. Indian Journal of Nematology*, 11; 42–46.

Vaishnav, M. U. & Sethi, C. L. (1978). Interaction of root-knot and stunt nematodes with *Sclerospora graminicola* on *bajra. Indian Phytopathology*, 31: 497–500.

Van Berkum, J. A. & Seshadri, A. R. (1970). Some important nematode problems in India. *Xth International Nematology Symposium*, Pescara, Italy, 136–137.

Van Gundy, S. D., Perez, B. J. G., Stolzy, L. H. A. & Thomason, I. J. (1974). A pest management approach to the control of *Pratylenchus thornei* on wheat in Mexico. *Journal of Nematology*, 6:107–116.

Vazquez, J. T. (1976). Infestaciones de nematodos fitoparásitos como factor limitante en la producción de maiz en el Antiplano Mexicano. Folleto. DAGEN 76 pp.

Waele De D. & Jordaan, E. M. (1988). Plant-parasitic nematodes on field crops in South Africa. 1: Maize. *Revue de Nématolgie*, 11 (1): 65–74.

Wallace, H. R. (1965). The ecology and control of the cereal root nematode. *Journal of Australian Institute of Agricultural Science*, 31: 178–186.

Walters, M. C. (1979). The possible status of parasitic nematodes as limiting factors in maize production in South Africa. *Proceedings Second South Africa Maize Breeding Symporium, Pietermaritzburg, 1976. Technical Service Republic of South Africa*, 142: 112–118.

Williams, T. D. (1978). Cyst nematodes. Biology of *Heterodera* and *Globodera*. In: Southey, J. F. (Ed.) *Plant Nematology*, H.M.S.O. London, 156–171.

Williams, T. D. & Beane, J. (1972). Effect of temperature and root exudates on *H. avenae* hatch. *Report Rothamsted Experiment Station for 1973*, 171–172.

Winslow, R. D. (1955). The hatching responses of some root eelworms of the genus *Heterodera*. *Annals of Applied Biology*, 45: 19–36.

Zirakparvar, M. E. (1980). Host range of *Pratylenchus hexincisus* and its pathogenicity on corn, soybean and tomato. *Phytopathology*, 70: 749–573.

Zirakparvar, M. E., Norton, D. C. & Cox, C. P. (1980). Population increase of *Pratylenchus hexincisus* on corn as related to soil temperature and type. *Journal of Nematology*, 12: 313–318.

Chapter 5

Nematode Parasites of Root and Tuber Crops

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Root and tuber crops are the most important food commodities produced in many subtropical and tropical countries. World production figures for 1986 (FAO, 1987) show that root and tuber crops are the most important source of carbohydrates in the tropical world and are second only to cereals in total world supply. They all produce starchy storage organs which are modified stems or roots, generally referred to as rhizomes, corms, or tubers.

The origin and history of root and tuber crops are well documented (Leon, 1977; Coursey & Booth, 1977; Coursey & Haynes, 1970; Salaman, 1949; Burton, 1966; Yen, 1982). However, the actual contribution and potential of these crops in the world's food supply is poorly understood. The most widely grown are potato (*Solanum tuberosum*), sweet potato (*Ipomoea batatas*), cassava (*Manihot esculenta*), yams (*Dioscorea* spp.), taro (*Colocasia esculenta*), and tannia (*Xanthosoma* spp.). A further 27 root and tuber crops have been described, many of which are not grown on a wide scale, but are of local importance (Kay, 1987).

Aside from the various production constraints, these crops are attacked by many pests and pathogens that can cause significant yield losses. Nematodes are amongst some of the most important factors that cause yield or quality reduction. Nematological investigations have mainly been concentrated on the major root and tuber crops, such as, potato, with comparatively little work having been done on most of the minor crops. All relevant information on nematodes of these crops is included in this chapter.

Potato

Potato, *Solanum tuberosum* L., originating from the Andean highlands of South America, is a major food crop in many countries. Potatoes are grown in more countries than any other single crop, with the exception of maize, and it is the only tuber crop produced in any significant amount in developed countries. While potato occupies fourth place in importance amongst the major food crops, in terms of dry matter production per hectare, it is the third highest on the list. It ranks first and third in the list of edible energy, and protein production per hectare per day, respectively (Horton *et al.*, 1984).

In recent years, in subtropical and tropical countries, potato production has spread gradually out of its traditionally cool environmental conditions at higher altitudes into hotter and, generally, drier areas. It is increasingly grown as a winter crop in many irrigated, arid areas of large, commercial

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farms. Recently, the production of this crop has been expanded to relatively warm and humid zones which are optimum for the development of many pathogens and pests, including nematodes.

So far, the possibilities of reducing the total production cost per hectare have been rather limited (Vander Zaag & Horton, 1983). However, recent developments in the production of potatoes from true potato seed (TPS) can provide an alternative to overcome the increasing cost of production.

Of the factors which adversely influence the production of potatoes from seed tubers or TPS, nematodes are amongst the most important pest constraints. Currently, distribution of nematodes in most temperate potato-growing areas of the world is well known. While infestation in some countries and production areas may be regarded as minor, in other areas high infestations cause severe yield losses and/or affect quality.

Nematodes of Potato

Nematodes recognized as major parasites of potato are *Globodera* spp., *Meloidogyne* spp., *Nacobbus aberrans, Ditylenchus* spp., and *Pratylenchus* spp.

However, many other species are found associated with potato, such as *Belonolaimus longicaudatus, Thecavermiculatus andinus, Xiphinema* spp., *Rotylenchulus* spp., *Radopholus similis, Longidorus* spp., *Paratrichodorus* spp., *Trichodorus* spp., and *Paratylenchus* spp.; most of these are of minor importance.

Globodera

Potato cyst nematodes, *Globodera pallida* and *G. rostochiensis*, are, by far, the most important nematodes of potatoes and have received the greatest attention (Jensen *et al.*, 1979). They are distributed in cooler areas of subtropical and tropical regions, as well as temperate regions of the world. They are believed to have evolved along with their principal hosts, potatoes, probably in Peru and Bolivia. Brucher (1960) suggested, however, that the mountains of northern Argentina, where these nematodes occur in accessible places, may be their centre of origin. The fact remains that they were introduced to Europe, probably in the mid or late 19th century, on South American potatoes imported for breeding purposes (Winslow, 1978). They have since spread to most potato-growing areas in the tropical and subtropical zones, e.g. Pakistan, India, Morocco, Philippines.

Symptoms of damage

There are no specific above-ground symptoms of diagnostic value associated with potato cyst nematode infections. However, root injury causes stress and reduces the uptake of water and nutrients which in turn cause stunting, yellowing and other discolouration (Plate 3A), and wilting of the foliage under drought conditions. Early senescence and proliferation of lateral roots are often associated with nematode infection. Small immature females of white and yellow stages can be observed on the roots at flowering (Brown, 1969) (Fig. 1). Females of *G. rostochiensis* will go through a yellow stage while *G. pallida* females remain white until dead (Guile, 1970) (Plate 3B). Females can also be observed on the tuber surface, but with less frequency (Franco, 1981). When females die they become cysts, and their cuticles become brown or leathery, and contain as many as 500 nematode eggs.

Biology

Eggs remain viable in soil for a long period of time and encysted eggs are stimulated to hatch by root exudates. Juveniles become active at 10°C and maximum root invasion takes place at 16°C (Franco, 1979). The mature, enlarged females rupture the root tissue, but remain attached to the root by their heads and protruding necks which stay inserted in the root tissue. The fertilized females become large and subspherical and go through a sequence of colour change prior to dying and

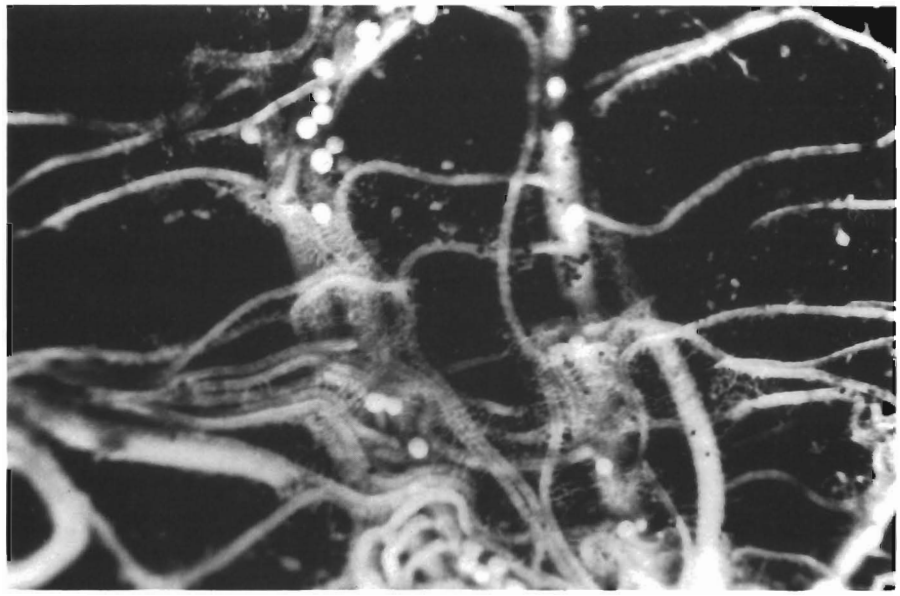

Fig. 1. Females and cysts of *Globodera pallida* on roots of potato.

becoming cysts. Potato cyst nematodes generally complete one generation during a growing season (Morris, 1971).

Races

Due to morphological differences noted between certain nematode populations, *Heterodera rostochiensis* was divided into *Globodera pallida* and *G. rostochiensis* (Mulvey & Stone, 1976; Stone, 1973). However, different populations of *G. rostochiensis* and *G. pallida* behaved differently on resistant cultivars. Different designations and various host differentials were used in Europe to distinguish different races of these two nematode species. Kort *et al.* (1977) introduced a standard system for differentiating various races designated Ro 1–5 as races of *G. rostochiensis* and Pa 1–3 for races of *G. pallida* from Britain, the Netherlands, and Germany. Canto and Scurrah (1977), however, found the European differentials unsuitable for distinguishing races of these nematodes from the Andean regions of South America. They used a set of four differentials that separated four European races of *G. rostochiensis* and three of *G. pallida* in addition to three races of *G. pallida* from the Andes (Table 1). It is known that 5–6 years of monoculture of resistant potatoes will lead to changes in the existing races to one which reproduces on resistant cultivars (Cole & Howard, 1966).

Survival and dissemination

Eggs will remain viable in cysts for over 20 years in soils under severe environmental stress (Oostenbrink, 1966). They withstand temperatures of extreme cold (−15°C) and soil desiccation for long periods. A large portion of eggs will hatch only if they are stimulated by potato root exudates. These nematodes are disseminated as cysts by movement of infested soil by farm implements and the planting of contaminated seed tubers. Irrigation water can also disseminate the nematodes (Jones, 1970).

Environmental factors

The conditions which favour successful potato production are also favourable for nematode multiplication and survival. They flourish in cool soil temperatures, and high soil temperatures for prolonged

TABLE 1. Differential hosts used for separating races of *Globodera rostochiensis* and *G. pallida* as proposed in European and S. American schemes.

	Globodera rostochiensis				*Globodera pallida*					
S. American Scheme	R_1A	R_1B	R_2A	R_3A	P_1A	P_1B	P_2A	P_3A	P_4A	P_5A
European Scheme	Ro1	Ro4	Ro2	Ro3	Pa1				Pa2	Pa3
Differential host										
Solanum tuberosum ssp. *tuberosum*	+	+	+	+	+	+	+	+	+	+
Solanum tuberosum ssp. *andigena* CPC 1673 hybr.	–	–	+	+	+	?	?	?	+	+
Solanum kurtzianum hybr. 60.21.19	–	+	–	+	+	+	–	+	+	+
Solanum vernei hybr. 58.1642/4	–	+	–	–	+	+	+	–	+	+
Solanum vernei hybr. 62.33.3	–	–	–	–	–	+	–	–	–	+
Solanum multidissectum hybr. P55/7	+	+	+	+	–	–	+	+	+	+

After, Kort *et al.*, 1977; Canto & De Scurrah, 1977

periods will limit development and reproduction (Jones, 1970). Soil moisture of field capacity will enhance juvenile movement while soil nutritional status has no effect on nematodes, other than that caused by crop performance. The nematodes tolerate the same soil pH which is tolerated by the potato plants (Jones, 1970).

Other hosts

Potato cyst nematodes are rather host specific and have a limited host range. Eggplant, tomatoes, and a few solanaceous weeds are known to harbour the nematodes, but are not considered as efficient hosts (Evans & Stone, 1977).

Disease complexes

Potato cyst nematodes are known to interact with other pathogenic organisms in development of disease complexes. Interactions have been reported between *G. pallida* and *Pseudomonas solanacearum* (Jatala, 1976) and between *G. pallida* and *Verticillium dahliae* (Harrison, 1971; Franco & Bendezu, 1985).

Economic importance

High losses occur in areas of intensive potato cultivation. Yield losses of as high as 80% are not uncommon in some potato-growing areas of the tropics where infestation levels are high and continuous potato cultivation is practiced.

Control measures

It is virtually impossible to eradicate the potato cyst nematodes. Use of resistant cultivars is the best means of controlling them. A list of such resistant cultivars to European races of *Globodera* is given by Stegemann and Schnick (1985). Long term rotations of 3–7 years also reduce nematode populations; members of the Gramineae and Leguminoseae are crops generally used in these rotations. Restricted shipment of seed tubers from infested areas and high dosages of soil fumigants can be effective in controlling nematodes. Nematicides usually reduce densities and give early crop protection (Whitehead, 1975). Utilization of these various control measures in an integrated management programme will help in keeping the populations below the damage threshold and reduce chances of dissemination, as well as the development of new races. Sikora (1984) developed a number of rotations for control of potato cyst nematode in the upland tropical growing areas of the Philippines. A combination of resistant, susceptible and early maturing potato cultivars integrated with non-host crops were used to suppress population densities. In addition, rotations were designed to take

advantage of nematode diapause to escape damage and to trap late penetrating segments of the population.

Diagnosis

Nematode cysts on roots can be observed if plant roots are examined at the flowering stage (Fig. 1, Plate 3B). Soil analysis for extraction of cysts will also provide an excellent means of diagnosis. It is important, however, to note that it takes 7–8 years from the time of introduction until the nematodes become established and reach the detection level. It is, therefore, important to conduct annual surveys for diagnosing the presence of nematodes.

Meloidogyne

Root-knot nematodes are cosmopolitan in distribution attacking almost all major crops and many weed species. Although many species of *Meloidogyne* are known to attack potato, only five species are considered of global importance. *M. incognita* is the most widely distributed species followed by *M. javanica, M. arenaria, M. hapla*, and *M. chitwoodi*. *M. incognita* and *M. javanica* are principally found in the warm temperate, tropical, and subtropical regions of the world, while *M. hapla* and *M. chitwoodi* are found in the cool temperate regions; *M. arenaria* occurs in most locations (Taylor & Sasser, 1978).

Symptoms of damage

There are no diagnostic above-ground symptoms. Infected plants exhibit stunting, yellowing, and tend to wilt under moisture stress. Infected roots will have galls or knots of various sizes and shapes (Fig. 2). Galling incidence and size is dependent upon nematode density and the nematode species. *M. hapla* and *M. chitwoodi* galls are usually smaller than those caused by other species and have extensive lateral root formation. Under favourable environmental conditions tubers of all shapes and sizes can become infected (Jatala, 1975). Infected tubers have galls which give a warty appearance or can become completely deformed on the surface (Fig. 3, Plate 3C). Depth of penetration of tubers varies but, depending on the tuber size, nematode females are usually found 1–2 cm below the skin feeding on vascular elements (Jatala, 1975).

Biology

The biology and life cycle of *Meloidogyne* species on potatoes follow the general patterns described for this genus (Chapter 1). Both roots and tubers are infected, however, the first generation occurs mainly on the root systems, while the succeeding generations attack tubers. There are up to five generations on the susceptible host under favourable environmental conditions.

Races

There are several races of *Meloidogyne* species (see Chapter 7). All races of these nematodes attack potatoes in varying degrees.

Survival and dissemination

Since *Meloidogyne* species attack a large number of plant species, their population can be maintained on weeds and volunteer crops. However, in the absence of a suitable host, their populations are drastically reduced. They overwinter usually in the form of eggs, although the ability of juveniles to go through anhydrobiosis may contribute to the survival of some *Meloidogyne* species. Infected tubers, plant parts, and planting material, as well as movement of infested soil by farm machinery, and irrigation water are the main avenues of disseminating *Meloidogyne* species. Infected weeds and volunteer crops can also be sources of inoculum.

Fig. 2. Galls on roots of potato caused by *Meloidogyne incognita*.

Environmental factors

M. incognita, M. javanica, and *M. arenaria* develop better in higher temperatures and cannot withstand cool temperatures. Hence, they are of great economic importance in the tropics and warm temperate regions of the world. *M. hapla* and *M. chitwoodi* on the other hand, are cool temperature nematodes and have an optimum temperature of 20°C (Taylor & Sasser, 1978). They are basically distributed in the northern part of North America and in Europe, but *M. chitwoodi* is also found in Mexico (Sosa-Moss, pers. comm.).

Other hosts

Meloidogyne species have a wide host range and attack many agriculturally important crops and weeds. Most of the tuber-bearing *Solanum* species are susceptible to *Meloidogyne* species.

Disease complexes

Meloidogyne species often interact with other pathogenic organisms in development of disease complexes. Perhaps the most important interaction of these nematodes on potatoes is their association with *Pseudomonas solanacearum* (Jatala *et al.*, 1975). Resistance of potatoes to bacterial wilt

Fig. 3. Swellings on surface of potato tubers caused by *Meloidogyne incognita*.

is broken in the presence of *M. incognita* (Jatala *et al.*, 1975; Jatala & Martin, 1979). Other interactions include their association with the *Verticillium* wilt organism and *Rhizoctonia solani*.

Economic importance

Although losses vary depending upon the cultivar and environmental conditions, losses can reach 25% or more (Mai *et al.*, 1981). Loss consists of direct damage to the plant, as well as reduction in tuber quality. Infected tubers are economically undesirable and can serve as an inoculum source (Jatala, 1975). Since potatoes are predominantly grown in cooler climates, there is no great global economic importance associated with *Meloidogyne* infestation. However, the extension of potato cultivation into the tropics could drastically change this situation.

Control measures

Since *Meloidogyne* species deposit their eggs in a gelatinous matrix (usually outside of the root surface) which is relatively unprotected, chemical control has been most successful in reducing their populations (Taylor & Sasser, 1978). The use of resistant cultivars and rotation with non-host crops are probably the most economical means for controlling *Meloidogyne* species. For example, susceptible tomato crops increase *M. hapla, M. arenaria* and *M. incognita* populations. If the species is not *M. hapla* or race 1 of *M. arenaria*, the tomato crop can be followed by peanuts without any damage to peanuts and nematode populations will be reduced (Taylor & Sasser, 1978). Resistant potato material with adaptation to warm temperatures of the tropics has been developed at the International Potato Centre. Utilization of these sources constitute the most practical means of controlling these nematodes.

Diagnosis

Sampling and extraction procedures are presented in Chapter 2. Additional methods of diagnosis include direct observation of roots and tubers. Staining the tuber and root tissues may aid in detection of nematodes.

Nacobbus aberrans

The false root-knot nematode, *Nacobbus aberrans*, is found in tropical and temperate regions of Argentina, northern Chile, Peru, Bolivia, Ecuador, Mexico, USA, and USSR (Mai *et al.*, 1981). Glasshouse populations have been reported from England (Franklin, 1959) and the Netherlands. Although there is a report on the occurrence of this nematode in India, its presence cannot be confirmed (Sher, 1970). It is considered the most important constraint to potato production in southern Peru and Bolivia (Mai *et al.*, 1981). In the USA, it is primarily a nematode pest of sugar beets (Thorne & Schuster, 1956; Inserra, 1983).

Symptoms

No specific above-ground symptoms are associated with *N. aberrans* infection. However, infected plants are stunted and wilt under moisture stress. Galls similar to those produced by root-knot nematodes are formed and usually the infected plants lack normal fibrous root growth. Galls caused by *N. aberrans* are usually formed laterally on roots in a rosary bead-like fashion (Fig. 4) and, hence, the common name of rosary nematode is given to *N. aberrans*. Although it does not cause

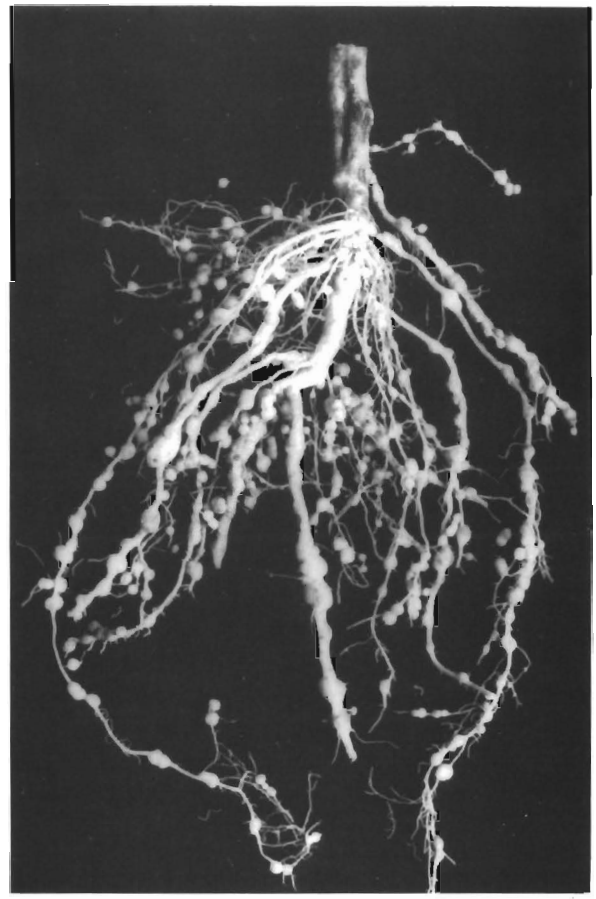

Fig. 4. Bead-like galls on roots of potato caused by *Nacobbus aberrans*.

easily recognizable symptoms on tubers, it usually penetrates the tubers to a depth of 1–2 mm below the skin (Mai *et al.*, 1981).

Biology and life cycle

N. aberrans will undergo the first moult within eggs; second stage juveniles emerge and invade small roots. They will then undergo an additional two moults before leaving the root system as preadults (Mai *et al.*, 1981). Under certain conditions they remain in the root system in a quiescent stage for some time. The quiescent or dormancy stage can be reduced by drying or cooling factors. Once the preadults become active they invade the root system and produce small necrotic lesions prior to gall formation. Production of necrotic lesions by juvenile invasion is not as frequent as those caused by preadults. A portion of those that leave the root system become males. After the establishment of preadult females and gall formation, the nematodes develop to maturity, depositing a portion of their eggs in a gelatinous matrix on the root surface. Females often retain a portion of their eggs in their bodies in addition to depositing them in a gelatinous matrix. Preadults and juveniles also attack tubers, penetrating approximately 1–2 mm below the skin surface. There is no tuber galling or deformation associated with nematode infection. Depending upon the host, temperature, and race of the nematode, generation time is usually between 25–30 days (Mai *et al.*, 1981).

Races

There are indications of the presence of several races of *N. aberrans* attacking potatoes (Jatala, unpubl.). Occurrence of races of this nematode on other crops is known (Inserra, 1983).

Survival and dissemination

False root-knot nematodes are quite resistant to low temperatures withstanding temperatures of −15°C. They can also survive in desiccated soil, a characteristic which makes this nematode quite unique in its biology (Jatala & Kaltenbach, 1979). Exposure of infested soil to cool temperatures for two weeks prior to planting with potatoes enhances infection and severity of the nematode damage. *N. aberrans* has a wide host range and can survive on weeds and alternate hosts, such as tomatoes and other Solanaceous crops. Planting infected tubers, as well as movement of infested soil that adheres to potatoes and farm implements, are the major means of dissemination of this nematode.

Environmental factors

False root-knot nematodes have a wide temperature adaptability surviving and reproducing most rapidly at a temperature range of 20–26°C. However, in the Andes they are associated with potatoes at temperatures of 15–18°C and are not limited by soil types (Mai *et al.*, 1981). Periods of soil cooling and desiccation aid in revival of nematode activity during spring, causing subsequent root infection (Jatala & Kaltenbach, 1979).

Disease complexes

N. aberrans is often associated with *Meloidogyne* spp. The nature of this association is not understood. Similarly, in the Andes this nematode often occurs together with *Globodera* spp., as well as with *Spongospora subterranea*. The effect of such association on potato cultivation is not well documented (Mai *et al.*, 1981).

Economic importance

N. aberrans plays an important role in reducing the yield of potatoes in Bolivia, Argentina, and Peru. Under favourable conditions for nematode development, potato losses of as high as 90% have been observed in Peru and Bolivia (Mai *et al.*, 1981). In Bolivia, this nematode is considered as the number one constraint to potato production. Strict quarantine regulations are imposed in northern Argentina for movement of tubers, as seed pieces, from infested fields (Costilla, pers. comm.).

Control measures

Utilization of nematicides has been the most commonly practised method of controlling *N. aberrans* on potatoes. Because of its extensive host range, control by crop rotations is difficult, although members of Gramineae and most of the Leguminoseae are non-hosts (Mai *et al.*, 1981). Limited work has been done on the development of resistant potato cultivars. Hot water treatment of tubers prior to planting will eliminate nematode infestation. Chemical dips and hot water treatment can be a practical means of controlling nematode spread and establishment (Jatala & Scurrah, 1975).

Diagnosis

Sampling and extraction of *N. aberrans* from soils and roots are similar to those described for *Meloidogyne* spp. Diagnosis of symptoms on roots can be problematic and often are mistaken for those caused by *Meloidogyne* spp. However, *N. aberrans* galls are characteristically formed on the lateral part of the roots and the galls often occur in a bead-like fashion with or without the presence of small root extensions from galls, as with *M. hapla*.

Ditylenchus

Potato rot or tuber nematode, *Ditylenchus destructor*, and potato stem nematode, *D. dipsaci*, have been reported from temperate climates, particularly eastern and western Europe. They also occur in North America and certain parts of South America (Mai *et al.*, 1981). However, the lack of economic damage or recognition of this pest from the potato fields in the tropics and subtropics is evident by the lack of extensive literature citations. Potato rot nematode occurs in many potato producing countries, but the damage is only apparent in temperate zones.

Symptoms of damage

D. dipsaci is mainly a parasite of the foliage where it attacks leaves and petioles, causing shortened, thickened, and malformed foliage. This nematode also injures tubers producing conical pits often accompanied by skin splitting (Mai *et al.*, 1981).

D. destructor mainly damages tubers. The earliest below ground symptoms are small, white, chalky, or light-coloured spots just below the surface of the tuber. The symptoms become evident in the advanced stages of development when the tuber surface is marked by sunken, dark-coloured pits or skin cracks. Sub-surface tissue will develop a brown, matted, wool-like appearance. As the affected areas coalesce, tissue darkens and are invaded by bacteria and fungi.

The tuber skin becomes paper thin and cracks as the underlying tissue dries and shrinks. Under certain environmental conditions, bacterial wet rot may cause complete destruction (Mai *et al.*, 1981).

Biology

D. destructor enters small potato tubers through lenticels on the skin near eyes. Nematodes at first exist singly or in small numbers in the tissue just beneath the skin of the tubers, and small white lesions are present during early and midseason tuber formation. More tuber tissue becomes involved as populations increase. The nematode continues to live and develop in harvested tubers (Winslow, 1978; Mai *et al.*, 1981).

Survival, dissemination, and host range

D. destructor has a wide host range, can survive on weeds, and on a wide range of soil-inhabiting fungi (Winslow, 1978; Jensen *et al.*, 1979). It can also survive on infected tubers left in the field. Dissemination occurs by introduction of infected tubers and in soil adhering to seed pieces (Mai *et al.*, 1981). Irrigation water and cultivation by infested farm tools and machinery are other sources of inoculum dissemination.

The nematode will survive in soils at temperatures as low as −28°C. However, major infestation

will occur at 15–20°C and a rather high relative humidity of 90–100%. Apparently, high relative humidity is a very important factor in the establishment of the nematode. The nematode cannot survive under drought or low (below 40%) relative humidity (Winslow & Willis, 1972; Winslow, 1978; Jensen *et al.*, 1979).

Economic importance and control

High yield losses occur in the areas where climatological conditions favour establishment of the potato rot nematodes. The effect of nematodes will manifest itself at harvest or storage when infected tubers will rot. The use of healthy tubers and soil fumigation are the most effective measures in controlling the nematodes. Rotation of potatoes with sugar beet and other non-host crops can reduce nematode populations (Winslow, 1978). Various cultural control programmes have successfully contributed to the management of these nematodes (Winslow & Wilis, 1972; Winslow, 1978; Jensen *et al.*, 1979).

Pratylenchus

Root-lesion nematodes, *Pratylenchus* spp., are known to damage potatoes in the temperate, tropical, and subtropical regions. *P. crenatus, P. minyus, P. thornei, P. scribneri, P. brachyurus, P. andinus, P. penetrans, P. coffeae, P. vulnus*, and *P. flakkensis* are the most important species associated with potatoes (Jensen *et al.*, 1979; Mai *et al.*, 1981). High populations of lesion nematodes cause areas of poor growth; plants are less vigorous, turn yellow and cease to grow. Damage is often caused by direct feeding and, usually, only cortical tissues are affected. Large nematode populations cause extensive lesion formation and cortex destruction of unsuberized feeder roots (Mai *et al.*, 1981).

Tubers are often attacked and small lesions are formed on the surface (Fig. 5). Infected tubers are sources of nematode inoculum and aid in the survival of the nematodes. *Pratylenchus* spp. have a wide host range and are extensively distributed in the tropics, subtropics, and temperate regions. Because of their extensive host range, crop rotations are not normally practical and should be developed with caution. These nematodes interact with a series of pathogenic organisms in development of disease complexes (Jensen *et al.*, 1979; Mai *et al.*, 1981). Soil fumigation and utilization of resistant potato clones have been identified (Dunn, 1973; Canto, pers. comm.). Hot water treatment of infected tubers at 50°C for 45 to 60 min may also be an aid to reducing nematode spread (Koen, 1969; Yokoo & Matsunobu, 1975).

Other Nematodes of Potatoes

Although many other nematodes are reported to cause serious damage to potatoes, few are of global concern. Other important nematodes of potatoes in the tropics and subtropics are *Thecavermiculatus andinus, Trichodorus*, and *Paratrichodorus* spp. *Thecavermiculatus andinus* is an important nematode of potatoes in some Andean regions of Peru (Jatala, 1989) (Fig. 6). However, the extent of distribution and economic damage of this nematode to potatoes is not well documented. *Trichodorus* and *Paratrichodorus* spp. are of importance because of their involvement in the dissemination of potato viruses (Jensen *et al.*, 1979). In addition to their role in the transmission of viruses, they can also cause severe damage to the root system, leading to stunting and early senescense of the potato plant (Jensen *et al.*, 1979).

Other nematodes, such as *Belonolaimus longicaudatus, Radopholus similis*, and *Rotylenchulus reniformis*, are also known to be of importance to potato production (Winslow, 1978; Jensen *et al.*, 1979). However, they are generally of no major global consequence to potato production.

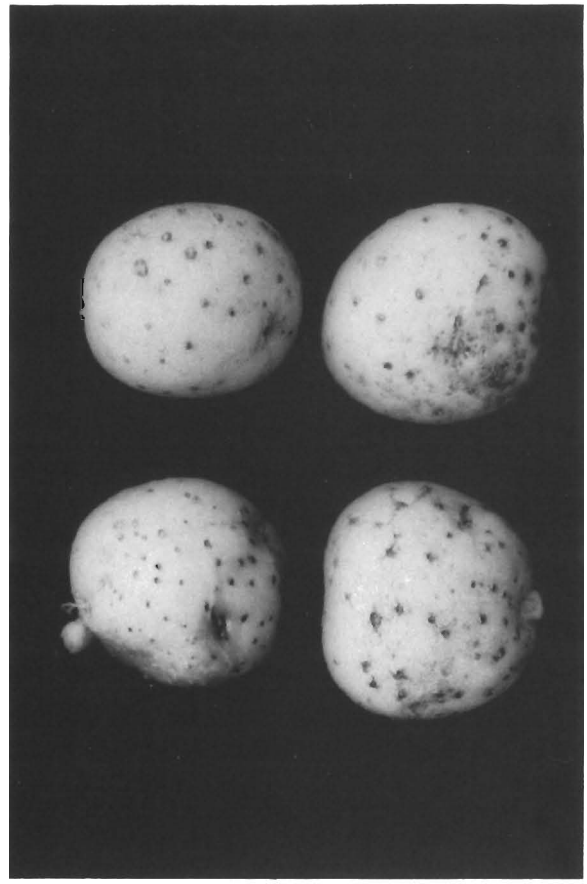

Fig. 5. Lesions caused by *Pratylenchus* sp. on potato tubers.

Sweet Potato

Sweet potato, *Ipomoea batatas* (L.) Lam., a native of tropical America, is more widely grown in developing countries than any other root crop. It is grown in tropical, subtropical, and warmer temperate zones. Of all the world's root and tuber crops, sweet potato is second only to white potato in importance. Asia accounts for the largest portion of sweet potato cultivation in the world.

The recent taxonomic revision of the *I. batatas* complex includes *I. trifida, I. littoralis*, and *I. leucantha* within a single group on anatomical grounds. Although there are several other *Ipomoea* species consisting of an anatomically differentiated group of genomes comprised of diploids and tetraploids, their values are primarily for breeding research (Yen, 1982).

Sweet potato is a perennial herb with vine-like habits and variations in leaf form. The storage roots become swollen as the plant matures. It is vegetatively propagated and can be grown in relatively infertile soils with few imputs and can withstand periods of irregular drought and rainfall (Horton *et al.*, 1984). Storage roots can be left in the ground after maturity, but once harvested, they generally have a short storage life. Sweet potato ranks 4th and 6th on the list of dry matter production per hectare and edible energy production per hectare per day, respectively.

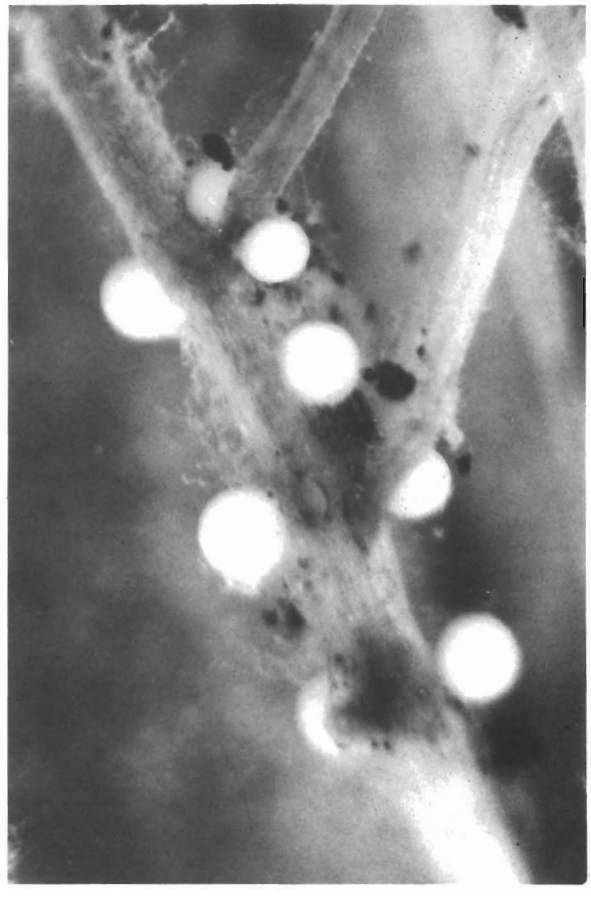

Fig. 6. Females of *Thecavermiculatus andinus* on potato roots.

Nematodes of Sweet Potato

Although a large number of nematode species are associated with sweet potatoes, few are of economic concern. The most important nematode genera attacking sweet potatoes are *Meloidogyne* spp., *Rotylenchulus reniformis, Pratylenchus* spp., and *Ditylenchus destructor.*

Meloidogyne

Root-knot nematode, *Meloidogyne* spp., are widely distributed in the tropics, subtropics, and warmer temperate regions of the world. *M. incognita* is the most important *Meloidogyne* species attacking sweet potatoes and has a wide global distribution. *M. hapla* may also attack this crop, but its distribution is limited to the cooler temperate regions of the world. *M. arenaria* and *M. javanica* are also found infecting sweet potato, although some isolates of *M. javanica* cannot complete their life cycle on the crop (Jatala, 1989).

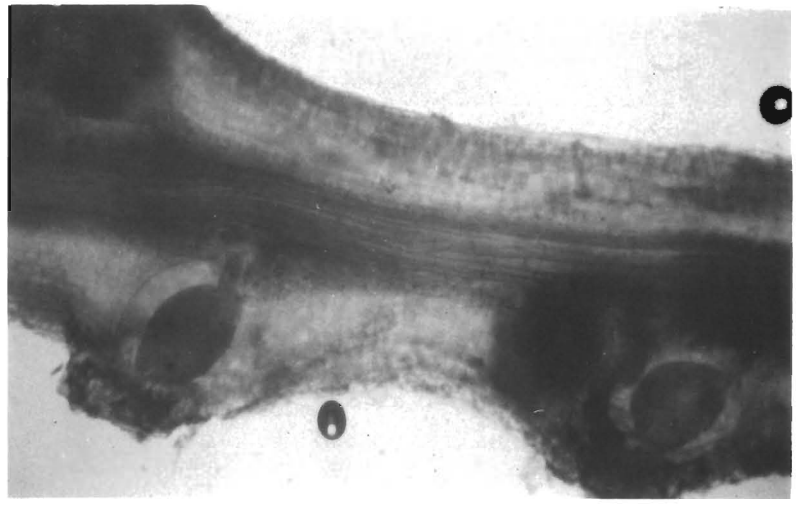

Fig. 7. Females of *Meloidogyne incognita* within sweet potato roots.

Symptoms

Meloidogyne species attack both roots (Fig. 7) and storage roots, causing swellings or knobs of different shapes. If the initial nematode population is high, they cause a pruning effect which can be overcome by vigorous growth and excessive lateral root production (Jatala, 1989). They also cause root-tip necrosis in hypersensitive and resistant plants, while causing a somewhat general root necrosis in roots of susceptible cultivars. Infected storage tubers tend to crack upon maturity, allowing the establishment of secondary organisms and subsequent rotting (Lawrence *et al.*, 1986). Females can be observed on sliced storage roots and are usually associated with necrotic cells around them (Plate 3D). Infected plants exhibit general symptoms of damage associated with poor root growth, such as, yellowing, stunting, and the tendency to wilt during the warmer periods of the day.

Biology

The life cycle of *Meloidogyne incognita* on sweet potato follows the general pattern specific to this genus (Chapter 1). Feeder and storage roots are attacked at the same rate. Depth of penetration is dependent upon the time of penetration of storage roots. The nematode may complete several generations during the cultivation of this crop with the length of time required to complete the life cycle being dependent upon the susceptibility of the host and the prevailing environmental conditions (Jatala, 1989). Apparently, all races of *M. incognita* can attack sweet potatoes at varying degrees.

Survival and dissemination

Meloidogyne juveniles and/or eggs survive in storage roots and can be disseminated in root, but not stem, propagative material. Irrigation water and unclean farm tools and machinery can aid dissemination of the nematodes. Nematodes can survive on many alternate weed hosts.

Environmental factors

Meloidogyne species seem to do well in light, friable, sandy loam soil which happens to predominate and constitute the major portion of the world's sweet potato growing areas. *M. incognita* requires warm temperature for completion of its life cycle. During a normal growing season it can undergo 4–5 generations (Jatala & Russell, 1972). Therefore, it is capable of increasing its population to a level of economic importance in a short period.

Disease complexes

M. incognita interacts with *Fusarium* spp. and *Pseudomonas solanacearum* causing severe wilting and premature death (Jatala, 1989). Although there are several *Fusarium* resistant cultivars, their resistance may be broken in the presence of *M. incognita*.

Economic importance

Meloidogyne species can reduce plant growth and yield. In addition, infected storage roots crack easily and the cracks provide the avenue for penetration and establishment of many secondary and/or pathogenic organisms affecting the quality of storage roots. An important economic factor in *Meloidogyne* infestation is its interaction with other pathogens in the establishment of disease complexes.

Control measures

Crop rotation and intercropping for reducing nematode populations is difficult with *Meloidogyne* species because of their extensive host range. A crop highly susceptible to root-knot nematodes should be avoided in the cropping system. Since sweet potato cultivation is generally conducted on a low cash input, the application of chemical control measures is usually cost prohibitive. Nevetheless, many organophosphates and carbamates are effective in controlling *Meloidogyne* species, such as nemacur and aldicarb (Clark *et al.*, 1980; Gapasin, 1981) and soil fumigation is practised on the sandy soils in California.

Sweet potato cultivars that carry various degrees of resistance to *Meloidogyne* spp., particularly *M. incognita*, have been developed in the USA and Japan. Examples of these are the cvs Heartogold, Norin no. 2, Norin no. 5, Nemagold, Ruby, Taihaku, and Tirivan (Sasser & Kirby, 1979). Many local Peruvian cvs such as Nemanete, and those in the world germplasm collection kept at the International Potato Centre have resistance to *M. incognita* (Jatala, unpubl.). Thus, a resistant gene base is available and could be readily utilized.

Hot water treatment of 65 min at 47°C (Burk & Tennyson, 1941) and hot air treatment of 4 to 8 hr at 50°C (Martin, 1962) is effective in eliminating *Meloidogyne* from root propogative material. Similarly, chemical dip treatment of the propagation material in a solution of oxamyl or side dressing with nematicides at the time of planting will allow the establishment of the crop by providing early protection against nematodes (Rodriguez-Kabana *et al.*, 1978).

Diagnosis

Damage to roots can be assessed by rating the number of galls on roots, taking into account the root necrosis as they relate to the total root mass. Degree of storage root infection can be determined by slicing the roots at 0.5 cm thickness and observing the tissue for the presence of females. Staining the tissue will aid in detection of females with egg masses.

Rotylenchulus reniformis

Rotylenchulus reniformis, the reniform nematode, has been reported in most of the southeastern United States and many other tropical and subtropical areas of the world where sweet potatoes are grown (Martin, 1960; Birchfield & Martin, 1965; Fassuliot & Rau, 1967; Bird *et al.*, 1973; Brathwaite, 1977; Gapasin & Valdez, 1979). Infestation by *R. reniformis* may cause cracking of storage roots (Clark & Wright, 1983). The induced cracks are deep and the exposed surfaces are healed over by formation of callus and periderm. No juveniles and adults are found within the cracked sweet potatoes. The population level necessary for cracking may be very low and is probably less than that for yield reduction. Selection P–104 is reported resistant to cracking (Clark & Wright, 1983).

R. reniformis may also interact with other pathogenic organisms, such as *Fusarium* spp., in development of disease complexes. Thomas and Clark (1983*a*) showed that *R. reniformis* and *M. incognita* were capable of inhibiting the other and becoming the predominant species in a sweet

potato field. Glasshouse studies, however, showed that *R. reniformis* was inhibited and *M. incognita* became predominant in concomitant infection of sweet potato (Thomas & Clark, 1983*b*). Data on control of these nematodes on sweet potatoes is rather limited. Birchfield and Martin (1968) demonstrated that, under field conditions, reniform nematodes can be controlled by in-row treatment with some nematicides in the halogenated hydrocarbon group. Some nematicides in the organophosphate and carbamate group also showed good control of nematodes, resulting in improved quality and yields of sweet potatoes.

Other Nematode Parasites of Sweet Potatoes

Other nematodes of possible importance to sweet potato production when present in large populations are *Pratylenchus* spp. *Ditylenchus destructor, Paratrichodorus* spp., *Belonolaimus longicaudatus, Radopholus similis* and *Scutellonema* spp. Of these, *Pratylenchus* spp. are probably the most important.

Pratylenchus

The *Pratylenchus* species most commonly found with sweet potatoes are *P. brachyurus* and *P. coffeae* causing necrotic lesions of both feeder and storage roots. Apparently a certain degree of resistance is available in some of the existing sweet potato cultivars. Some local Peruvian cvs, such as nemanete, with resistance to *M. incognita* are known to also exhibit resistance to another species, *P. flakkensis* (Canto & Jatala, unpubl.). Because of their relatively large host range, control measures such as rotation may not be very effective.

Cassava

Cassava, *Manihot esculenta* Crantz, originated in tropical America but its occurrence in a wild state is not known and its evolution as a species is directly linked to selection under cultivation by man (Horton *et al.*, 1984). There are two main groups – sweet and bitter cassavas. The enlarged storage roots have hydrocyanic glycosides in varying quantities. It was originally selected for its enlarged roots, ability to propagate from stem cuttings, and erect plant type (Jennings, 1976). Because of its long growth period, its cultivation is primarily limited to the tropics and subtropics. It is the most widely grown root crop in varying agro-climatic conditions (Flach, 1982). It has the ability to produce economic yields under relatively marginal soil and rainfall conditions, and has the highest carbohydrate yield per unit of land and labour. It is compatible with a variety of associated crops and is essentially a small farm and subsistence crop with minimal cash input for production.

Nematodes of Cassava

Several factors may influence the production of this crop.Because of its distribution in the warm tropics, the cassava roots are associated with a large number of nematode species.

Comprehensive lists of nematode species associated with cassava and their distribution are reported by Hogger (1971) and Caveness (1980). Although the list of associated nematodes is rather large, only a few are of some concern. The plant parasitic nematodes most frequently found associated with cassava are *Pratylenchus brachyurus, Rotylenchulus reniformis, Helicotylenchus erythrinae, H. dihystera, Scutellonema bradys, Meloidogyne incognita*, and *M. javanica*. Although *M. arenaria* and *M. hapla* are also reported on cassava (Tanaka *et al.*, 1979), they are not of major concern. *M. incognita* and *M. javanica* are probably the most important nematodes followed by *P. brachyurus, Helicotylenchus* spp., and *R. reniformis*, as they are found in abundance around the roots of cassava. These nematodes have wide host ranges and, therefore, intercropping susceptible hosts with cassava is not recommended. Most of these nematodes may interact with other pathogenic

organisms in development of disease complexes. However, information of such interactions on cassava is rather scarce. It is important to note that as cassava production moves into monoculture and new high yielding cultivars are released, nematodes have the potential of becoming limiting factors in production. Varietal responses of cassava to *M. incognita* and *M. javanica* suggest that the use of tolerant and resistant cultivars may be the most practical method for managing these nematodes on this crop. Limited information on the use of nematicides for controlling nematodes indicates that, in general, nematodes are not major production constraints. Gapasin (1981), however, reported that preplant application of aldicarb, carbofuran and bunema increased yield. Cassareep, a by-product of the cassava industry, was apparently effective in controlling *M. incognita* and *M. javanica* on cassava (Da Ponte & Franco, 1981). Utilization of resistant cultivars and intercropping with non-hosts are economical means of nematode control on cassava.

Yams

Yams, *Dioscorea* spp., are probably one of the oldest food crops known to man (Alexander & Coursey, 1969). Their large-scale cultivation as food crops is restricted largely to three main areas of the world – West Africa; the Pacific area (including Japan); and the Caribbean, but are also of importance in parts of eastern Africa and tropical America.

The genus *Dioscorea* consists of over 600 species but only ten of these are important food yams: *D. rotundata* Poir., *D. cayenensis* Lam., *D. dumetorum* (Kunth) Pax., *D. hispida* Dennst., *D. alata* L., *D. esculenta* (Lour.) Burk., *D. bulbifera* L., *D. opposita* Thunb., *D. japonica* Thunb. and *D. trifida* L. In addition to the edible yams, a number of *Dioscorea* species have been commercially grown to provide a source of diosgenin which is used in the manufacture of oral contraceptives, sex hormones and cortisone (Coursey, 1967; Purseglove, 1972; Kay, 1987).

Some yams produce single, large tubers, while others produce many small tubers. Yams can also form bulbils in the leaf axils as in *D. bulbifera*. Most yams have good storage qualities and can survive for periods of 3–4 months or longer. Yams are normally vegetatively propogated from whole small tubers (seed tubers), portions of tubers (setts) or bulbils. The small seed tubers can be formed by cutting and removing the main tuber during the growing season. They can also be produced by the use of "minisetts" or "microsetts" cut from tubers (International Institute of Tropical Agriculture, 1984). Yams can be monocropped but are more often intercropped. The ideal growing conditions are a long rainy season with rainfall of at least 1500 mm, a temperature of 30°C, and deep, loose, fertile soils (Coursey, 1972).

Nematodes of Yams

Many different nematode species have been found associated with yams. The nematodes of particular importance are endoparasites of roots and tubers. Those known to cause serious damage are *Scutellonema bradys, Pratylenchus coffeae* and *Meloidogyne* spp.

Scutellonema bradys

The yam nematode, *S. bradys*, is the cause of a decay of yam tubers known as "dry rot disease". It is found in many yam growing areas of the world having been reported from West Africa (The Gambia, Cameroon, Ivory Coast, Nigeria, Senegal, Togo), the Caribbean (Cuba, Dominican Republic, Guadeloupe, Haiti, Jamaica, Martinique, Puerto Rico), Brazil and India.

Symptoms of damage

Dry rot of yams occurs in the outer 1 to 2 cm of tubers directly associated with *S. bradys* (Fig. 8). The initial stage of dry rot consists of cream and light yellow lesions below the outer skin of the

Fig. 8. Dry rot of yam *(Dioscorea rotundata)* tuber (left) caused by *Scutellonema bradys* compared with healthy tuber (right) in Cameroon.

tuber. There are no external symptoms at this stage. As the disease progresses it spreads into the tuber, normally to a maximum depth of 2 cm but sometimes deeper. In these later stages of dry rot, infected tissues first become light brown and then turn dark brown to black. External cracks appear in the skin of the tubers and parts can flake off exposing patches of dark brown, dry rot tissues (Plate 3E). The most severe symptoms of dry rot are seen in mature tubers especially during storage when it is often associated with general decay of tubers.

No foliar symptoms have been observed on yams growing in soil infested with *S. bradys*.

Biology and life cycle

S. bradys is a migratory endoparasite present in yam soils, roots and tubers. It invades the young, developing tubers through the tissues of the tuber growing point, alongside emerging roots and shoots, through roots and also through cracks or damaged areas in the tuber skin (Bridge, 1972).

Nematodes feed intracellularly in tuber tissues resulting in rupture of cell walls, loss of cell contents and the formation of cavities (Goodey, 1935; Bridge, 1973; Adesiyan *et al.*, 1975*a*). They are mainly confined to the sub-dermal, peridermal and underlying parenchymatous tissues in the outer 1 to 2 cm of tuber. *S. bradys* continues to feed and reproduce in yams stored after harvesting. Populations can increase 9 to 14-fold in *D. rotundata* tubers over a 5 to 6 month storage period, and 5 to 8-fold in *D. alata* and *D. cayenensis* respectively over the same period (Bridge, 1973; Adesiyan, 1977). In tubers with partial dry rot, more nematodes are found in the oldest, apical portions, adjacent to the stems (Adesiyan, 1977).

Survival and dissemination

No true survival stage is known with *S. bradys* but populations are maintained in the absence of yams probably on other host plants. Sizeable populations of the nematode can be found in soil at the beginning of the yam growing season (Obigesan & Adesiyan, 1981; Adesiyan & Badra, 1982).

Yams are propogated from whole tubers or pieces of tuber which are the principal means of

dissemination of *S. bradys*. Comparatively low populations of the nematodes in tubers do not produce external symptoms of damage (Bridge, 1973) and thus the risk of dissemination by this means is greater. Infested seed tubers rather than soil are probably the main source of nematode inoculum in yam fields.

Environmental factors affecting parasitism

Nematodes in stored tubers are affected by storage conditions; populations of *S. bradys* increase at twice the rate in tubers stored at 22–32°C and relative humidity 40–85% compared to those in tubers stored at 16–18°C and relative humidity 80–85% (Adesiyan, 1977).

Other hosts

The most commonly grown food yams are all hosts of *S. bradys* and susceptible to dry rot disease. In West Africa, the *Dioscorea* species known to be attacked are *D. alata, D. bulbifera, D. cayenensis, D. dumentorum, D. esculenta* and *D. rotundata* (Baudin, 1956; Caveness, 1967*a*; Smit, 1967; Bridge, 1982). Two wild *Dioscorea* spp. in Nigeria have been shown to support low populations in tubers (Bridge, 1982), and also tubers of a wild *Dioscorea* sp. from forest soil in Cameroon have been found infested with *S. bradys* causing dry rot (Bridge & Price, unpubl.).

D. alata, D. bulbifera, D. cayenensis, D. rotundata, D. trifida, and *D. transversa* are hosts of *S. bradys* in the Caribbean (Decker *et al.*, 1967; Ayala & Acosta, 1971; Belliard & Kermarrec, 1978; Kermarrec *et al.*, 1987); *D. cayenensis* in Brazil (Moura *et al.*, 1978) and *D. alata* in India (Nadakal & Thomas, 1967).

There are many other crop and weed hosts of *S. bradys* (Luc & de Guiran, 1960; Adesiyan, 1976*b*; Bridge, 1982), but most plants are relatively poor hosts in comparison to yams. Sesame and cowpea, support high root populations, and melon can increase soil populations.

Disease complexes

Dry rot disease can be caused by *S. bradys* in the absence of other organisms (Bridge, 1973; Adesiyan *et al.*, 1975*a*) although it has been suggested that the disease is caused by a bacterium, *Corynebacterium* sp., in association with *S. bradys* which acts as a wounding agent (Ekundayo & Naqvi, 1972). The more extensive, internal decay of tubers known as "wet rot", "soft rot" or "watery rot" is associated with fungal and bacterial pathogens (Adeniji, 1970; Ogundana *et al.*, 1970; Ekundayo & Naqvi, 1972). This general decay of tubers, which is a serious problem in stored yams, is increased when tubers are wounded or damaged (Adeniji, 1970; Ogundana *et al.*, 1970). The damage caused by nematodes can predispose the tubers to invasion by decay organisms resulting in complete rotting of the tubers (Goodey, 1935). The principal fungi causing internal tuber decay are *Botryodiplodia theobromae* and *Fusarium* sp. although other fungi and a bacterium, *Erwinia* sp., are frequently isolated from decaying tissues (Coursey, 1967; Adeniji, 1970; Ogundana *et al.*, 1970; Ekundayo & Naqvi, 1972; Moura *et al.*, 1976; Demeaux *et al.*, 1982). Nematodes and fungi are found together in the transitional stage between dry rot and wet rot but nematodes do not occur in the "late wet rot" stage deep in the tubers (Adesiyan *et al.*, 1975*a*).

In the West Indies, *S. bradys* infrequently occurs together in the same tubers with *P. coffeae*, however, and the most usual situation is infestation by one species only. The establishment of one species in tuber tissues apparently prevents concomitant infection by the other species (Castagnone-Sereno & Kermarrec, 1988).

Economic importance

The primary importance of *S. bradys* is in the direct damage it causes to the tubers, but the relationships between this damage and loss in total yield is difficult to determine (Wood *et al.*, 1980). However, weight differences between healthy and diseased tubers harvested from the field have been estimated to be 20 to 30% in the Ivory Coast (Smit *in* Bridge, 1982) and 0 to 29% in Nigeria (Wood *et al.*, 1980). Weight reduction due to moisture loss is more likely to occur in late harvested

tubers left in dry soil (Bridge, 1982). Water loss from tubers continues during storage and is significantly greater in tubers infected with *S. bradys* compared to healthy tubers (Adesiyan *et al.*, 1975*b*).

Dry rot of yams alone causes a marked reduction in the quality, marketable value and edible portions of tubers, and these reductions are more severe in stored yams. When dry rot is followed by wet rot in stored yams, losses of whole tubers can be as high as 80 to 100% (Adesiyan & Odihirin, 1975). The degree of pre-harvest damage to tubers by *S. bradys* varied from 0 to 40% in Nigeria (Wood *et al.*, 1980). Nearly 47% of all tubers on sale in Nigerian markets were infested with *S. bradys* (Bridge, 1973) and both dry rot and wet rot diseases of tubers have been observed in all Nigerian yam barns and markets sampled (Adesiyan & Odihirin, 1977).

Populations in the outer peelings of rotted yam tubers can average 100 000 nematodes (Adesiyan *et al.*, 1975*a*) and can exceed 300 000 nematodes/50 g of tuber peelings (Bridge, 1973). Low populations of the nematode produce only discrete areas of yellow necrotic tissues or dry rot internally, and populations in excess of 1000 nematodes/50 g of tuber peelings are necessary to produce observable, external symptoms of damage (Bridge, 1973).

Control

The control measures that can be used are (1) controlling nematodes in field soil by chemical and cultural means (2) use of nematode-free planting material or treatment of seed tubers and setts prior to planting to reduce or eliminate nematodes from propogative material, and (3) treatment of tubers after harvesting to prevent storage losses.

Cultural

Keeping fallow land free of all host plants is a suggested control of *S. bradys* in Cuba (Decker *et al.*, 1967) but this will not always be economic or practical.

Rotation of crops to control *S. bradys* is not always an option open to all growers as yams are normally grown as the first stage in a rotation after fallow. However, soil populations of *S. bradys* will be reduced if a non-host or poor-host crop, such as, peanut, chillie pepper, tobacco, Indian spinach, cotton, maize or sorghum are grown prior to yams (Adesiyan, 1976*b*). Crops which are known to support high populations of *S. bradys* should be avoided, eg. cowpea (cvs New era, Ife brown), sesame, greengram, pigeonpea, kenaf, okra, tomato and melon.

Yams are frequently intercropped, sometimes with as many as five other crops (Coursey, 1967). If these crops are hosts of *S. bradys* they will encourage build-up of nematode densities increasing the chances of damage to the tubers. Similar results are to be expected with host weeds such as *Eupatorium, Synedrella* and *Chromolaena*. Weed control and the exclusion of hosts of *S. bradys* from around yams will help to reduce nematode damage (Adesiyan, 1976*b*).

The use of nematode-free propogative material is an obvious means of preventing nematode damage. Seed tubers showing symptoms of dry rot (cracking and flaking) should not be used for planting. The presence of dry rot in tubers without external symptoms can be determined by scraping away sections of tuber skin, or by the use of tuber pieces rather than whole tubers enabling the grower to examine for dry rot symptoms before planting. Pieces from different parts of the tubers often contain varying population levels of *S. bradys* (Adesiyan, 1977). The bottom or distal portions have the least nematodes and can be selected for planting where possible.

Any foliar material used for propogative material will be completely free of *S. bradys*. Yams, such as *D. bulbifera* and some forms of *D. alata*, can be readily propogated from bulbils or aerial tubers. A number of yams, such as *D. alata, D. rotundata* and *D. dumentorum*, can be produced from vine cuttings (Coursey, 1967). Even true seed can be used for propogating *D. rotundata* (Sadak & Okereke, 1975). Although these methods of propogation are not a practical means of producing ware tubers, they can be used to produce nematode-free seed tubers.

The method used to produce large numbers of seed tubers from relatively few yams by growing "microsetts" or "minisetts" cut from mature tubers (International Institute of Tropical Agriculture,

1984) will effectively produce nematode-free propogative material as long as clean, healthy "mother seed yams" are selected.

The use of wood ash to coat yam setts before planting is a traditional practice amongst some yam growers and can enhance tuber formation but does not markedly decrease numbers of nematodes in tubers. Mixing cow dung in yam mounds before planting at a rate of 1.5 kg per mound (1886.3 kg/ha) can increase yields of tubers and significantly decrease nematode numbers (Adesiyan & Adeniji, 1976). Other organic manures may have a similar effect on nematode populations in yam mounds.

NPK fertiliser can reduce *S. bradys* populations in tubers of *D. alata* to a very low level. In contrast, nitrogen alone can increase both populations of *S. bradys* and the percentage of infested tubers of *D. rotundata*, whereas phosphorus alone can decrease percentage of infested tubers. These results support observations by farmers in certain yam growing areas of Nigeria that yams fertilised with nitrogen alone do not store well, but yams fertilised with mixtures that contain phosphorus store longer (Adesiyan & Adeniji, 1976).

Hot water treatment

Hot water treatment can reduce or eliminate *S. bradys* from tubers. The expense of heating equipment, and the difficulties of maintaining constant temperatures, are the main prohibitive factors against its large scale use. However, it is feasible for small scale operations and for establishing nematode-free planting material.

Most studies have shown that a water temperature of 50° to 55°C for up to 40 min gives the best control of *S. bradys* without damaging tubers. The age of the tuber, the species of *Dioscorea* being treated, and the severity of infestation of the tubers, will affect nematode control by hot water treatment (Ayala & Acosta, 1971; Bridge, 1975; Acosta & Ayala, 1976; Adesiyan & Adeniji, 1976). The time of treatment can be critical. *D. rotundata* tubers treated immediately after harvesting rot completely, but those treated after a storage of 2 to 6 months show little sign of deterioration, although those treated soon after dormancy has broken are slower to sprout (Bridge, 1975; Adesiyan & Adeniji, 1976).

Resistance and tolerance

There is no firm evidence of resistance to *S. bradys* in yams, and all the main food yams (*D. alata, D. bulbifera, D. cayenensis, D. esculenta, D. rotundata*) are susceptible to damage. *D. dumetorum* is generally less readily invaded than other species. All cultivars of *D. alata, D. cayenensis* and *D. rotundata* that have been examined in West Africa are susceptible to infection by *S. bradys* (Adesiyan, 1977; Bridge, 1982). In Puerto Rico, a casual observation suggests that *D. alata* cv Florido is not susceptible to nematode attack (Ayala & Acosta, 1971).

Chemical

Chemical control of *S. bradys* on yams has had some success but information on the economics of this means of control is lacking for large scale use.

DD and DBCP applied as soil treatments have, at best, only produced moderate yield increases and control of *S. bradys* (Anon., 1964; Ayala & Acosta, 1971)

Four granular nematicides (aldicarb, oxamyl, carbofuran and miral or isazophos) applied as post-plant treatments in yam mounds two weeks after planting at a rate of 2 kg a.i./ha reduced soil populations of *S. bradys* to very low levels with remarkable yield increases recorded. There was some accumulation of toxic residues in harvested tubers (Adesiyan & Badra, 1982).

Although chemotherapy of tubers as a practical means of nematode control for yam growers has not been ascertained, results from laboratory experiments suggest that this could be an economic proposition. Significant increases in yield have been obtained by soaking tuber pieces of *D. alata* infected with *S. bradys* for 30 minutes in 1000 ppm a.i. aqueous solutions of the nematicides DD, carbofuran, and oxamyl; the disinfectants calcium hypochlorite and formalin; and nitrogenous

fertilizers ammonium sulphate and calcium nitrate. Tuber pieces are drained and air dried before planting. All treatments reduced *S. bradys* populations in tuber tissues but none of them eliminated nematodes from the yams (Badra & Caveness, 1979).

Diagnosis

Assessment of the incidence and extent of dry rot disease in yam tubers can be done by direct observation. In tubers without obvious external symptoms of damage, it will be necessary to scrape away the surface layers, or section tubers to determine the presence of dry rot.

Nematodes will be found in soil and roots which can be sampled, particularly at the end of the growing season. However, most nematodes will be found in tuber tissues and sampling of these is the most appropriate means of assessing populations and importance of *S. bradys*. Peelings of a known thickness (1 or 2 cm) are cut from tubers. These are chopped finely, teased apart or preferably macerated before placing on a support tissue or sieve in water (see Chapter 2). Thirty to 50% of nematodes will emerge from tissues in the first 3 days but they will continue migrating from the tissues for over 20 days.

Pratylenchus coffeae

P. coffeae, is widely distributed on many different crops throughout the tropics. It is recorded as a parasite of yams in Barbados, Jamaica and Puerto Rico (Ayala & Acosta, 1971; Brathwaite, 1977; Coates-Beckford & Brathwaite, 1977), and in the Pacific islands of Papua New Guinea, Fiji, Niue, Tonga, Vanuatu and Solomon Islands (Bridge, 1988). *P. coffeae* is the cause of tuber dry rot disease of yams, known locally in Jamaica as "burn".

Symptoms of damage

The dry rot symptoms caused by *P. coffeae* in yam tubers are indistinguishable from those caused by *S. bradys* (Plate 3F). Brown, irregular dry rot extends 1 to 2 cm into the outer tissues of *D. rotundata* tubers (Acosta, 1974), but can occur as deep as 5 cm in *D. alata* tubers (Bridge & Page, 1984). The dry rot can be more pronounced in the oldest apical portions of the tubers adjacent to the vines (Acosta, 1974), or even restricted to these portions in newly harvested tubers (Bridge & Page, 1984). External symptoms observed on tubers of *D. alata, D. cayenensis* and *D. rotundata* are deep cracks, a corky appearance, exposed dark brown rotted areas, and diseased tubers being spongy to the touch (Thompson *et al.*, 1973; Acosta & Ayala, 1975; Bridge & Page, 1984). Necrosis or rotting caused by *P. coffeae* has also been observed in tubers of *D. esculenta* (Bridge & Page, 1984) and *D. trifida* (Hickling, 1974).

Above-ground symptoms of damage are not as obvious. Vines from tubers severely infected with *P. coffeae* are shorter and unthrifty (Coates-Beckford *et al.*, 1978). Planting material with a high proportion of dry rot can result in non-sprouting of tubers and poor stands in yam fields (Coates-Beckford & Brathwaite, 1977).

Biology

P. coffeae is a migratory endoparasite of yam roots and tubers. It is assumed to have a life cycle of three to four weeks on *Discorea* spp. (Thompson *et al.*, 1973) and the general behaviour of *P. coffeae* in yam tubers is probably very similar to that of *S. bradys*.

No information is available on whether *P. coffeae* of yams is a separate biological race from those that are important parasites of other crops although this possibility does exist.

P. coffeae reproduces and multiplies in stored yams and is disseminated in seed tubers. It can also be introduced into yam fields in the roots and plant tissues of other crops. The nematodes can survive in field soil between yam crops on other hosts.

Temperature can have a marked affect on nematodes. During storage, at ambient temperatures

of 24–31°C, *P. coffeae* populations can rise to very high levels (939/g), but in tubers stored at 12–13°C numbers of nematodes remain very low (< 1/g) (Thompson *et al.*, 1973).

Other hosts

P. coffeae is a parasite of *D. alata, D. cayenensis, D. esculenta, D. rotundata* and *D. trifida*. It has also been found associated with *D. bulbifera* in the Pacific (Orton Williams, 1980). In addition to yams, *P. coffeae* has an enormous host range covering almost all plant families.

Disease complexes

Dry rot of yams caused by *P. coffeae* is associated with other soft and wet rots in stored tubers (Coates-Beckford & Brathwaite, 1977; Bridge & Page, 1984). It is likely that similar interrelationships between nematodes and other organisms that have been described or suspected with *S. bradys* also occur with *P. coffeae*.

Economic importance

P. coffeae is important as a parasite of the tubers reducing their edible portions, marketable value and, particularly, their storage qualities. Where the nematode occurs it can be very widespread. In Jamaica, 67 to 100% of *D. rotundata* and *D. cayenensis* tubers were found to be infected with *P. coffeae* (Thompson *et al.*, 1973), and over 50% of *D. alata* tubers examined in Papua New Guinea had obvious signs of dry rot and were infested with *P. coffeae* sometimes in numbers in excess of 60 000 nematodes/50 g tissues (Bridge & Page, 1984).

Yield reductions, as measured by weight of tubers, mainly results from planting seed tubers infested with *P. coffeae*. But yield reductions in relation to numbers of high quality tubers produced can occur when *P. coffeae* is initially present in the soil. Soil populations of 600 *P. coffeae*/plant of *D. rotundata* can produce significant tuber damage, and 1000 nematodes/plant can cause complete deterioration and severe reduction in tuber quality. However, neither of these populations cause reduction in total weight of harvested tubers (Acosta & Ayala, 1975, 1976*a*). If seed tubers are badly affected by dry rot, they can be so weakened that sprouting does not occur (Coates-Beckford & Brathwaite, 1977).

Control measures

The control methods that have been described against *S. bradys* are, in most cases, applicable to control of *P. coffeae*. The main exception is in the use of crop rotations because of the different host range of *P. coffeae*.

Cultural

Using plant material which is free of nematodes is an effective means of controlling or reducing damage by *P. coffeae* as detailed for *S. bradys*. As with *S. bradys*, central or distal tuber pieces, which generally contain least *P. coffeae*, are recommended for propogative material (Acosta, 1974).

P. coffeae has an extremely wide and varied host range. Until it has been shown that there exist resistant crops against the yam isolates of *P. coffeae*, it is not possible to recommend any effective crop rotation practises.

Physical

The theoretical, but not always practical, control of *P. coffeae* in yam tubers can be achieved by hot water treatment similar to that for *S. bradys*. Immersion of tubers in hot water can markedly reduce tuber populations of *P. coffeae* but rarely eliminate them without damaging the tuber. Hot water at 46° to 52°C for 15 to 30 min has been recommended for control of *P. coffeae* in *D. rotundata* tubers (Acosta & Ayala, 1976*b*). Use of seed tubers with extreme dry rot should be avoided as the treatment of these is less effective. Treatments in water at 51°C for 15 to 45 minutes have also effectively suppressed populations of *P. coffeae* and dry rot in *D. rotundata* tubers as well as

increasing vine growth (Coates-Beckford *et al.*, 1978). However, hot water treatment can cause severe physiological damage (Thompson *et al.*, 1973; Coates-Beckford *et al.*, 1977).

Resistance and tolerance

It is suggested that *D. alata* cv Florido is not susceptible to attack by *P. coffeae* (or *S. bradys*) in Puerto Rico (Ayala & Acosta, 1971). *D. esculenta* is possibly less susceptible to *P. coffeae* because of its different growth habit (Bridge & Page, 1984).

Chemical

Chemical treatments of tubers prior to planting or storage have been tested for control of *P. coffeae*, but no treatment with chemicals has been found to completely eliminate nematodes from tubers.

Field treatments to control *P. coffeae* are reported to be successful but, as with *S. bradys* on yams, the economics of their use in different situations have not been determined. Aldicarb as a single application at planting at a rate of 5.4 kg a.i./ha can give 72% control of *P. coffeae* (and *Rotylenchulus* sp.) and significantly increase high quality tuber yields of *D. rotundata* in Puerto Rico. This nematicide is more effective than carbofuran and fensulfothion (Roman *et al.*, 1984*a*). Significant increases in yield of *D. rotundata* have also been obtained by a combination of foliar and seed tuber treatments with oxamyl (Roman *et al.*, 1984*b*).

Meloidogyne

The root-knot nematodes, *Meloidogyne* spp., have been found on yams in Africa (Ghana, Ivory Coast, Nigeria), Caribbean (Jamaica, Martinique, Puerto Rico, Trinidad), Pacific (Fiji, Kiribati, Niue, Papua New Guinea, Western Samoa), Brazil, Guatemala and Japan.

The species of *Meloidogyne* identified as parasites of yams are *M. arenaria, M. hapla, M. incognita* and *M. javanica*, but worldwide, *M. incognita* is the most important.

Symptoms of damage

Meloidogyne spp. cause typical knotting or galling of yam roots. In addition, nematodes parasitizing the tubers produce galls in the outer tuber tissues giving rise to abnormal, warty or knobbly tubers. In older tubers, dark necrotic spots can be observed in the outer tuber tissues surrounding individual females. Internal rotting of tubers has also been found associated with *Meloidogyne* spp. in certain yam species. Sprouting from galled tubers can be reduced or suppressed, and root proliferation from galls on tubers can occur (Schieber, 1961; Jenkins & Bird, 1962; Bridge, 1973; Kermarrec, 1974; Adesiyan & Odihirin, 1978; Nwauzor & Fawole, 1981).

Foliar symptoms on food yams are occasionally observed. Early yellowing, leaf fall and termination of vine growth have been seen on *D. rotundata* infected with *M. incognita*, but infection only rarely reduces total tuber yield of these yams (Adesiyan & Odihirin, 1978; Nwauzor & Fawole, 1981; Atu *et al.*, 1983). *M. incognita* produces obvious galling on tubers of *D. trifida* (Kermarrec, 1974). Seedlings of "medicinal" yams (*D. composita* Hemsl., *D. floribunda* Mart. et Gal., *D. spiculiflora* Hemsl.) used for the production of cortisone precursors can be severely stunted or killed by *M. arenaria* and *M. incognita*, mainly the latter, with foliar chlorosis and leaf die-back (Schieber & Lassman, 1961; Jenkins & Bird, 1962; Bruhn & Koch, 1963).

Biology and life cycle

The behaviour of *Meloidogyne* in yam roots is similar to that in other crops (Chapter 1) but in tubers there are some unusual features.

The life cycle of *M. incognita* in *D. rotundata* or *D. alata* tubers is 35 days (Nwauzor & Fawole, 1981). In *D. alata*, most nematodes are concentrated to a depth of 2 mm with none beyond the 8 mm depth; in *D. rotundata* they are concentrated at depths between 4 to 6 mm with few at 14 mm (Nwauzor & Fawole, 1981). Females and egg masses produced in tuber tissues of *D. composita, D.*

floribunda and *D. spiculiflora* become surrounded by lignified cells preventing migration of hatched juveniles into surrounding tissues and causing their death (Bruhn & Koch, 1962; Jenkins & Bird, 1962; Koch, 1975). In *D. rotundata*, a similar host reaction occurs with *M. incognita* which either kills, or decreases juvenile and egg populations in stored tubers (Bridge, 1973; Nwauzor & Fawole, 1981). *M. hapla* develops in tubers of *D. batatas*(= *D. opposita*) until eggs are produced and these only hatch when the tuber decays (Kawamura & Hirano, 1961).

Races

Host races are known in *Meloidogyne* (see Chapter 7), but it has not been determined which races, if any, are peculiar to yams. *M. incognita* race 2 is reported to infest *D. alata, D. bulbifera, D. cayenensis, D. esculenta* and *D. rotundata* in Nigeria (Atu *et al.*, 1984).

Survival and dissemination

Where *Meloidogyne* juveniles and/or eggs survive in stored tubers, they will be disseminated in propagative material. However, *Meloidogyne* species have extremely wide host ranges and damaging populations will come from field soil having survived on other weed hosts, or be introduced into yam fields on infested seedlings of other crops.

Other hosts

Susceptible yam hosts of *M. incognita* are *D. alata, D. bulbifera, D. cayenensis, D. composita, D. esculenta, D. floribunda, D. praehensilis, D. rotundata, D. spiculiflora* and *D. trifida*; hosts of *M. javanica* are *D. alata, D. opposita* and *D. rotundata*, and *D. batatas* is a host of *M. hapla*. In addition to yams, *Meloidogyne* spp., have a very wide host range.

Disease complexes

Yam tubers infested with *Meloidogyne* spp. are more prone to fungal and/or bacterial rot during storage than tubers free of the nematodes (Schieber, 1961; Schieber & Lassmann, 1961; Badra *et al.*, 1980; Nwauzor & Fawole, 1981).

Economic importance

Meloidogyne spp. adversely affect the marketable value of tubers because of the unappealing, warty appearance, and they are associated with rot of stored yams.

M. incognita completely destroyed a crop of *D. trifida* in Martinique at soil populations of 30 000 juveniles/100 g soil (Kermarrec, 1974), and in Nigeria a combination of root-knot nematodes and *S. bradys* caused the abandonment of large areas of yam farms (Adesiyan & Odihirin, 1977). *M. javanica* populations of 30 000 nematodes/plant can reduce yields of *D. opposita* by over 50% (Nishizawa, 1973). Lower populations (5000 nematodes/plant) of both *M. incognita* and *M. javanica* significantly reduce yields of *D. alata* but not of *D. cayenensis* or *D. rotundata* (Adesiyan & Odihirin, 1978). Other results suggest that reduction in yield is not the important part of nematode damage with *D. rotundata* as both relatively low and very high populations of *M. incognita* and *M. javanica* (100 000 and 156 000 eggs or juveniles/plant) do not appreciably decrease tuber weights (Acosta & Ayala, 1975; Nwauzor & Fawole, 1981; Atu *et al.*, 1983; Atu & Ogbuji, 1986).

The tuber quality as it relates to marketable value is often of primary importance in determining the economic damage caused by root-knot nematodes. The proportion of yams with galled tubers collected from yam barns and markets in Nigeria can be as high as 90% for *D. alata* and 70% for *D. rotundata* (Adesiyan & Odihirin, 1978). It is estimated that there is a reduction of 39 to 52% in the price of galled tubers compared to healthy ones (Nwauzor & Fawole, 1981). In Nigeria, the economic threshold at which control measures should be initiated is suggested to be the point at which 40% or more of tubers are galled. This is based on differences in market value between infected and healthy tubers. Experimentally, this has been shown to occur when soil populations of *M. incognita* at planting are 50 to 250 eggs/plant (Atu *et al.*, 1983).

Other losses caused by *M. incognita* and *M. javanica* in stored tubers are reduction in the edible portion (more peel has to be removed), a weight loss, and an increase in the number of rotted tubers in both *D. alata* and *D. rotundata* (Nwauzor & Fawole, 1981).

Control measures

There are a few specific control measures that can be used against root-knot nematodes, but in general many of those described above for other yam nematodes can be applied.

Cultural

The carry over of high populations of nematodes in seed tubers is not as serious a problem with *Meloidogyne* as it is with the dry rot nematodes, but it does occur (Nwauzor & Fawole, 1981) and the use of obviously galled tubers for propogative material should be avoided. Local practises need to be changed, for example, in Nigeria, where most farmers deliberately keep galled tubers for use as planting material because of the low selling price (Nwauzor & Fawole, 1981).

Crop rotation will be difficult with *Meloidogyne* spp. because of their very wide host range, but crops highly susceptible to root-knot nematodes should be excluded from a cropping system. Severe damage to yam seedlings can occur when yams are grown alongside, or immediately after, a root-knot susceptible crop (Bridge, 1982). In Nigeria, intercropping highly susceptible crops such as okra, pumpkin and yam bean (*Sphenostylis stenocarpa*) with yam increases the damage by *M. incognita* to *D. rotundata* tubers (Atu & Ogbuji, 1986).

Physical

Hot water treatment can be used to control *Meloidogyne* spp. in tubers. As before, the economics and the success of the method will depend on many factors including species and age of yam tubers, nematode densities, and depth of infestation. Dipping tubers of *D. alata, D. rotundata* and *D. floribunda* in water at 50–51°C for 30 minutes can effectively eliminate *Meloidogyne* (mainly *M. incognita*) from galled tubers (Hawley, 1956; Nwauzor & Fawole, 1981).

Resistance and tolerance

The only yam species consistently found to be resistant to attack by *M. incognita* is the cluster yam, *D. dumentorum* (Caveness, 1979; Nwauzor & Fawole, 1981; Atu *et al.*, 1984). *D. alata* cv Obunenyi is reported to be resistant to *M. incognita* in Nigeria (Atu *et al.*, 1984) and *D. cayenensis* can be resistant to *M. incognita* and *M. javanica* (Adesiyan & Odihirin, 1978; Nwauzor & Fawole, 1981) although at least two cultivars of *D. cayenensis*, Oku and Apani, are known to be susceptible to *M. incognita* (Atu *et al.*, 1984).

Chemical

In Nigeria, some farmers use carbofuran granules applied to yam planting stations at a rate of 3 kg a.i./ha to control nematodes in fields infested with *Meloidogyne* (Atu & Ogbuji, 1986). This is reported to be an economic proposition when over 40% of yam tubers are found to be galled (Atu *et al.*, 1983). Granular oxamyl at rates of 3 or 6 kg a.i./ha applied at planting and at three, four-week intervals can control *M. javanica* on *D. rotundata*. In the presence of both *M. javanica* and *Pratylenchus brachyurus*, tuber yields can be increased by over 40% when granular oxamyl at 3 kg a.i./ha applied at planting is combined with subsequent applications of calcium nitrate or ammonium sulphate incorporated at three, four-week intervals, each 60 kg N. These treatments also reduce the incidence of rot in stored yams associated with the nematodes (Badra *et al.*, 1980).

Diagnosis

Sampling and extraction of *Meloidogyne* spp. from yam roots and soil is as described in Chapter 2. Damage to tubers can be assessed by rating the number of galls or percentage area of tubers covered in galls. Population counts of juveniles hatched from eggs in the outer tuber layers can be done by

the standard methods for extraction from plant tissues. Estimating populations of females in the outer tissues requires cutting the part of the tuber to be sampled into thin slices. Nematodes can be removed manually by teasing the tissue under a microscope, or the slices can be stained in the normal way and nematodes counted directly whilst embedded in the tissues.

Other Nematode Parasites of Yams

Other species of *Pratylenchus* are known to be parasites of yam. *P. brachyurus* has been found in tubers, roots and yam soil in Nigeria (Caveness, 1967*b*), Ivory Coast (Miege, 1957), Guatemala (Jenkins & Bird, 1962), Fiji and Tonga (Bridge, 1988).

Radopholus similis has been found causing dry rot of yam tubers in Papua New Guinea. The dry rot disease is similar to that caused by *P. coffeae* and *S. bradys* but diseased tissues tend to be lighter brown in colour (Bridge & Page, 1984). *R. similis* has also been found infesting tubers in Fiji (Butler & Vilsoni, 1975) and yam roots in the Solomon Islands (Bridge, 1988).

Aphelenchoides besseyi, a foliar nematode, is known to occur in large populations in the foliage and tubers of *D. trifida* in Guadeloupe associated with drying and blackening of the foliage, and wasting and cracking of tubers with internal decay (Kermarrec & Anais, 1973).

A "black scurf-like syndrome" of Chinese yam, *D. opposita*, was shown to be caused by *Trichodorus porosus* (= *Paratrichodorus porosus*) in Japan (Nishizawa, 1973). Symptoms of the disease are blackening, cracking and corkiness of the tuber tips. The disease increases in severity with successive planting of yams. *P. porosus* also reduces weight of the tubers and greatly inhibits their elongation resulting in small rounded rather than long thin tubers.

Of the remaining nematodes associated with yams, the only other species identified as parasites of yam roots or tubers are *Rotylenchulus reniformis, Scutellonema clathricaudatum* and *Helicotylenchus dihystera*.

Taro

Taro (*Colocasia esculenta* (L.)Schott.), also known as cocoyam, dasheen and eddoe, is grown throughout the tropics, subtropics and warmer regions of the temperate zone. It is mostly a staple food or subsistence crop but is grown commercially in some countries. There are two botanical varieties of *Colocasia*, the "eddoe type" *C. esculenta* var. *antiquorum* which has a relatively small corm surrounded by large well developed cormels; and the "dasheen type" *C. esculenta* var. *esculenta* which has a large central corm and numerous but small cormels. They can be grown in dry upland or flooded areas depending on the type and cultivar. They grow best with daily average temperatures of 20°C–27°C and rainfall of 2500 mm per annum or more (Purseglove, 1972; Kay, 1987).

Taros are propagated vegetatively using whole corms or cormels, pieces of corms or the leaf bearing tops of mature corms (the lower 30–50 cm of the petiole with the top 1–2 cm of the corms). They can be grown in flat wet areas, steep hillsides where rainfall is sufficient, or in "patches" or pits in swampy areas (Purseglove, 1972; Kay, 1987).

Nematodes of Taro

The nematodes known to be damaging parasites of taro are *Meloidogyne* spp., *Hirschmanniella miticausa* and *Pratylenchus coffeae*. Other nematodes found associated with tissue damage or present in high populations on the crop are *Radopholus* sp. and *Rotylenchulus reniformis*.

Meloidogyne

The root-knot nematodes, *Meloidogyne* spp. (*M. incognita, M. javanica* and *M. arenaria*) have been reported on *Colocasia* from Cuba (Lorenzo & Fernandez, 1982), Puerto Rico (Ayala, 1969), Trinidad

(Brathwaite, 1972*a*), Florida (Byars, 1917; McSorley, 1983), Hawaii (Parris, 1940), East Africa (Whitehead, 1969), Nigeria (Caveness, 1967), Philippines (Timm, 1965), Papua New Guinea (Bridge & Page, 1984), Niue, Western Samoa, Tonga, Fiji (Orton Williams, 1980; Fliege & Sikora, 1981) and Solomon Islands (Gowen, 1985), Taiwan (Huang *et al.*, 1972), Egypt (Byars, 1917) and from India (Nirula, 1959).

Symptoms of damage

Both *M. incognita* and *M. javanica* can cause galling of roots and corms. On young feeder roots galls are small and irregular. Infested older roots become thickened with large swellings although the symptoms are not always obvious. On corms, nematodes cause blister like swellings which later become large round or oblong galls, 2–15 mm in diameter, deforming the corms. Such infested corms are known to rot in storage. Nematodes can be present in yellow areas of variable size internally even though external symptoms are not present on the corms. The above-ground symptoms occur in patches in the field. Affected plants are stunted and unhealthy with yellowed leaves which can turn brown and die (Nirula, 1959; Srivastava *et al.*, 1971; Brathwaite, 1972; Lorenzo & Fernandez, 1982)

Survival and means of dissemination

Meloidogyne spp. can be carried over from one *Colocasia* crop to the next in the wide range of other host crops and weeds. As the nematodes feed and reproduce in corm tissues, they can be disseminated in corms and cormels if infested material is used for propagation.

Environmental factors affecting parasitism

Root-knot nematodes are especially serious on the eddoe type or upland taro, *C. esculenta* var. *antiquorum*; *Meloidogyne* populations could be suppressed when taro is grown in very wet or flooded conditions (McSorley *et al.*, 1983).

Economic importance

Losses caused by *Meloidogyne* have been described as severe in India where local farmers have in the past had to abandon cultivation of *Colocasia* because of the nematodes (Srivastava *et al.*, 1969). It is suggested that *Colocasia* (and *Xanthosoma*) are more tolerant of *M. incognita* than other crops and high preplant populations of the nematode have to be present in field soil for damage to occur (McSorley *et al.*, 1983). The malformation of corms due to galling reduces their marketable value (Srivastava *et al.*, 1971).

Control measures

Information on control of *Meloidogyne* on taro is limited and the economics of any measures taken have not been reported.

Use of nematode-free planting material will prevent dissemination into the field; seed corms or cormels should be free of any external symptoms of root-knot damage. Selecting planting material from land with no previous records of nematode attack will reduce the risk of damage. Root-knot can be controlled in corms by dipping in hot water at 50°C for 40 minutes (Byars, 1917) but this is unlikely to be an economic measure for large scale farming.

Most root-knot damage to taro is likely to occur if the crop is grown in field soils with high populations of *Meloidogyne* present. Planting taro intercropped with, or after, susceptible crops should be avoided.

The number of contradictory reports on damage, by *Meloidogyne* may be due to the different host reactions of the many taro cultivars that are grown worldwide (McSorley *et al.*, 1983). One cultivar, "Dodare" in Japan, was found to be completely resistant to both *M. incognita* and *M. javanica* (Inagaki, 1981), while cultivar "Samra" in Fiji is described as moderately susceptible to these two species (Kirby, 1977).

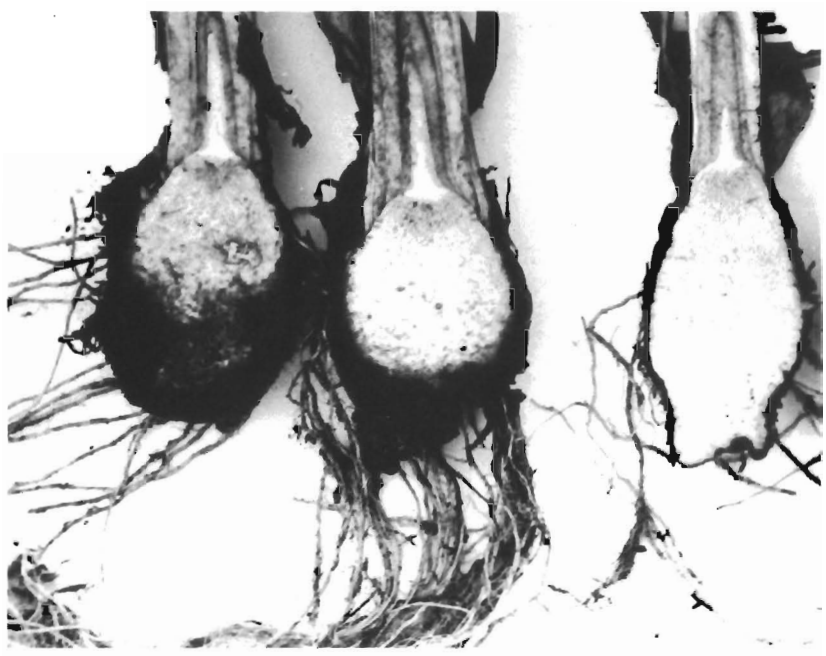

Fig. 9. Miti miti disease of taro *(Colocasia esculenta)* corms caused by *Hirschmanniella miticausa* (left) plus secondary rot (Bridge et al., 1983).

Diagnosis

Standard methods for the extraction of nematodes from soil and roots can be used (Chapter 2). Assessing *Meloidogyne* populations in corms and the damage they cause can be done in a similar way to that used for yam tubers.

Hirschmanniella miticausa

H. miticausa is the causal organism of a taro corm rot disease known as "miti-miti" in the Solomon Islands. The disease and nematode have been reported from four islands in the Solomon Islands group (Mortimer *et al.*, 1981) and the highlands of Papua New Guinea (Bridge & Page, 1984). A *Hirschmanniella* sp. has also been recorded associated with taro in Taiwan (Huang *et al.*, 1972).

Symptoms of damage

The initial foliar symptoms of miti-miti disease are wilting of the older leaves, which eventually become chlorotic, while the new central leaf, instead of bending, remains straight. Taro plants with the disease die prematurely as a result of corm damage.

Corms with the disease, cut longitudinally, at first show red streaks radiating from the base of the corm. These later become irregular, 1–10 mm wide, zones of dry brown rot with the advancing diseased tissues remaining red (Plate 3G). The basal portions of severely diseased corms are often completely decayed due to a brown soft rot (Fig. 9). The numbers of cormels are reduced in plants with the disease (Mortimer *et al.*, 1981; Bridge *et al.*, 1983).

Biology

H. miticausa is a migratory endoparasite. In growing taro plants, highest populations occur in the corms with less in roots and relatively few in surrounding soil. Nematodes are found in, or immediately around, red necrotic tissues of the corm in the basal portion (Fig. 10); relatively small numbers

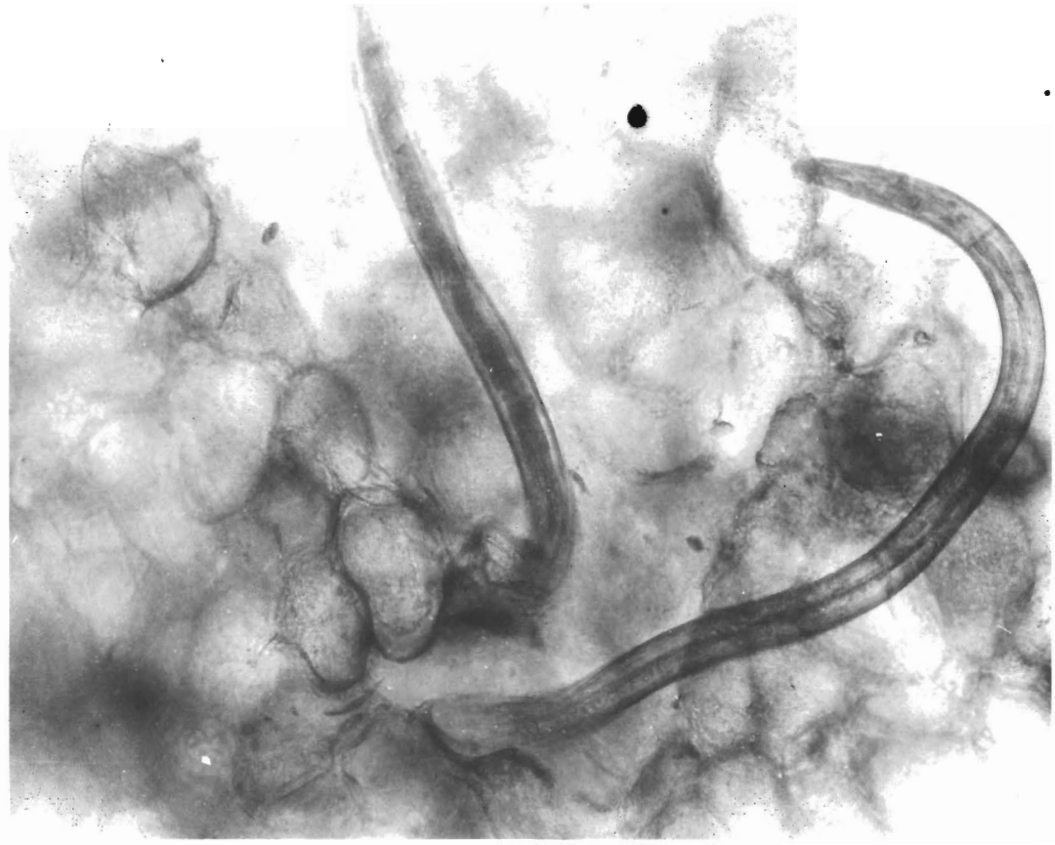

Fig. 10. *Hirschmanniella miticausa* in diseased tissue of taro corm (Bridge, et al., 1983).

occur in the white centre tissues, and nematodes are rarely found in the crown (the top 1 cm). Numbers of nematodes commonly exceed 1000/10 g and can be over 3000/10 g of corm tissue.

The nematode is disseminated in diseased corm planting material. Other hosts are not known but the nematode probably can survive for some period of time in field soil without hosts. It is found causing miti-miti disease of taro in dryland soils, rainfed mountain slopes and in flooded swamp pits.

Disease complexes

Nematode activity in corm tissues probably predisposes the corms to invasion of secondary pathogens causing the extensive outer, soft rot invariably associated with the disease. Fungi isolated from areas of soft rot in corms with miti-miti are *Corticum solani, Pythium vexans, Fusarium solani* and *F. oxysporum* (Bridge *et al.*, 1983).

Economic importance

Miti-miti disease renders taro corms inedible and, when severe, can destroy almost all consumable corm tissues of the crop. In parts of the Solomon Islands, the disease is so devastating that taro cultivation has been almost entirely abandoned particularly where continuous cultivation has occurred in swamp pits (Patel *et al.*, 1984).

Control measures

The disease is at present restricted to those areas of the Pacific where taro is a subsistence crop. This limits the control measures that can be recommended, particularly the use of expensive nematicides.

Planting material infested with *H. miticausa* is the main source of inoculum in new land. Nematodes can be eliminated from normal planting material (corm top and 40 cm of leaf base) by immersing in hot water at 50°C for 15 minutes without damaging the tissues (Mortimer *et al.*, 1981). Because of the difficulties of treatment it cannot be generally recommended to taro growers, but it could be used to establish a source of nematode-free planting material.

The most practical measure for small growers is to completely remove all nematodes from planting material manually. Nematodes rarely occur in the top few cms of the corm. Trimming the corm top back to white, healthy tissues will ensure that most, if not all, planting material is free of nematodes (Mortimer *et al.*, 1981). Planting corms or cormels, as compared to corm tops, will increase the risk of spreading nematodes.

Where taro is grown on hillsides, there is a risk of nematodes being carried downhill in run-off water. This can be avoided by making new plantings uphill from old taro gardens (Mortimer *et al.*, 1981).

These hygiene measures cannot be used in areas where there is intensive and continuous taro production such as in swamp pits in parts of the Solomon Islands. Where this occurs the only practical solution is the use of resistant cultivars. One such resistant cultivar has been identified, a taro that occurs wild and is used only when other foods are scarce, and crosses between this taro and high yielding cultivars are possible (Patel *et al.*, 1984).

Diagnosis

H. miticausa is a large nematode and is most efficiently extracted from soil by a sieving and sedimentation method (Chapter 2). But, as most nematodes are found in plant tissues, their extraction from corms will give the most accurate assessment of their presence and population levels using a standard tissue extraction method.

Pratylenchus coffeae

The lesion nematode, *P. coffeae*, has been found parasitic on taro in Papua New Guinea (Bridge & Page, 1984), Fiji (Kirby *et al.*, 1980; Orton Williams, 1980), Solomon Islands (Mortimer *et al.*, 1981) and in the warmer parts of Japan (Inagaki, 1985). However, it is reported causing injury to taro only in Japan (Nishizawa & Ohshima, 1972; Oashi, 1984; Inagaki, 1985).

Symptoms of damage

P. coffeae has consistently been found to be associated with a disease of taro in Japan causing poor plant growth, root decay and reduced number of cormels. Two months after planting, roots turn brown and then rot. This is followed by stunted top growth and, in serious cases, withering and death of the leaves five months after planting. The disease is most commonly seen in fields with continuous taro cultivation (Oashi, 1984). In Papua New Guinea, *P. coffeae* causes localised necrosis of root and corm tissues (Bridge & Page, 1984).

Biology

All stages of *P. coffeae* are found in roots, corms, and in soil around taro. Highest populations occur in roots and soil, with less in the "skin" of the corms (Oashi, 1984).

Economic importance

Field trials have shown that, by controlling *P. coffeae* in seed corms and field soil, yields of corms can be increased three-fold. The most serious damage and highest nematode populations occur

where taro is cultivated continuously, although there is a suggestion that nematodes may not be the only cause of problems with continuous taro cultivation (Oashi, 1984).

Control measures

The suggested control measures against *P. coffeae* on taro include disinfection of seed corms, reduction of soil populations and crop rotation (Oashi, 1984).

It is recommended that seed corms are selected from healthy parent plants and all roots are removed before planting. In Japan, nematodes can be eliminated from corms by soaking in a disinfectant ("cartap aqueous solution") for 30 minutes, but chemical residues may be a problem.

Lowest populations of *P. coffeae* are found in soils that have previously been flooded and planting taro in rice paddy field soil compared to dry, upland soil reduces the risk of damage. Combining disinfection of the seed corms with cultivation in paddy soil can almost eliminate nematodes from the crop, increasing corm germination and yields.

In Japan, taro is a comparatively low income crop and the use of nematicides is thought to be uneconomic. Crop rotation is considered a more appropriate control measure. Soil populations of *P. coffeae* are decreased in land planted to peanut, marigold and *Stevia rabaudiana* Cav., but the nematodes increase to large numbers as soon as taro is cultivated. It is recommended that a rotation of two or more years between taro crops is necessary (Oashi, 1984).

Diagnosis

Determining the presence of nematodes in association with diseased plants will require sampling and extraction from soil and plant tissues. It will not always be possible to obtain a direct association between visible root damage symptoms and nematode numbers as *P. coffeae* can be found in superficially healthy, white roots (Oashi, 1984).

Other Nematodes of Taro

Rotylenchulus reniformis, has been recorded associated with *Colocasia* in Puerto Rico (Ayala, 1969), Taiwan (Huang *et al.*, 1972), Fiji, Western Samoa, Solomon Islands, Tonga (Orton Williams, 1980; Fliege & Sikora, 1981), and Florida. Although high population levels of *R. reniformis* (1767 nematodes/100 cm^3 of soil) can be found with *Colocasia*, no affect on yield was noted in Florida (McSorley *et al.*, 1983).

An undescribed *Radopholus* sp. is reported from necrotic tissues of taro corms and roots in Papua New Guinea (Bridge & Page, 1984). *Radopholus* spp. have been found associated with taro in Fiji, Tonga and Western Samoa (Kirby *et al.*, 1980; Orton Williams, 1980).

Aphelenchoides besseyi is recorded in large numbers from taro corms with rot (Bridge & Page, 1984).

Xanthosoma

There are about 40 species of *Xanthosoma* with the common names of tannia, tanier, yautia, malanga and new cocoyam. They can be confused with the genus *Colocasia* because of their similar botany but are distinguished by their different leaves.

Xanthosoma is native of tropical America but has spread widely throughout the tropical world. Some species are grown for their edible tubers or leaves; others can be grown for their ornamental foliage. The most widely grown edible species is *X. sagittifolium* (L.) Schott., others are *X. atrovirens* Koch & Bouché, *X. violaceum* Schott, *X. caracu* Koch & Bouché, and *X. brasiliense* Engl. They can grow to a height of 2 m. A corm is produced which bears up to 10 or more lateral cormels (Purseglove, 1972; Kay, 1987).

Tannias are propogated vegetatively from pieces of main corm, cormels, or tops of main corm plus 20–30 cm of leaves. They can be grown in pure stands but are more often intercropped with

tree crops and other plants. They require well-drained soils and cannot withstand waterlogging, and prefer an average annual rainfall of 140–200 cm (Purseglove, 1972; Kay, 1987).

Nematodes of Xanthosoma

Comparatively little information is available on the importance of nematodes associated with *Xanthosoma*. Only *Meloidogyne* spp., *Rotylenchulus reniformis* and *Pratylenchus coffeae* are reported to cause damage to the crop.

Meloidogyne

Three species of *Meloidogyne* have been found with *Xanthosoma; M. arenaria* is reported from Cuba (Decker & Casamayor, 1966); *M. incognita* from Puerto Rico (Roman, 1978), Nigeria (Caveness *et al.*, 1981), Cuba (Decker & Casamayor, 1966) and Papua New Guinea (Bridge & Page, 1984); and *M. javanica* from Fiji and Tonga (Orton Williams, 1980), Colombia (Nacarro & Barriga, 1975), and Florida, USA (McSorley *et al.*, 1983). *Meloidogyne* spp. are also reported on tannia from Kiribate and Western Samoa in the Pacific (Orton Williams, 1980) and from Trinidad (Brathwaite, 1972).

M. incognita has been found in high populations causing galling and roughening of the surface of *Xanthosoma* corms (Acosta, 1979). Similarly *M. javanica* can cause obvious corm damage (Orton Williams, 1980). *M. arenaria* has been shown to cause severe galling and malformation of *X. sagittifolium* corms (Decker & Casamayor, 1966). *Meloidogyne* has also been reported in association with stunting and yellowing of *Xanthosoma* plants with nematode galls localised at root tips (Roman, 1978). However, most findings suggest that *Xanthosoma* spp. are generally tolerant of *Meloidogyne* except when preplant populations are high (McSorley *et al.*, 1983). Initial soil populations of 5000 *M. incognita* juveniles/litre of soil can reduce corm weight of *X. sagittifolium* but nematode populations decline to only 14/litre of soil at harvest suggesting that the crop is a very poor host (Caveness *et al.*, 1981).

It has been suggested that *M. incognita* is involved in a *Xanthosoma* root rot disease in Papua New Guinea (Bridge & Page, 1984).

Rotylenchulus reniformis

The reniform nematode, *R. reniformis* is reported on *Xanthosoma* spp., sometimes in high populations, in the Pacific islands of Fiji, Kiribati, Western Samoa, Tonga (Orton Williams, 1980) and Papua New Guinea (Bridge & Page, 1984), also from Puerto Rico (Ayala & Ramirez, 1964), Trinidad (Brathwaite, 1972*b*) and Florida (McSorley *et al.*, 1983).

Soil populations of 400 *R. reniformis*/100 cm^3 of soil can cause reduction in root weight and a 26% reduction in dry weight of marketable cormels of *X. caracu*. The same population levels did not affect yield of *X. atrovirens* (McSorley *et al.*, 1983). Populations of 100–1000 nematodes/100 cm^3 of soil have been found associated with small root lesions on *X. sagittifolium* (Brathwaite, 1972*b*). In Fiji, *R. reniformis* occurred in 80% of *X. sagittifolium* plantings (Orton Williams, 1980), but tannia was a non-host for the nematode in a host range trial (Vilsoni & Heinlein, 1982).

The amount and type of damage caused by *R. reniformis* will depend on the species and cultivars of *Xanthosoma*, as well as populations of the nematode present in the soil. Nematode control has been recommended only in sites heavily infested by *R. reniformis* but not where populations are low (McSorley *et al.*, 1983).

Pratylenchus

Pratylenchus spp., have been recorded on *X. violaceum* in Honduras (Pinochet & Ventura, 1980) and on *X. sagittifolium* in Fiji, Tonga and Western Samoa (Orton Williams, 1980). In Fiji, *P. coffeae*

was found associated with 50% of *Xanthosoma* plants examined, occasionally present in the outer corm layers in areas around the margin of blackened, rotted tissue.

Other Root and Tuber Crops

There are over 27 species of minor root and tuber crops that are of local importance in several tropical and subtropical regions of the world (Kay, 1987). Nematological information is not available for most of these crops. Those crops on which some nematological investigations have been done are giant taro (*Alocasia* spp.), giant swamp taro (*Cyrtosperma chamissonis*), Chinese water chestnut (*Eleocharis dulcis*), and crops in certain tropical regions of Central and South America, oca. *Oxalis tuberosa*, olluco, *Ullucus tuberosus*, arracacha, *Arracacia xanthorrhiza*, and mashua, *Tropaeolum tuberosum*, which constitute the basic diet of the population.

Giant Taro

Giant taros (*Alocasia* spp.) are grown for their large edible corms. The most common species is *A. macrorrhiza* (L.) G.Don.

A number of plant parasitic nematodes have been isolated from around *Alocasia* plants, but there is no information on their importance. Most records come from the Pacific (Orton Williams, 1980). Two species of *Meloidogyne*, *M. javanica* and *M. arenaria*, are reported causing root galls on *Alocasia* sp. in southern Africa (Martin, 1969).

Swamp Taro

The swamp taro, *Cyrtosperma chamissonis* (Schott) Merr., is a crop of the Pacific grown in flooded swamp land for its large edible corms.

There are very few records of plant parasitic nematodes associated with *Cyrtosperma*. *Criconemella denoudeni, C. onoensis, Helicotylenchus dihystera, Meloidogyne* sp., and *Pratylenchus coffeae* have been found around plants in Fiji (Orton Williams, 1980). However, there is now strong evidence that a corm rot of swamp taro is caused by the burrowing nematode, *Radopholus similis*, in the Pacific islands of Yap, Palau and Guam (Jackson, 1987). *R. similis* has been consistently isolated from roots and corms with the disease. Corms have small shallow holes, no more than 1–2 cm deep for the most part, except in severe instances when the entire basal part of the corm is decayed. Beneath these the rot is brown and superficial but sometimes extending as narrow channels deep into the centre of the corm (Jackson, pers. comm.).

Chinese Water Chestnut

Chinese water chestnut (*Eleocharis dulcis* Burm.f.Trin.ex Hensch) is commercially cultivated in S.E. Asia, Pacific and southern USA for its edible corms. *Dolichodorus heterocephalus*, the awl nematode, is reported to reduce growth of the crop in the USA (Tarjan, 1952).

Oca and Olluco

Oca, *Oxalis tuberosa* Molina, is an important crop of the cold areas of the Andes, grown at elevations of over 3000 m from Bolivia to Venezuela as a minor crop, considered of less importance than potato, but more important than olluco. There are several kinds of oca: the bitter, which has white tubers; and the sweet, with tubers of various colours. Because of high content of calcium oxalate in the tubers, they can only be eaten after days of exposure to sun.

Olluco, *Ullucus tuberosus* Caldas, is endemic to the Andes and constitutes one of the staple food

crops in the region from Bolivia to Colombia and is an important crop after potato and oca. Tubers vary in shape and colour. As in potatoes and oca, they are often dehydrated and made into chuno (frozen, thawed and dehydrated). It replaces potatoes in certain zones of the cold altiplano where the excess of humidity becomes a limiting factor to potato production.

Several nematode species are known to be associated with oca and olluco (Jatala, 1989). *Thecavermiculatus andinus* and *Nacobbus aberrans* are quite widely distributed in the areas of oca and olluco cultivation (Aztocaza Perez, 1980; Jatala, 1989). Although roots of these crops are severely infected by *T. andinus* and *N. aberrans*, the economic importance of these nematodes as production constraints is not well known. Reactions of these crops to *T. andinus* and *N. aberrans* indicate the possibility of an availabe resistant gene base. *Meloidogyne* species are often found in association with *T. andinus* and *N. aberrans* on the roots of these crops. This nematode, however, does not constitute a major concern in production. Because of the fact that these are primarily small farm crops with limited economic input for production, chemical control of nematodes is not practised.

Arracacha

Arracacha, *Arracacia xanthorrhiza* DC, is a perennial herb, native of areas from Mexico to Peru. Its fleshy tubers have an agreeable flavour which constitute an important food item amongst the people of Central America and the Andean regions of South America. From the Andean region of South America, its centre of origin, it was successfully introduced to mountainous regions of Brazil and Central America and recently, to India and eastern Africa. Colombia is, however, probably the largest producer of this crop.

Of the nematode species attacking arracacha, *Meloidogyne* spp. are of major importance. Severe and early root infection inhibits the development of tubers. Infected plants exhibit general symptoms of stunting, yellowing, and tendency to wilt readily during the hot and dry period (Jatala, unpubl.). In Brazil, both roots and tubers of arracacha (mandioquinha salsa) can be severely infested by *M. hapla* and *M. incognita* (Plate 3H). Lesion nematodes, identified as *Pratylenchus penetrans*, also cause necrosis of these organs. Suggested control is by nursery soil treatment and the use of nematode-free planting material (Lordello, 1981).

Mashua

Mashua or añu, *Tropaeolum tuberosum* Ruiz & Pav., probably originated in the altiplano zones of Peru and Bolivia. It is an annual crop that produces cone-shaped tubers similar to oca in form and colour. It is the least popular of the tubers and root crops of the region. The tubers are not palatable when eaten raw. They must be cured by the sun prior to cooking. They are also dehydrated to form chuno, as in potatoes, oca, and olluco.

Of the nematode species attacking this crop, *Nacobbus aberrans* and *Meloidogyne* spp. are of major importance, and *N. aberrans* can become a limiting factor to production (Jatala, 1989). However, its economic damage to mashua production has not been documented throughout the range of its production.

Although chemicals are successful in controlling the nematodes, the fact that mashua is a small farm crop with minimal economic input means that no control measures are taken to reduce nematode attack.

Conclusions

In general, tuber and root crops constitute the major food source for a great part of the world's population. Assessment of nematode damage to minor tuber and root crops and their economic

importance in production systems needs to receive greater attention. Although some tuber and root crops are the basic staple diet of the majority of the world population, nematological information regarding these crops is lacking. Similarly, a better understanding of the importance of several minor tuber and root crops and their utilization in the cropping systems may alleviate some of the food shortage experienced in many developing countries.

References

Acosta. N. (1974). Depth penetration of phytoparasitic nematodes in yam tubers. *Nematropica*, 4:7–11.

Acosta, N. (1979). *Meloidogyne incognita* in tanier corms in Puerto Rico. *Organization of Tropical American Nematologists Newsletter*, 11 (1):14.

Acosta, N. & Ayala, A. (1975). Pathogenicity of *Pratylenchus coffeae, Scutellonema bradys, Meloidogyne incognita* and *Rotylenchus reniformis* on *Dioscorea rotundata. Journal of Nematology*, 7:1–6.

Acosta, N. & Ayala, A. (1976*a*). Effects of *Pratylenchus coffeae* and *Scutellonema bradys* alone and in combination on Guinea yam (*Dioscorea rotundata*). *Journal of Nematology*, 8:315–317.

Acosta, N. & Ayala, A. (1976*b*). Hot water and chemical dips for nematode control in tubers of *Dioscorea rotundata. Journal of Agriculture of the University of Puerto Rico*, 60:395–402.

Adeniji, M. O. (1970). Fungi associated with storage decay of yam in Nigeria. *Phytopathology*, 60:590–592.

Adesiyan, S. O. (1976). Host range studies of the yam nematode, *Scutellonema bradys. Nematropica*, 6:60–63.

Adesiyan, S. O. (1977). Penetration and multiplication of *Scutellonema bradys* in yams (*Dioscorea* spp.). *Nematologia mediterranea*, 5:313–317.

Adesiyan, S. O. & Adeniji, M. O. (1976). Studies on some aspects of yam nematode (*Scutellonema bradys*). *Ghana Journal of Agricultural Science*, 9:131–136.

Adesiyan, S. O. & Badra, T. (1982). Granular nematicides for control of the yam nematode, *Scutellonema bradys*, and relevant residues in raw tubers. *Journal of Nematology*, 14:213–216.

Adesiyan, S. O. & Odihirin, R. A. (1977). Plant parasitic nematodes associated with yam tubers in Mid-West State, Nigeria. *Nigerian Journal of Plant Protection*, 3:178–179.

Adesiyan, S. O. & Odihirin, R. A. (1978). Root knot nematodes as pests of yams (*Dioscorea* spp.) in southern Nigeria. *Nematologica*, 24:132–134.

Adesiyan, S. O., Odihirin, R. A. & Adeniji, M. O. (1975*a*). Histopathology studies of the yam tuber (*Dioscorea rotundata* Poir) infected with *Scutellonema bradys* (Steiner & Le Hew). *International Biodeterioration Bulletin*, 11:48–55.

Adesiyan, S. O., Odihirin, R. A. & Adeniji, M. O. (1975*b*). Economic losses caused by the yam nematode, *Scutellonema bradys*, in Nigeria. *Plant Disease Reporter*, 59:477–480.

Alexander, J. & Coursey, D. G. (1969). The domestication of the yams. In: Ucko, P. J. & Dimbleby, C. W. (Eds). *The domestication and exploitation of plants and animals*. Gerald Duckworth, London: 405–425.

Anon. (1964). Nematode control trials with yam. *Annual Report for the Ministry of Agriculture Nigeria for 1962–63*.

Atu, U. G., Odurukwe, S. O. & Ogbuji, R. O. (1983). Root-knot nematode damage to *Dioscorea rotundata. Plant Disease*, 67:814–815.

Atu, U. G. & Ogbuji, R. O. (1986). Root-knot nematode problems with intercropped yam (*Dioscorea rotundata*). *Phytoprotection*, 67:35–38.

Atu, U. G., Okoli, O. O. & Ogbuji, R. O. (1984). Reactions of yams (*Dioscorea* spp.) to *Meloidogyne incognita* race 2. *International Nematology Network Newsletter*, 1:10–12.

Ayala, A. (1969). Nematode problems in Puerto Rican agriculture. In: Abad-Ramos, J. (Ed.) *Proceedings of the Symposium on Tropical Nematology*. Agricultural Experimental Station, University of Puerto Rico: 135–145.

Ayala, A. & Acosta, N. (1971). Observations on yam (*Dioscorea alata*) nematodes. *Nematropica*, 1:39–40.

Ayala, A. & Ramirez, C. T. (1964). Host-range, distribution and bibliography of the reniform nematode,

Rotylenchulus reniformis, with special reference to Puerto Rico. *Journal of Agriculture of the University of Puerto Rico*, 48:140–161.

Aztocaza Perez, E. P. (1981). *Nematodo esférico atacando cultivos andinos en el Perú*. M. S. Thesis, Universidad Nacional Agraria, La Molina, Lima, Peru. 95p.

Badra, T. & Caveness, F. E. (1979). Chemotherapy of *Dioscorea alata* for disinfestation of *Scutellonema bradys*. *Nematropica*, 9:135–137.

Badra, T., Steele, W. M. & Caveness, F. E. (1980). The employment of a non-fumigant nematicide for control of root-knot and lesion nematodes on yams and crop preservation in storage. *Nematropica*, 10:81–85.

Baudin, P. (1956). Les maladies parasitaire des ignames en Côte d'Ivoire. *Revue de Mycologie*, Paris 21 Supplement colon No. 2:87–111.

Belliard, A. & Kermarrec, A. (1978). Présence du nématode de l'igname (*Scutellonema bradys*) dans les tubercules de *Dioscorea trifida* en Republique Dominicaine. *Nouvelles Agronomiques des Antilles et de la Guyane*, 4:49–51.

Birchfield, W. & Martin, W. J. (1965). Effects of reniform nematode populations on sweet potato yields. *Phytopathology*, 55:497.

Birchfield, W. & Martin, W. J. (1968). Evaluation of nematicides for controlling reniform nematodes in sweet potatoes. *Plant Disease Reporter*, 52:127–131.

Bird, G. W., Crawford, J. L & McGlohon, N. E. (1973). Distribution, frequency of occurrence and population dynamics of *Rotylenchulus reniformis* in Georgia. *Plant Disease Reporter*, 57:399–401.

Brathwaite, C. W. D. (1972*a*). *Colocasia esculenta* a new host of *Meloidogyne incognita* in Trinidad. *Plant Disease Reporter*, 56:618.

Brathwaite, C. W. D. (1972*b*). Preliminary studies of plant parasitic nematodes associated with selected crops at the University of the West Indies. *Plant Disease Reporter*, 56:1077–1079.

Brathwaite, C. W. D. (1977*a*). Outbreaks and new records in Barbados. *FAO Plant Protection Bulletin*, 25:210.

Brathwaite, C. W. D. (1977*b*). The response of sweet potato to nematode infection. *Newsletter International Society Tropical root Crops*, 10:32–38.

Bridge, J. (1972). Nematode problems with yams (*Dioscorea* spp.) in Nigeria. *PANS*, 1:89–91.

Bridge, J. (1973). Nematodes as pests of yams in Nigeria. *Mededelingen Faculteit Landbouwwetenschappen Gent*, 38:841–852.

Bridge, J. (1975). Hot water treatment to control plant parasitic nematodes of tropical crops. *Mededelingen Faculteit Landbouwwetenschappen Gent*, 40:249–259.

Bridge, J. (1982). Nematodes of yams. In: Miege, J. & Lyonga, S. N. (Eds.). *Yams. Ignames* Clarendon Press, Oxford: 253–264.

Bridge, J. (1988). Plant-parasitic nematode problems in the Pacific islands. *Journal of Nematology*, 20:173–183.

Bridge, J. & Page, S. L. J. (1984). Plant nematode pests of crops in Papua New Guinea. *Journal of Plant Protection in the Tropics*, 1:99–109.

Bridge, J., Mortimer, J. J. & Jackson, G. V. H. (1983). *Hirschmanniella miticausa* n.sp. (Nématoda: Pratylenchidae) and its pathogenicity on taro (*Colocasia esculenta*). *Revue de Nématologie*, 6:285–290.

Brown, E. B. (1969). Assessment of the damage caused to potatoes by potato cyst eelworm, *Heterodera rostochiensis* Woll. *Annals of Applied Biology*, 63:493–502.

Brucher, H. (1960). Über das Wild-Vorkommen des Nematoden *Heterodera rostochiensis* in Nord-Argentinien. *Die Naturwissenschaften*, 47:21–22.

Bruhn, C. & Koch, W. (1962). Beobachtungen über den Befall mittelamerikanischer Dioscoreenarten durch *Meloidogyne incognita* (Kofoid & White). *Nematologica*, 8:307–312.

Bruhn, C. & Koch, W. (1963). Control of root-knot nematodes in *Dioscorea* tubers. *Phytopathology*, 53:24.

Burk, E. F. & Tennyson, G. (1941). Hot water treatment for control of nematodes in sweetpotato seed roots. *Proceedings of the American Society for Horticultural Science*, 39:299–302.

Burton, W. G. (1966). In: Veeman, N. and Zonen, N. V. (Eds.). *The potato, a survey of its history and of factors influencing its yield, nutritive value, quality, and storage*. 2nd. ed. Holland.

Butler, L. & Vilsoni, F. (1975). Potential hosts of the burrowing nematode in Fiji. *Fiji Agricultural Journal*, 37:38–39.

Byars, L. P. (1917). A nematode disease of the dasheen and its control by hot water treatment. *Phytopathology*, 7:66.

Canto-Saenz, M. & Mayer de Scurrah, M. (1978). Races of potato cyst nematode in the Andean region and a new system of classification. *Nematologica*, 23:340–349.

Castagnone-Sereno, P. & Kermarrec, A. (1988). Association between *Pratylenchus coffeae* and *Scutellonema bradys* in yam tubers under agronomic conditions in the French West Indies. *Nematropica*, 18:155–157.

Caveness, F. E. (1967*a*). Shadehouse host ranges of some Nigerian nematodes. *Plant Disease Reporter*, 51:115–119.

Caveness, F. E. (1967*b*). *Nematology studies 1960–1965*. End of tour progress report. Ministry of Agriculture and Natural Resources, Nigeria, 135 p.

Caveness, F. E. (1980). Plant parasitic nematodes on cassava. In: Ezumah. H. C., (Ed.) *Proceedings of the Workshop on Cassava Production and Extension in Central Africa*, Mbanza-Ngungu, Zaire. International Institute of Tropical Agriculture, 4:83–106.

Caveness, F. E., Wilson, J. E. & Terry, R. (1981). Root-knot nematodes on tannia (*Xanthosoma sagittifolium*). *Nematologia mediterranea*, 9:201–203.

Clark, C. A. & Wright, V. L. (1983). Effect and reproduction of *Rotylenchulus reniformis* on sweet potato selections. *Journal of Nematology*, 15:197–203.

Clark, C. A., Birchfield, W., Yik, C. P. & Boniol, D. P. (1980). Application rates and methods for Nemacur 3SC for nematode control on sweet potato, 1979. *Fungicide and Nematicide Tests*, 35:222.

Coates-Beckford, P. L. & Brathwaite, C. W. D. (1977). Comparison of various treatments for the control of *Pratylenchus coffeae* in yam. *Nematropica*, 7:20–26.

Coates-Beckford, P. L., Hutton, D. G. & Jones, A. G. (1978). Effect of various treatments for the control of nematodes in the initial growth of yam. *Nematropica*, 8:6–7.

Cole, C. S. & Howard, H. W. (1966). The effects on a population of potato-root eelworm (*Heterodera rostochiensis*) of growing potatoes resistant to pathotype B. *Annals of applied Biology*, 58:487–495.

Coursey, D. G. (1967). *Yams*. Longmans, London 230p.

Coursey, D. G. & Booth, R. H. (1977). Root and tuber crops. In: Leakey, C. L. A. & Willis, J. B. (Eds.) *Food Crops of the Lowland Tropics*. England, Oxford University Press: 75–96.

Coursey, D. G. & Haynes, P. H. (1970). Root crops and their potential as food in the tropics. *World Crops*, 22:261–265.

Decker, H. & Casamayor, G. R. (1966). Algunas, observaciones sobre la presencia de nemátodos formadores de agallas en las raices (*Meloidogyne* spp.) en Cuba. *CENTRO, Boletin de Ciencias y Tecnologia de la Universidad Central de las Villas, Cuba*, 2:19–29.

Decker, H., Casamayor, G. R. & Bosch, D. (1967). Observaciones sobre la presencia del nemátodo *Scutellonema bradys* en al tuberculo de ñame en la provincia de Oriente (Cuba). *CENTRO, Boletin de Ciencias Tecnología de la Universidad Central de Las Villas*, 2:67–70.

Demeaux, M., Babacauh, K. D. & Vivier, P. (1982). Problèmes posés par la conservation des ignames en Cote d'Ivoire et essais de techniques pour les résoudre. In: Miège, J. & Lyonga, S. N. (Eds.). *Yams. Ignames*. Clarendon Press, Oxford: 320–328.

Dunn, R. A. (1973). Resistance in potato (*Solanum tuberosum*) to *Pratylenchus penetrans*. *International Congress of Plant Pathology (2nd), Minneapolis, Minnesota, September 5–12. Abstracts of the Papers*. St. Paul, Minnesota, USA. American Phytopathological Society Inc. No. 0860.

Ekundayo, J. A. & Naqvi, S. H. Z. (1972). Preharvest microbial rotting of yams (*Dioscorea* spp.) in Nigeria. *Transactions of the British Mycological Society*, 58:15–18.

Evans, K. & Stone, A. R. (1977). A review of the distribution and biology of the potato cyst nematodes *Globodera rostochiensis* and *G. pallida*. *PANS*, 23:178–189.

Fassuliotus, G. & Rau, G. J. (1967). The reniform nematode in South Carolina. *Plant Disease Reporter*, 51:557.

Flach, M. (1982). Ecological competition among the main moisture-rich starchy staples in the tropics and subtropics. *Proceedings of the 5th International Symposium on Tropical Root and Tuber Crops*. 17–21 Sept. 1979. Los Banos, Laguna, Philippines: 345–375.

Fliege, F. H. & Sikora, R. A. (1981). Occurrence and distribution of plant-parasitic nematodes in W. Samoa. *Alafua Agricultural Bulletin*, 6:33–41.

Franco, J. (1979). Effect of temperature on hatching and multiplication of potato cyst nematodes. *Nematologica*, 25:237–244.

Franco, J. (1981). Potato cyst nematodes, *Globodera* spp. *Technical Information Bulletin 9*. International Potato Centre, Lima, Peru, 21 p.

Franco, J. & Bendezú, E. (1985). Estudio del complejo *Verticillium dahliae* Kleb. y *Globodera pallida* Stone y su efecti en el comportamienti de algunos cultivares peruanos de papa. *Fitopatologia*, 20:21–27.

Franklin, M. T. (1959). *Nacobbus serendipiticus* n.sp., a root-galling nematode from tomatoes in England. *Nematologica*, 4:286–293.

Gapasin, R. M. (1981). Control of *Meloidogyne incognita* and *Rotylenchulus reniformis* and its effect on the yield of sweet potato and cassava. *Annals of Tropical Research*, 3:92–100.

Goodey, T. (1935). Observations on a nematode disease of yams. *Journal of Helminthology*, 13:173–190.

Gowen, S. R. (1985). *Report on nematode survey in the Solomon Islands and Vanuatu*. Report to U.K. Overseas Development Administration, London, 34 p.

Guile, C. T. (1970). Further observations on cyst colour changes in potato cyst eelworm pathotypes. *Plant Pathology*, 19:1–6.

Harrison, J. A. C. (1971). Association between the potato cyst nematode, *Heterodera rostochiensis* Woll. and *Verticillium dahliae* Kleb. in the early-dying disease of potatoes. *Annals of applied Biology*, 67:185–193.

Hawley, W. O. (1956). Hot water treatment for the control of root-knot nematodes on *Dioscorea floribunda*. *Plant Disease Reporter*, 40:1045–1046.

Hemeng, O. B. & Hemeng, B. S. (1976). Root-knot nematodes in Ghana. In: *Proceedings of Research Planning Conference on Root-knot Nematodes, Meloidogyne spp*. Ibadan, Nigeria: 48–52.

Hickling, G. E. (1974). Nematode pests of yams in Jamaica. In: *Proceedings of the 12th Annual Meeting of the Caribbean Food Crops Society, Jamaica*. Jamaica, Ministry of Agriculture: 63–67.

Hogger, C. H. (1971). Plant parasitic nematodes associated with cassavas. *Tropical Root and Tuber Crops Newsletter*, 4:4–9.

Horton, D., Lynam, J. & Knipscheer, H. (1984). Root crops in developing countries – An economic appraisal. *Proceedings of sixth symposium of the International Society for Tropical Root Crops*. International Potato Centre, Lima, Peru, 21–26 Feb. 1983: 9–39.

Huang, C. S., Tsai, Y. P., Tu, C. C., Lin, Y. Y. & Huang, S. P. (1972). Plant parasitic nematodes in Taiwan. *Monograph Series No. 1. Institute of Botany Academia Sinica Taipei, Taiwan*, 61 p.

Hutton, D. G., Wahab, A. H. & Murray, H. (1982). Yield response of yellow yam (*Dioscorea cayenensis*) after disinfesting planting material of *Pratylenchus coffeae*. *Turrialba*, 32:493–496.

Inagaki, H. (1981). Introductory reports of studies on Meloidogyne spp. in Japan. In: *Proceedings of the Third Research Planning Conference on Root-Knot Nematodes,* Meloidogyne *spp. Region VI*. Jakarta, Indonesia: 40–49.

Inagaki, H. (1985). The plant parasitic nematodes important in Japan and the related researches. *JARQ*, 18:194–201.

Inserra, R. N. (1983). *Development and pathogenicity of the false root-knot nematode* Nacobbus aberrans *and its relationship with* Heterodera schachtii *and* Meloidogyne hapla *on sugarbeet*. Ph.D. thesis, Utah State University, Logan.

International Institute of Tropical Agriculture. (1984). A system to increase seed yam production. *Research Highlights for 1983*. Ibadan, Nigeria: 103–107.

Iwahashi, T. (1977). [Control of root-lesion nematode of dasheen, I: soaking method of seed tuber.] *Kyushu Agricultural Research*, 38:81 [In Japanese]

Jackson, G. V. H. (1987). Corm rot of *Cyrtosperma* in Guam. Report to the Federated States of Micronesia and Palau.

Jatala, P. (1975). Root-knot nematodes (*Meloidogyne* species) and their effect on potato quality. *6th Triennial Conference of the EAPR. 15–19 September 1975, Wageningen, Netherlands*, 194p.

Jatala, P. (1989). Nematodes in tuber and root crops and their management. *Proceedings of the 11th International Congress in Plant Protection Manila, Philippines.*

Jatala, P. & Kaltenbach, R. (1979). Survival of *Nacobbus aberrans* in adverse conditions. *Journal of Nematology*, 11:303.

Jatala, P. & Martin, C. (1977). Interaction of *Meloidogyne incognita acrita* and *Pseudomonas scolanacearum* on *Solanum chacoense* and *S. sparsipilum. Proceedings of the American Phytopathological Society*, 4:178.

Jatala, P. & Russell, C. C. (1972). Nature of sweet potato resistance to *Meloidogyne incognita* and the effect of temperature in parasitism. *Journal of Nematology*, 4:1–7.

Jatala, P. & de Scurrah, M. M. (1975). Mode of dissemination of *Nacobbus* spp. in certain potato growing areas of Peru and Bolivia. *Journal of Nematology*, 7:324–325.

Jatala, P., French, E. R., & Gutarra, L. (1975). Interrelationships of *Meloidogyne incognita acrita* and *Pseudomonas solanacearum* on potatoes. *Journal of Nematology*, 7:325.

Jatala, P., Gutarra, L., French, E. R., & Arango, J. (1976). Interaction of *Heterodera pallida* and *Pseudomonas solanacearum* on potatoes. *Journal of Nematology*, 8:289–290.

Jenkins, W. R. & Bird, G. W. (1962). Nematodes associated with wild yam, *Dioscorea* sp., with special reference to the pathogenicity of *Meloidogyne incognita incognita. Plant Disease Reporter*, 46:858–860.

Jennings, D. L. (1976). Cassava. In: Simmonds, N. W., (Ed.) *Evolution of Crop Plants*. London, England.

Jensen, H. J., Armstrong, J., & Jatala, P. (1979). Annotated bibliography of nematode pests of potato. *Joint Publication of the International Potato Centre*, Apartado 5969, Lima, *Peru, and Oregon State University Agricultural Experiment Station*, Corvallis, Oregon, 97331. Oct. 1979, 315 p.

Jones, F. G. W. (1970). The control of the potato cyst nematode. *Journal of the Royal Society of Arts*, 118:179–199.

Kawamura, T. & Hirano, K. (1961). [Host-parasite relationship of *Meloidogyne hapla* Chitwood on yam (*Dioscorea batatas* Decne).]. *Annals of the Phytopathological Society of Japan*, 26:7–15 [In Japanese].

Kay, D. E. (revised by Gooding, E. G. B.). (1987). *Crop and Product Digest No. 2 – Root crops (second edition)* London, Tropical Development and Research Institute, 380 p.

Kermarrec, A. (1974). Les nématodes de l'igname dans les Antilles. *Nouv. Maraich. et Viv de l'INRA*, 7/8:95–105.

Kermarrec, A. & Anais, A. (1973). Presencia en Guadalupe de *Aphelenchoides besseyi* Christie 1942 (Nematoda, Aphelenchoididae) en foliage del mapuey: *Dioscorea trifida* L. *Turrialba*, 23:389–393.

Kermarrec, A., Degras, L., & Anais, A. (1981). Le nematode de l'igname *Scutellonema bradys* dans la Caraibe: distribution et quarantaine internationale. *Agronomie Tropicale*, 36:364–368.

Kermarrec, A., Castagnone-Sereno, P., Degras, L., Anais, A. & Denon, D. (1987). Nouvelle distribution *Scutellonema bradys* (Tylenchida: Hoplolaiminae) dans le Caraibe. Le cas des Antilles Francaises. *Medelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent*, 52:617–624.

Kirby, M. F. (1977). Control of root knot nematodes in Fiji. *Fiji Agricultural Journal*, 39:87–95.

Kirby, M. F., Kirby, M. E., Siddiqi, M. R. & Loof, P. A. (1980). Fiji nematode survey report: plant parasitic nematode distributions and host associations. *Bulletin No. 68, Ministry of Agriculture and Fisheries, Fiji*, 28 p.

Koch, W (1975). Control of diseases, pests and weeds in cultivating steroid plants. In: *International Plant Protection Congress (8th), Moscow, August 21–16, 1975. Reports and Informations. Section VI.* Moscow, USSR: 239–244.

Koen, H. (1969). Thermotherapeutic control of *Pratylenchus brachyurus* in potato tubers. *Phytophylactica*, 1:67–69.

Kort, J., Ross, H., Rumpenhorst, H. J., & Stone, A. R. (1977). An international scheme for identifying and classifying pathotypes of potato cyst nematodes *Globodera rostochiensis* and *G. pallida*. *Nematologica*, 23:333–339.

Lawrence, G. W., Clark, C. A. & Wright, V. L. (1986). Influence of *Meloidogyne incognita* on resistance and susceptible sweet potato cultivars. *Journal of Nematology*, 18:59–65.

Leon, J. (1977). Origin evolution, and early dispersal of root and tuber crops. In: Cock, J., MacIntyre, R. & Graham, M. (Eds.) *Proceedings of the Fourth Symposium of the International Society for Tropical Root Crops CIAT*, Cali, Colombia: 20–36.

Lordello, L. G. E. (1959). A nematosis of yam in Pernambuco, Brazil, caused by a new species of the genus *Scutellonema*. *Revista Brasileira de Biologia*, 19:33–41.

Lordello, L. G. E. (1981). *Nematóides das Plantas Cultivadas* 6*a* edicão. Livraria Nobel S. A., 314p.

Lorenzo, E. & Fernandez, E. (1982). Reporte de nematodos noduladores en la malanga "Isléna Japonesa" (*Colocasia esculenta*) en Cuba. *Ciencia y Técnica en la Agricultura. Proteccion de Plantas*, 5:31–38.

Luc, M. & Guiran, G. de (1960). Les nematodes associes aux plantes de l'Ouest Africain. Liste preliminaire. *Agronomie Tropicale*, 15:434–449.

Mai, W. F., Brodie, B. B., Harrison, M. B., & Jatala, P. (1981). Nematodes. In: Hooker, W. J. (Ed.) *Compendium of Potato Diseases*. American Phytopathological Society: 93–101.

Martin, G. C. (1969). Plants infected with root-knot nematodes (*Meloidogyne* spp.) in Rhodesia, Malawi and Zambia. *Technical Bulletin No. 8, Rhodesia Ministry of Agriculture, Salisbury*, 14 p.

Martin, W. J. (1962). Elimination of root-knot nematodes from infested sweet potato roots and plants. *Plant Disease Reporter*, 46:21–23.

McSorley, R., O'Hair, S. K. & Parrado, J. L. (1983). Nematodes associated with the edible aroid genera *Xanthosoma* and *Colocasia* and their effects on yield. *Nematropica*, 13:165–180.

Miège, J. (1957). Influences de quelques caractères des tubercules semences sur la levée et le rendement des ignames cultivées. *Journal d'Agriculture Tropicale et de Botanique Appliquée*, 4:315–342.

Morris, R. F. (1971). Distribution and biology of the golden nematode, *Heterodera rostochiensis* in Newfoundland. *Nematologica*, 17:370–376.

Mortimer, J. J., Bridge, J. & Jackson, G. V. H. (1981). *Hirschmanniella* sp., an endoparasitic nematode associated with miti-miti disease of taro corms in the Solomon Islands. *FAO Plant Protection Bulletin*, 29:9–11.

Moura, R. M., Coêlho, R. S. B. & Pio-Ribeiro, G. (1978). Estudo etiológico e efeito de 1,2-dibromo–3-cloropropano no controle à caxa preta do inhame (*Dioscorea cayenensis* Lam.). *Fitopatologia Brasileira*, 3:47–53.

Moura, R. M., Pio-Ribeiro, G., Coêlho, R. S. B. & Silva-Junior, J. N. (1976). *Penicillium sclerotigenum* Yamamoto, principal fungo causador de podridão em túberas de inhame (*Dioscorea cayenensis* Lam.) no Estado de Pernambuco. *Fitopatologia Brasileira*, 1:67–76.

Mulvey, R. H., & Stone, A. R. (1976). Description of *Punctodera matadorensis* n.gen., n. sp. (Nematoda Heteroderidae) from Saskatchewan with list of species and generic diagnosis of *Globodera* (n. rank), *Heterodera*, and *Sarisodera*. *Canadian Journal of Zoology*, 54:772–785.

Nadakal, A. M. & Thomas, N. (1967). Observations of nematodes associated with dry rot of *Dioscorea alata* L. *Science and Culture*, 33:142–143.

Navarro, R. & Barriga, R. (1975). Identifications of *Meloidogyne* spp., root-knot nematodes, in Columbia. *Proceedings of the American Phytopathological Society*, 2:77–78.

Nirula, K. K. (1959). Root knot nematode on Colocasia. *Current Science*, 28:125–126.

Nishizawa, T. (1973). Pathogenicity of *Trichodorus porosus* to Chinese yam. *Japanese Journal of Nematology*, 3:33–37.

Nishizawa, T. & Ohshima, Y. (1972). [Annual changes in the nematode fauna in experimental fields with

continuous or rotational cropping with 4 crops.] *16th Annual Meeting of the Japanese Society of Applied Entomology and Zoology*, Shizuoka, Japan: 120 [In Japanese].

Nwauzor, E. C. & Fawole, B. (1981). Root-knot nematodes on yams in eastern Nigeria. *Proceedings of the 3rd Research Planning Conference on root-knot nematodes*, Meloidogyne *spp., Regions IV and V.* Ibadan, Nigeria: 161–167.

Oashi, K. (1984). [On the damage and ecological control of *Pratylenchus coffeae* infesting taro in south Kyushu.] *Japanese Journal of Nematology*, 14:61–62 [In Japanese].

Obigbesan, G. O. & Adesiyan, S. O. (1981). The influence of fertilizer nutrients on population levels of *Scutellonema bradys* in three yam species. *Nematologia mediterranea*, 9:21–28.

Ogundana, S. K., Naqvi, S. H. Z. & Ekundayo, J. A. (1970). Fungi associated with soft rot of yams (*Dioscorea* spp.) in storage in Nigeria. *Transactions of the British Mycological Society*, 54:445–451.

Oostenbrink, M. (1966). Major characteristics of the relation between nematodes and plants. *Mededelingen Landbouwhogeschool Wageningen*, 66:1–46.

Orton Williams, K. J. (1980). Plant-parasitic nematodes of the Pacific. *Technical Report, Volume 8, UNDP/FAO-SPEC Survey of Agricultural Pests and Diseases in the South Pacific*. Commonwealth Institute of Helminthology, St. Albans, UK, 192 p.

Parris, G. K. (1940). A check-list of fungi, bacteria, nematodes and viruses occurring in Hawaii, and their hosts. *Plant Disease Reporter Supplement*, 121:1–91.

Patel, M. Z., Saelea, J. & Jackson, G. V. H. (1983). Breeding strategies for controlling diseases of taro in Solomon Islands. *Proceedings - Sixth Symposium of the International Society for Tropical Root Crops*, Lima, Peru: 143–149.

Pinochet, J. & Ventura, O. (1980). Nematodes associated with agricultural crops in Honduras. *Turrialba*, 30:43–47.

Ponte, J. J. Da, & Franco, A. (1981). Manipueira, un nematicida nao convencional de comprovada potencialidade. In: *Trabalhos apresentados Reuniae de Sociedade Brasileira de Nematologia, Piracicaba*, Brasil, 5:25–33.

Purseglove, J. W. (1972). *Tropical Crops. Monocotyledons*. Longmans, London, 607 p.

Rodriguez-Kabana, R., Turner, J. L., & Ingram, E. G. (1978). Tratamiento de raíces de batata con el nematocida sistémico oxamyl para el control de nematodos fitoparásitos, *Nematropica*, 8:26–31.

Roman, J. (1978). *Fitonematologia Tropical.* Universidad de Puerto Rico, Estacion Experimental Agricola, Rio Piedras, Puerto Rico, 256 p.

Roman, J., Oramas, D. & Green, J. (1984*a*). Nematicide evaluation for the control of the nematodes of yam (*Dioscorea rotundata* Poir). *Journal of Agriculture of the University of Puerto Rico*, 68:157–162.

Roman, J., Oramas, D. & Green, J. (1984*b*). Use of oxamyl for the control of nematodes in yam (*Dioscorea rotundata* Poir). *Journal of Agriculture of the University of Puerto Rico*, 68:383–386.

Sadik, S. & Okereke, O. U. (1975). A new approach to improvement of yam, *Dioscorea rotundata. Nature*, 254:134–135.

Salaman, R. (1949). *The history of social influence of the potato*. London, England, Cambridge University Press.

Sasser, J. N. & Kirby, M. F. (1979). *Crop cultivars resistant to root-knot nematodes*, Meloidogyne *species*. International Meloidogyne Project Contract No. AID/ta-c–1234. Raleigh, North Carolina State University, USA, 24p.

Schieber, E. (1961). Parasitic nematodes on *Dioscorea* in Guatemala. *Plant Disease Reporter*, 45:425.

Schieber, E. & Lassmann, D. K. (1961). Root-knot nematode on *Dioscorea* in Guatemala. *Plant Disease Reporter*, 45:981.

Sher, S. A. (1970). Revision of the genus *Nacobbus* Thorne and Allen, 1944 (Nematoda: Tylenchoidea). *Journal of Nematology*, 2:228–235.

Sikora, R. A. (1984). Importance of diapause, resistant and early maturing potato cultivars, chicken manure and non-host crops for *Globodera rostochiensis* integrated control in the upland tropics. *Mededelingen Faculteit Landbouwwetenschappen Gent*, 49:613–620.

Smit, J. J. (1967). Nematodes. In: Coursey, D. G. (Ed.) *Yams*. Longmans, London: 115–120.

Srivastava, A. S., Verma, R. S. & Pandey, R. C. (1971). Comparative efficacy of different nematicides tested

against root-knot nematode infesting *Colocasia* (*C. anticorum*). *Labdev Journal of Science and Technology. Life Sciences*, 9:142–144.

Srivastava, A. S., Gupta, R. L., Singh, B. & Ram, S. (1969). Damage and control of *Meloidogyne javanica* (Treub) in *Colocasia* (*C. antiquorum*). *Labdev Journal of Science and Technology. Life Sciences*, 7:306–307.

Stegemann, H. & Schinck, D. (1985). *Index 1985 of European Potato Varieties. National registers, characteristics, genetic data.* Mitteilungen aus Biologischen Bundesanstalt für Land-und Forstwirtschaft. Berlin-Dahlem, 227p.

Steiner, G. (1937). Observations on the yam nematode (*Rotylenchus bradys* (Steiner & Le Hew, 1933) Filipjev, 1936). *Phytopathology*, 27:865–867.

Stone, A. R. (1973). *Heterodera pallida* n.sp. (Nematoda: Heteroderidae), a second species of potato cyst nematode. *Nematologica*, 18:591–606.

Tanaka, M. A. de S., Chalfoun, S. M., & Abreu, M. S. de. (1979). Doencas de mandioca en seu controle. *Informe Agropecuario*, 5:70–78.

Tarjan, A. C. (1952). Awl nematode injury on Chinese water chestnuts. *Phytopathology*, 42:114.

Taylor, A. L. & Sasser, J. N. (1978). Biology, identification and control of root-knot nematodes (*Meloidogyne* species). *International Meloidogyne Project. North Carolina State University Graphics*, 111 p.

Thomas, R. J. & Clark, C. A. (1983*a*). Effects of concomitant development on reproduction of *Meloidogyne incognita* and *Rotylenchulus reniformis* on sweet potato. *Journal of Nematology*, 15:215–221.

Thomas, R. J. & Clark, C. A. (1983*b*). Population dynamics of *Meloidogyne incognita* and *Rotylenchulus reniformis* alone and in combination and their effects on sweet potato. *Journal of Nematology*, 15:204–211.

Thompson, A. K., Been, B. O. & Perkins, C. (1973). Nematodes in stored yams. *Experimental Agriculture*, 9:281–286.

Thorne, G., & Schuster, M. L. (1956). *Nacobbus batatiformis* n.sp. (Nematoda: Tylenchida), producing galls on the roots of sugar beets and other plants. *Proceedings of helminthological Society of Washington*, 23:128–134.

Timm, R. W. (1965). *A preliminary survey of the plant parasitic nematodes of Thailand and the Philippines.* SEATO Thai Sambhand Printing Press, Bangkok, 71 p.

Unny, K. L. & Jerath, M. L. (1965). Parasitic nematodes on *Dioscorea* spp. in eastern Nigeria. *Plant Disease Reporter*, 49:875–876.

Vander Zaag, D. E. & Horton, P. (1983). Potato production and utilization in world perspective with special reference to the tropics and sub-tropics. In: Hooker, W. J. (Ed.) *Research for the Potato in the year 2000. Proceedings of the International Congress in Celebration of the Tenth Anniversary of the International Potato Centre.* Lima, Peru, 22–26 Feb. 1982. CIP:44–58.

Vilsoni, F. & Heinlein, M. (1982). Host range and reproductive capacity of the reniform nematode *Rotylenchulus reniformis* on some crop cultivars in Fiji. *Fiji Agricultural Journal*, 44:61–66.

Whitehead, A. G. (1969). The distribution of root-knot nematodes (*Meloidogyne* spp.) in tropical Africa. *Nematologica*, 315–333.

Whitehead, A. G. (1975). Chemical control of potato cyst nematode. *Research review*, 8:17–23.

Winslow, R. D. (1978*a*). An overview of the important nematode pests of potato. *Development in Control of Nematode Pests of Potato. Report of the 2nd Nematode Planning Conference.* International Potato Centre, Lima, Peru: 16–30.

Winslow, R. D. (1978*b*). Other nematode pests: importance and control. *Developments in the Control of Nematode Pests of Potato. Report of the 2nd Nematode Planning Conference.* International Potato Centre, Lima, Peru: 138–153.

Winslow, R. D. & Willis, R. J. (1972). Nematode diseases of potatoes. In: Webster, J. M. (Ed.) *Economic Nematology* London, U.K., Academic Press: 17–48.

Wood, T. G., Smith, R. W., Johnson, R. A. & Komolafe, P. O. (1980). Termite damage and crop loss studies

in Nigeria – pre-harvest losses to yams due to termites and other soil pests. *Tropical Pest Management*, 26:355–370.

Yen, D. E. (1982). Sweet potato in historical perspective. In: Villareal & Griggs, T. D. (Eds.) *Sweet Potato, Proceedings of the First International Symposium*. Tainan, Taiwan, AVRDC: 17–30.

Yokoo, T., & Matsunobu, K. (1975). On thermal death point of the potato lesion nematode *Pratylenchus pratensis*. *Agricultural Bulletin. Saga University*, 5:97–102.

Chapter 6

Nematode Parasites of Food Legumes

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The family Leguminosae, with approximately 650 genera and 18 000 species is the third largest family of flowering plants. Although legumes are found throughout the world the greatest diversity exists in the tropics and subtropics. The family is divided into three subfamilies: Caesalpinioideae with approximately 2800 species, mainly trees of tropical savannas and forests; Mimosoideae with about 2800 species, mostly small trees and shrubs of semiarid tropical and subtropical regions; and Papilionoideae with about 12 000 species, containing the majority of food legumes and herbs with a worldwide distribution (NAS, 1979; Purseglove, 1974).

Archeological excavations have demonstrated that lentil, chickpea, lupin, string bean, broad bean, kidney bean, pea, and soybean, among others, have played an important role as essential foods in the ancient civilizations of China, India, the Americas, and the Near East as far back as 7000 B.C. (Brothwell & Brothwell, 1969). Of the more than 18 000 known legume species less than 20 are of worldwide economic importance as food crops. However, over 200 have been considered important on a regional, local or future basis (NAS, 1979). For practical purposes legume crops are often grouped under a variety of names including: legumes, pulses, grain legumes or beans. The use of any one term can be misleading, because these crops have a multitude of uses. These plants can be used as a grain, vegetable, green manure, pasture, cover crop to reduce erosion or as a source of fodder, cooking oil, or protein supplement as well as for raw material in the food processing industry. Therefore, we have decided to use the broader term "food legumes" for the crops discussed in this chapter. The main climatic zones, uses, distribution and relative economic importance of the major food legumes are presented in Table 1.

Legumes rank second to cereal crops in degree of nutritional importance for humankind. In many countries they are the major source of protein, often containing two to three times more protein than cereals. It has been estimated that 80% of the protein in the diet of many tropical and subtropical countries are derived from vegetable products, among which food legumes predominate. In India where in excess of 10 million tons are consumed per year, they supply the only high-protein component of the diet (Kay, 1979). Legumes are the cheapest and most direct form of protein. They can be transported easily when dried and can be stored for long periods of time at room temperature without losing substantially on nutritional content.

The land area in food legume production, yield/ha and overall production, is given in Table 2. The figures on production by crop and continent (Table 3) demonstrate the importance of the

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

TABLE 1. Common name, growing zone, uses, distribution and importance of food legumes in tropical and subtropical climatic areas*.

Common names	*Climatic zones*[1]				*Uses*			*Distribution*	*Importance*
	T	ST	UT	D/SA	Grain	Veg.	Animal[2]		
Adzuki bean		x			x		x	Worldwide, Ch,Jap, SE Asia	++
Black gram, Urd	x	x			x		x	India	++
Broad bean, faba bean	x	x			x	x	x	Worldwide	+++
Catjang bean	x	x				x	x	Worldwide, SE Asia	++
Chickpea	x	x		x	x	x	x	Worldwide	+++
Cowpea	x	x		x	x	x	x	Worldwide	+++
Grass pea, Chickling pea		x	x		x		x	Worldwide	+
Haricot, Kidney, Bush, French, String bean	x	x			x	x		Worldwide	+++
Horse bean	x			x	x		x	Asia, Africa	+
Horse gram	x			x	x		x	Asia, Africa	+
Hyacinth bean, Lablab	x	x		x	x		x	SE Asia	++
Lentil		x	x	x	x		x	Worldwide	+++
Lima bean, Butter bean	x	x			x	x		Worldwide	++
Lupin, Tarwi		x			x		x	N & S Am, Med	+
Moth bean	x	x		x	x		x	Worldwide, Ind, S. Am	+
Mung bean, Green gram	x	x			x	x	x	Worldwide, Ind,Ch, SE Asia	+++
Pea		x	x		x	x	x	Worldwide	+++
Pigeonpea, Red gram	x	x		x	x	x	x	Worldwide	++
Winged bean	x				x	x	x	Worldwide, SE Asia	+
Rice bean, Red bean	x	x			x		x	Worldwide, SE Asia	++
Soybean, Soya	x	x			x	x		USA, China, Brazil	+++

*(Brothwell & Brothwell, 1969; Rehm & Espig, 1976; *NAS*, 1979 *Ward et al.*, 1981)
[1]T = tropical, ST = subtropical, UT = upland tropics, D/SA =dry/semi-arid tropics
[2]Animal = fodder, green manure, protein supplement, or straw.

different food legumes in Asia where roughly 50% are consumed. The importance of plant parasitic nematodes, insects and diseases as well as abiotic constraints are reflected in the low per hectare yields in tropical agriculture when compared to yields in temperate agriculture (Table 2).

The symbiotic relationship between legumes and nitrogen fixing *Rhizobium* bacteria gives these crops an economic advantage over crops requiring fertilizer. Part of the fixed nitrogen remains in the soil within crop residues after harvest, thus improving soil fertility. Food legumes are, therefore,

TABLE 2. Worldwide production of food legumes according to region in 1985*.

Region	Total area 1000 HA	Yield KG/HA	Production 1000 MT
World	67508	729	49226
Africa	12486	469	5861
N & C America	3982	841	3351
St. America	6440	534	3436
Asia	34010	679	23110
Europe	3012	1553	4678
Oceania	810	1061	860
USSR	6766	1172	7929

*(FAO Production Yearbook, Vol. 39, 1985)

TABLE 3. World food legume production in 1000 metric tons[1].

Continent	Bean	Broad bean	Dry pea	Chickpea	Lentil	Pigeonpea[2]	Cowpea[2]	Total Legumes[3]	Soybean
Africa	1732	1062	277	284	106	70	1003	5861	365
N. & C America	2600	77	342	150	110	41	57	3351	59099
S. America	3131	105	100	26	44	4	–	3436	25746
Asia	6268	2393	2398	5866	1288	1845	27	23110	14033
Europe	794	522	2290	90	88	–	6	4678	929
Oceania	6	11	246	–	–	–	3	860	111
Australia	6	11	168	–	–	–	–	776	111
World Total	14615	4170	11644	6416	1650	1960	1097	49226	100833

*(FAO Production Yearbook Vol 28, 1974; [2]Vol. 39. 1985)
[1]Includes other grain legumes, soybean is not included.

an important component in tropical cropping systems, where they are rotated with such nutrient demanding crops as rice and maize. In the subtropics, where soils are often deficient in organic matter, legumes can be used as green manure.

Cultivation techniques

Food legumes are adapted to a wide range of climatic conditions particularly warm climates. Their deep root system favours survival during periods of drought, making them important crops in the semi-arid and dry regions of the tropics. In addition, a number of species grow well in moist climatic areas and are important crops in the humid tropics. Many food legumes are adapted to a wide range of soil types, high temperatures, low nutrient levels, alkalinity, acidity and high salt concentrations, making them important crops in marginal areas and in subsistence agriculture. Their capacity to grow under poor soil conditions also may be related to their ability to form symbiotic relationships with endomycorrhizal fungi which are known to increase plant tolerance to a wide range of abiotic and biotic stress factors (Dehne, 1987) and in some cases to nematode infection (Sikora, 1981; Hussey & Roncadori, 1982).

Methods of cultivation vary greatly between climatic regions and within individual countries. The majority are sown by drilling or broadcasting either as a single crop or interplanted with other crops. When intercropped, the main crop is planted in rows and the legumes are broadcasted after the main crop has been established (Kay, 1979; Ward *et al.*, 1981).

Nematodes of Food Legumes

Many plant parasitic nematodes have been found associated with legume crops (Goodey *et al.*, 1965; Sitaramaiah *et al.*, 1971; Bridge, 1981; Mani *et al.*, 1982). Those affecting forage, pasture and legumes grown mainly for cooking oil have been the subject of other review articles (Eriksson, 1972; Griffin, 1984; Schmitt & Noel, 1984; Sikora, 1987). The identification, races, biology and complex disease interrelationships of the cyst nematodes affecting legumes in the *Heterodera trifolii* complex group were discussed by Sikora and Maas (1986).

Only those nematodes that are known to cause yield loss will be covered in this chapter, those that only are known to parasitize the crops and complete their life cycle on the plant will not be discussed in detail.

When food legumes are cultivated in semi-arid areas under rainfed conditions or in the dry season after the monsoon rains, infected plants are often severely damaged. Nematodes induce vascular disorders and reduce root penetration of the soil profile increasing the negative impact moisture stress exerts on plant health.

Plant parastic nematodes also affect plant vigour in some food legumes by suppressing *Rhizobium*

root nodulation and nitrogen fixing activity. Complex interrelationships between nematodes and soil-borne fungal pathogens also play a significant role in reducing yield. The importance of these complex interrelationships has received only minor attention (Sikora & Maas, 1986).

Control measures, in the vast majority of cases where nematodes have been shown to be limiting factors, have not been adequately developed; leaving the farmer to his traditional cropping systems and ultimate poor yield. Furthermore, the effects of traditional multicropping rotation patterns on nematode population dynamics and crop growth are lacking for many parts of the tropical and subtropical zones. Many of these traditional cropping systems may be effective in checking nematode damage.

Although many breeding lines have shown different degrees of resistance to important nematodes, only a handful of resistant cultivars are available to the farmer. In many cases the techniques used for testing have led to misinterpretation of results with retesting often failing to produce good sources of resistance for breeding programmes. Because breeding lines have little value to the grower, we have decided not to list all the lines tested. Lists of cultivars with resistance in food legumes have been compiled (Armstrong & Jensen, 1978; Sasser & Kirby, 1979; Bridge, 1981).

Black Gram, Urd, Mash

Black gram (*Vigna mungo* (L.) Hepper, syn. *Phaseolus mungo* L.) also known as urd or mash probably originated in India and is a bushy annual common in Asia, Africa and America. The plant which is very similar to mung bean, is resistant to high temperatures and is reasonably drought resistant. It is often grown intercropped with cotton, maize or sorghum.

Rotylenchulus reniformis has been detected on gram in Puerto Rico (Ayala & Ramirez, 1964). In India *Heterodera cajani, R. reniformis*, and *Tylenchorhynchus mashhoodi* have been found associated with the crop (Sitaramaiah, 1984). The root-knot nematodes *Meloidogyne incognita* and *M. javanica* are known to infect black gram in Brazil (Freire *et al.*, 1972). Root-knot has also been detected on the crop in India (Nadakal, 1964). In the Rajasthan area of India, *M. incognita* was found in 54% of the 176 fields sampled (Datta *et al.*, 1987).

Economic threshold level

M. incognita and *R. reniformis* were shown to cause significant growth reductions at 1 juvenile/cm^3 of soil in pot tests (Mishra & Gaur, 1981). Growth reduction increased with level of infestation and both nematodes reduced the number of *Rhizobium* nodules. Zaki and Bhatti (1986) reported that *H. cajani* at 1 juvenile/g of soil did not affect shoot growth, but caused reductions in root weight. Gupta and Yadav (1979) in pot studies showed that plant growth was significantly reduced by *R. reniformis* in densities of $\geq$ 2 nematodes/g of soil. *M. incognita* reduced the number, weight and activity of *Rhizobium* nodules in pot tests (Chahal & Chahal, 1987).

Control

Although crop rotations designed specifically to control nematodes on the crop have not been developed, the use of non-hosts in cropping systems would be the most economical means of preventing damage. Resistant cultivars are not available, but moderate levels of resistance have been detected in some lines (Routaray *et al.*, 1986; Midha & Trivedi, 1988).

Broad Bean

Broad bean (*Vicia faba* L.) also known as faba, field, common, horse, tick and Windsor bean is a subtropical or temperate crop that is probably native to the Mediterranean region or Southwest Asia. It is grown in the winter season in the subtropics. Whereas the dried seeds are eaten as a porridge or consumed after baking as Foul in the Middle East, the immature seeds are eaten as a

vegetable after boiling. The seeds are also widely used as livestock and poultry feed. The crop is sometimes used as green manure and the dried residues as animal fodder.

A wide range of plant parasitic nematodes have been found associated with *V. faba*, but only a few are of widespread economic importance in the tropical and subtropical zones (Hooper, 1983*b*). In most cases, nematode damage occurs in the cooler winter growing seasons in the subtropics or in the upland tropical zones.

Ditylenchus

The stem nematode, *D. dipsaci*, is the most important nematode on broad bean in subtropical and temperate growing areas. The nematode has been detected attacking broad bean in many countries bordering the Mediterranean Sea – Syria, Jordan, Turkey, France, Tunisia, Algeria, Morroco, Cyprus, Spain, Italy, Greece – and because of the nematode's worldwide distribution it should be considered a potential pest in most areas where broad bean is grown (Hooper, 1972; Lamberti, 1981; Greco & Di Vito, 1987).

Biology

The stem and bulb nematode is a migratory endoparasite that feeds on stem, petiole, leaf, pod and seed tissue (see Chapter 1). The nematode does not cause damage to the root. Soil-borne *D. dipsaci* fourth stage juveniles penetrate the young seedling below the soil surface after germination. Damage is often more severe when seed-borne populations are already present in the tissue at planting. Cool, moist conditions, for example when present during the winter growing season in the Mediterranean region, favour nematode infection and disease development. As temperatures rise during the growing season, nematode development is often retarded, symptoms can disappear, and the plant seems to recover.

Survival and means of dissemination

The fourth stage juvenile can withstand desiccation for many years. The nematodes often clump together to form "nematode wool" when the plant tissue begins to dry. This wool can often be observed on the seeds in heavily infested pods. The presence of infective fourth stage juveniles in seed as well as in plant debris is important in the passive dissemination of the nematode over long distances. *D. dipsaci* is seed-borne in broad bean, lucerne, onion, clovers and teasel.

The nematode in this desiccated stage can survive passage through pigs and cattle on infested seed (Palmisano *et al.*, 1971). Augustin (1985) was unable to detect passage of the nematode on infested straw in sheep.

Although soil densities seem to decrease rapidly, Seinhorst (1956*a*) and Wilson and French (1975) have shown that the nematode can survive for years without a host plant. Nematode survival and damage are greater in heavy soils as compared to sandy soils (Seinhorst, 1956*b*).

Races

Races of *D. dipsaci* normally cannot be identified morphologically with one exception, those attacking broad bean. Broad bean is attacked by the normal "oat race" (1.2 to 1.4 mm adult or fourth-stage juvenile body length) in temperate regions and by the "giant race" (1.5 to 1.7 mm length) in the subtropical semi-arid regions of the Mediterranean. There are other races that can attack broad bean, but they are of marginal importance only in temperate regions.

The fact that the "giant race" causes damage in England (Hooper, 1983*a*) and can survive under environmental conditions existing in Germany (D. Sturhan, pers. comm.) warrants closer examination of imported broad bean seeds.

Fig. 1. Darkened and swollen stem, typical of *Ditylenchus dipsaci* 'Giant race' infection of *Vicia faba* (Photo: J. Bridge).

Symptoms

Although Hooper (1983*a*) suggested that the two races could be tentatively identified by the symptoms produced – the more severe symptoms being induced by the "giant race" – he considered measurement of body length a more exact means of identification. The nematode can induce stem swelling and deformation of stem tissue (Fig. 1) or lesions which turn reddish brown then black depending on cultivar and environmental factors. The lesions envelope the stem and increase in length, often advancing to the edge of an internode (Plate 4D). Leaf and petiole necrosis is also common under heavy infestations, but can be confused with symptoms produced by fungal leaf pathogens. Newly formed pods take on an even, dark brown appearance (Hooper, 1983*a*). Seeds

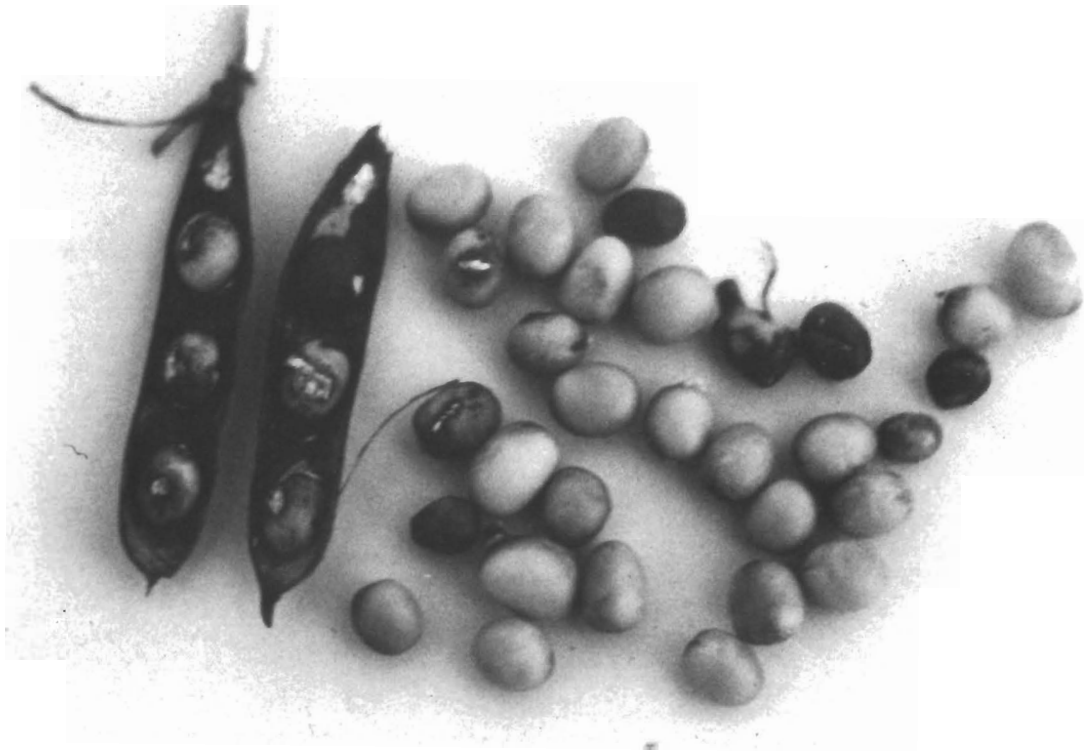

Fig. 2. Deformed and blackened seed and pods of *Vicia faba* infested with *Ditylenchus dipsaci* 'Giant race' (Photo: J. Bridge).

infested are darker, distorted, smaller in size and may have speckle like spots (Fig. 2) on the surface (Schreiber, 1977; Hooper, 1983*b*; Augustin, 1985). The percentage of seeds infested increases with infestation levels and is greatest when nematode contaminated seed is used for sowing. Heavy infestations often kill the main shoot which stimulates secondary tiller formation. These newly formed shoots are often free from infection.

The nematodes are found under the testa in depressions on either side of the radicle causing necrotic patches, visible when the testa is removed (Hooper, 1983*b*). Over 10 000 juveniles can be found in one infested seed.

Economic threshold level

Hooper (1983*a*) in field trials showed that the "giant race" was more damaging to broad bean than the "oat race", common to Europe, when *D. dipsaci* infested straw was incorporated into the field. The "giant race" caused 100 and 63% and the "oat race" 82 and 1.3% stem and seed infection, respectively.

The economic threshold level is not known for the "giant race" on broad bean. The threshold level for onion, celery and carrot is 2 nematodes/100g of soil (Decker, 1969).

Other hosts

Although *D. dipsaci* has over 450 host plants (Hooper, 1972), the host range of the "giant race" seems to be more limited. Certain weeds serve as hosts for the "oat race" (Green, 1981) and the

"giant race" of *D. dipsaci* (Augustin & Sikora, 1989*a*) and are important in maintaining high soil densities of the nematode.

Control

Prevention of introduction by establishment of quarantine laws should be promoted. Seed can be easily examined by the techniques outlined below and in chapter 2.

Fumigation has been used to eradicate the nematode from infested seed, but will not give 100% control when high infestation exist (Powell, 1974; Augustin, 1985). Soil treatment with non-fumigant nematicides will prevent seed infestations and can be used to protect breeding material (Augustin & Sikora, 1984; Augustin, 1985).

Resistance is known from Egypt (Oteifa, pers. comm.) where the nematode was not detected in a survey by Augustin (1985) and was reported for a local Moroccan cultivar by Schreiber (1977) and in Syria (Hanounik *et al.*, 1986). Hooper (1983*a*) stated that the production of uninfested tillers after the main stem was killed by the nematode may be confused with resistance.

Rotation of four years with non-host crops and weed control of other hosts is required for successful control.

Heterodera

The pea cyst nematode, *Heterodera goettingiana*, is an important parasite of broad bean in many temperate regions. The nematode is a limiting factor in the cool growing season in some countries of subtropical North Africa, West Asia, Italy and Spain (Stone & Course, 1974). The nematode causes stunting in heavily infested fields (Fig. 3).

Other hosts

Pisum sativum, species of *Vicia, Glycine max, Lens esculenta*, are economically important hosts (Jones, 1950; Winslow, 1954). Most host plants are in the tribe Vicieae of the family Leguminosae

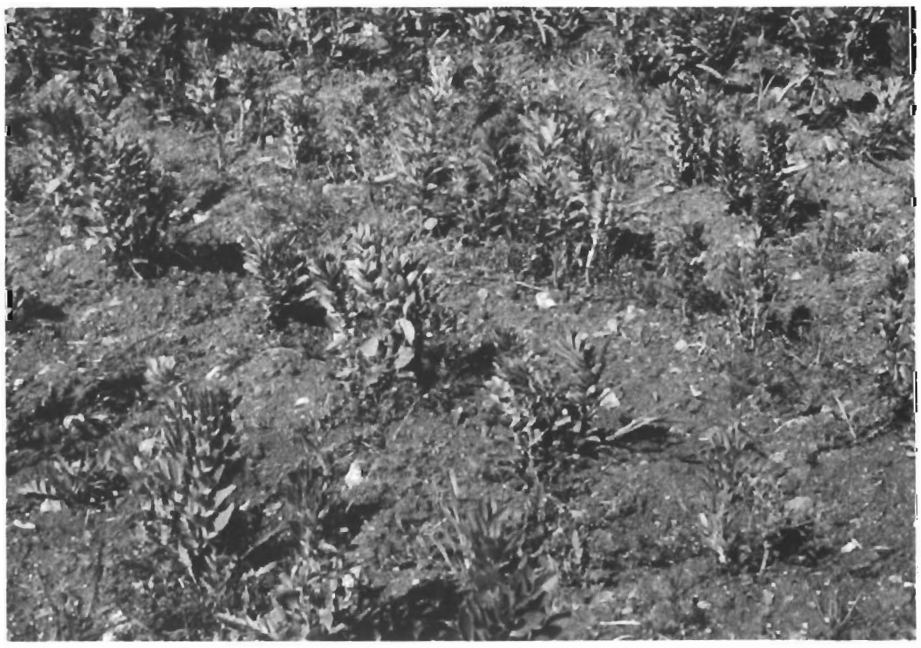

Fig. 3. Broad Bean crop showing a patch of stunted plants in a field infested with *Heterodera goettingiana*.

(Winslow, 1954). In addition, many weeds are considered good hosts and are responsible for maintaining populations in the absence of susceptible crop plants.

Biology

The biology and development of this cyst nematode is similar to that described for the other cyst nematodes in this, and in Chapter 1. Whereas on pea *H. goettingiana* only completes one generation/crop, multiple generations can be produced on *V. faba* (Hooper, 1983*a*). Survival in the absence of a host has been reported to exceed 10 years (Brown, 1958).

Economic threshold level

Threshold levels have not been determined for the nematode on broad bean. The crop is, however, less susceptible to damage than pea, which is severely affected at population densities of 127 eggs/g of soil (Winslow, 1955). Growing the crop every four years in infested fields caused crop failure under temperate climatic conditions (Brown, 1958).

Control

Effective control can be obtained by crop rotation with non-host crops. On uninfested land, Hooper (1983*a*) recommended reducing legume crops to once in four years. Where infestations are known, longer rotations are required (Brown, 1958).

Cicer arietinum L., *Glycine hispida* Moench., *Lupinus albus* L., *Medicago sativa* L., *Phaseolus vulgaris* L. and a number of clover species were found resistant to the nematode (Di Vito *et al.*, 1980).

Nematicides have been shown to be effective in control of *H. goettingiana* on peas, but have not been examined on broad bean. Oxamyl at 6g a.i./100 m row, applied in furrows caused increased yield of pea and was considered to be economical, even though the nematode population increased tenfold after harvest (Green *et al.*, 1981). Nematicides, however, can not be used economically for control of this nematode on broad bean.

Other Nematodes of Broad Bean

There are a number of other nematodes that parasitize broad bean in the tropics and subtropics that are of local, limited or unknown importance.

The root-knot nematodes *M. incognita, M. javanica, M. arenaria*, and *M. artiellia* are known to attack broad bean in the tropics and subtropics (Goodey *et al.*, 1965). Damage caused by root-knot nematodes has been reported from Rhodesia, Nyasaland, Malawi, East Africa, Libya and Iraq (Hooper, 1983*a*). The symptoms of damage and methods of diagnosis are the same described for other legumes in this chapter. Control is usually accomplished by rotation with non-host crops especially cereals. Care should be taken in selecting rotation crops, because of the nematodes wide host range and known variability in the genus. Resistance is not known and nematicides are too expensive for practical use.

Some species of *Pratylenchus* cause extensive necrosis of the root tissue and yield loss in the subtropics and tropics. The importance of this group of nematodes to broad bean, however, has not been determined. The burrowing nematode *Radopholus similis*, has been shown to reproduce on broad bean only in India (Sosamma & Koshy, 1977). The reniform nematode, *Rotylenchulus reniformis*, has only been reported on broad bean in Pakistan and is of unknown importance (Timm, 1956). Hooper (1983*a*) discussed the distribution and importance of stunt nematodes in the family Tylenchorhynchidae. The nematodes are of limited economic importance.

Chickpea

Chickpea (*Cicer arietinum* L.) also known as gram and bengal gram, originated from Turkey and Syria around 5450 B.C. (Saxena, 1987). Production is concentrated in Asia where 92% is grown

with India accounting for over 70% of the area in cultivation. Other countries with extensive cultivation are: Pakistan, Burma, Iran, Nepal, Ethiopia and Mexico. In the Mediterranean basin chickpea is an important crop in Turkey, Syria, Morocco, Tunisia, Spain, and Portugal. Although green pods and shoots of chickpea are also used for vegetables in India, this legume is mainly used as dried grains which are boiled, mashed or roasted, and used for flour in various foods. A minor portion is used as animal feed.

Two types of chickpea are commonly grown: 1) Desi – small seeded with a brown seed coat common to India and used for flour, and "Dhal", an important split-pea vegetable, and to a lesser extent as animal feed and 2) Kabuli – large seeded with a thin light coloured seed coat and usually consumed whole in West Asia.

Chickpea is moderately resistant to drought and sensitive to low temperature, therefore, it is cultivated as a winter crop in India and Pakistan and as a spring crop in Turkey and Syria. It can be successfully cultivated in areas with a minimum annual rainfall of 300 mm. Supplementary irrigation may double yields. Chickpea is irrigated in the Nile Valley of Egypt and Sudan, due to a lack of sufficient rainfall and in India in areas whose soils have low water holding capacity (Saxena, 1987).

Chickpea infested by nematodes are in general stunted, with chlorotic foliage. They flower poorly and give rise to few and small pods that are often empty. Senescence sets in earlier in heavily infested plants. The root system is reduced in size, *Rhizobium* nodulation is suppressed and the roots can show extensive necrosis. Since these symptoms are not specific, close examination of the root system is required for proper diagnosis. The nematodes associated with chickpea have been tabulated by Sharma (1985).

Meloidogyne

The root-knot nematodes *Meloidogyne javanica, M. incognita*, and *M. arenaria* damage chickpea in India (Mathur *et al.*, 1969; Nath *et al.*, 1979) and *M. arenaria* in Ghana (Edwards, 1956). Infected chickpea have heavily galled roots (Fig. 4) which may rot, because of concomitant infestations with fungal pathogens.

In the subtropical semi-arid Mediterranean basin, damage is conspicuous when chickpeas are planted in sandy-loam soils in late summer or early autumn. Conversely, crop injury is minimized when chickpeas are sown from late autumn into the winter season. Soil temperature suitable for nematode attack and development are not reached until late spring allowing the plant to escape the damaging early root invasion process. For this reason root-knot nematodes, although important on other summer crops, do not constitute a problem in the Mediterranean basin.

The nematodes, however, are a serious problem in tropical zones. In India, Upadhyay and Dwivedi (1987) treated field plots infested with 4.6 *M. incognita* juveniles/cm^3 soil with carbofuran and observed increases in yield of 40%. Yield losses of 31–37% were detected in nematicide trials when *M. incognita* was present at 2.5 juveniles/g of soil (Reddy, 1984).

Economic threshold level

In pot experiments the growth of chickpea was negatively affected when soil populations of *M. incognita* (Nath *et al.*, 1979) and *M. javanica* (Srivastava *et al.*, 1974) exceeded 0.2 juveniles/g of soil. Ahmad and Husain (1988) detected reductions in shoot length and total plant weight at densities of 1 juvenile/g of soil in pot studies. However, under field conditions yield losses differ greatly between countries. This variation is caused by differences in soil type, environmental factors existing during the growing season in the different climatic zones and to complex disease interrelationships. Therefore, field studies are required to estimate tolerance limits and make yield loss assessments.

Fig. 4. Root of chickpea showing galls caused by infestation of *Meloidogyne incognita*.

Control

Crop rotation, including fallow, is currently used to control root-knot on chickpea. Rotation is complicated by the wide host range of species of *Meloidogyne*. Nevertheless, peanut and winter cereals are non-hosts of *M. incognita* and *M. javanica* and cotton is a non-host of *M. incognita* and *M. arenaria*. Saka and Carter (1987) listed hosts and non-hosts of *M. incognita*.

Sowing in late autumn, when soil temperature drops below 18°C and harvesting in spring can limit or prevent nematode reproduction (Roberts *et al.*, 1981). Chickpea should not be planted in early autumn in fields planted in the previous season to a summer host plant. In India, postponing sowing to late autumn has also been shown to suppress yield loss (Gaur *et al.*, 1979).

Weeds are often excellent hosts for root-knot, therefore, good weed control can be important to a rotation programme both under non-host and fallow conditions.

Organic amendments have been incorporated into infested soils for control purposes. Attempts have also been made to control root-knot nematodes in pots with sawdust (Singh & Sitaramaiah, 1971) and plant leaves (Kaliram & Gupta, 1982). Although some nematode control and increased plant growth was obtained, the use of these materials in the field is often not practical on a expanded scale because of poor farmer access to the material, costs of transport, or the large amounts needed for adequate control.

Although nematicides are effective they can not be used to control nematodes economically on chickpea.

Resistance

Chickpea lines and a few cultivars have recently been identified as resistant to root-knot nematodes. The breeding material and cultivars available have poor agronomic characteristics and are presently of little importance to practical agriculture.

Meloidogyne artiellia

This root-knot nematode causes yellowing and stunting of plants and severe losses in yield (Fig. 5). *M. artiellia* was first reported from cabbage in England (Franklin, 1961) and later on chickpea in

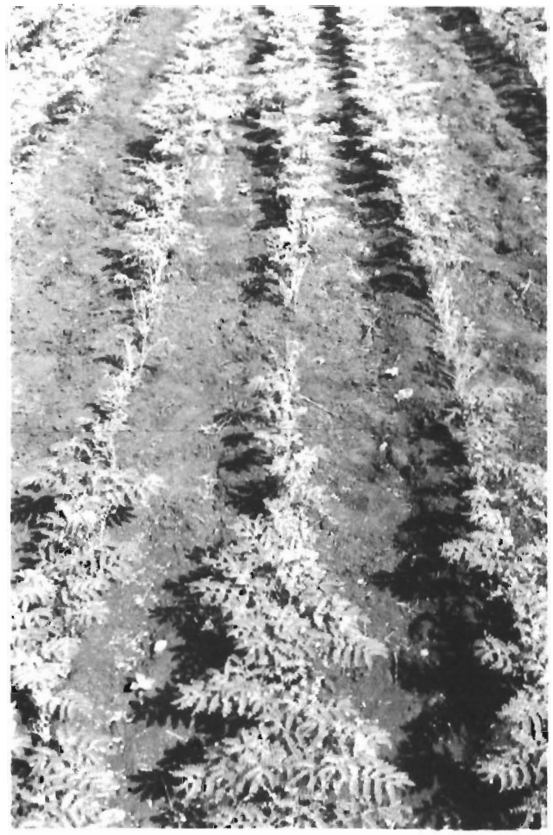

Fig. 5. A chickpea crop showing yellowing and stunting of plants infested by *Meloidogyne artiellia* in Syria.

Spain (Tobar-Jimenez, 1973), Italy (Greco, 1984) and Syria (Greco *et al.*, 1984). The nematode differs significantly from the previous mentioned species of *Meloidogyne* both in morphometrics and ecology. Galls produced on chickpea by Syrian populations of the nematode are indistinct and almost totally absent in Italian populations. The most obvious symptom of nematode attack is the presence of large egg-masses on the roots. Because of their size they can be confused with cyst nematode females when observed with the naked eye (Plate 4E).

Other hosts

The nematode has a wide host range. Di Vito *et al.* (1985) found many cruciferous spp., cereals (except oat and maize) and leguminous crops (except lentil, haricot bean, cowpea, lupin, soybean and sainfoin) as good or very good hosts for the nematode. All species in the Solanaceae, Rosaceae, Linaceae, Compositae, Cucurbitaceae, Chenopodiaceae and Umbelliferae, were poor or non-hosts.

Biology

Investigations by Di Vito and Greco (1988*a*) demonstrated that second stage juveniles can invade chickpea roots at 10°C, but at this temperature adult stages were not formed after 66 days (Fig. 6). Nematode development also was retarded at 30°C. In Italy and Syria large egg-masses can be observed in early April on the roots of chickpea sown the previous autumn and in early May on spring sown chickpea. Juveniles may hatch soon after the completion of embryogenesis.

The presence of a combination of insufficient rainfall and high temperature in spring in the Mediterranean basin often causes poor root growth which limits juvenile emergence from newly produced eggs. This interplay of biotic and abiotic factors is responsible for limiting the nematode to only one generation per growing season. However, if rainfall occurs late in the season, eggs hatch immediately and second stage juveniles survive during dry and hot summers in a anhydrobiotic condition (Di Vito & Greco, 1988*a*). The nematode seems to be adapted to a wide range of environmental conditions and develops well in a large variety of soil types including those containing 30–40% of clay.

Consistent damage is caused to chickpea in Syria where this crop is rotated with durum hard wheat and barley, both good hosts for the nematode. A survey conducted in 1983 (Greco *et al.*, 1984) revealed that 12% of chickpea fields in the northern part of the country were infested.

Economic threshold level

Microplot experiments have shown that chickpea are highly susceptible to nematode attack when population densities exceed 0.14–0.016 egg/cm^3 of soil for winter and spring sown crops, respectively (Di Vito & Greco, 1988*b*).

Control

The parasite can be effectively controlled by rotating chickpea with non-host crops. In the Mediterranean area cotton, sugar beet, potato, oat, maize, lentil, tomato and melon are poor or non-host crops suitable for *M. artiellia* control programmes. The length of the rotation should be designed to reduce soil densities below threshold levels, which generally requires a two to four year period with non-host crops.

Although nematicides have been shown to be effective experimentally, they cannot be used economically on the crop. No attempts have been made to screen chickpea lines or cultivars for resistance to this nematode.

Heterodera

A cyst nematode infesting chickpea was found in Syria by Mamluk *et al.* (1983) and was observed as the causal agent of severe chickpea decline in the Idleb province and other areas in the north of the country (Greco *et al.*, 1984). The nematode was described as *Heterodera ciceri* by Vovlas *et al.*

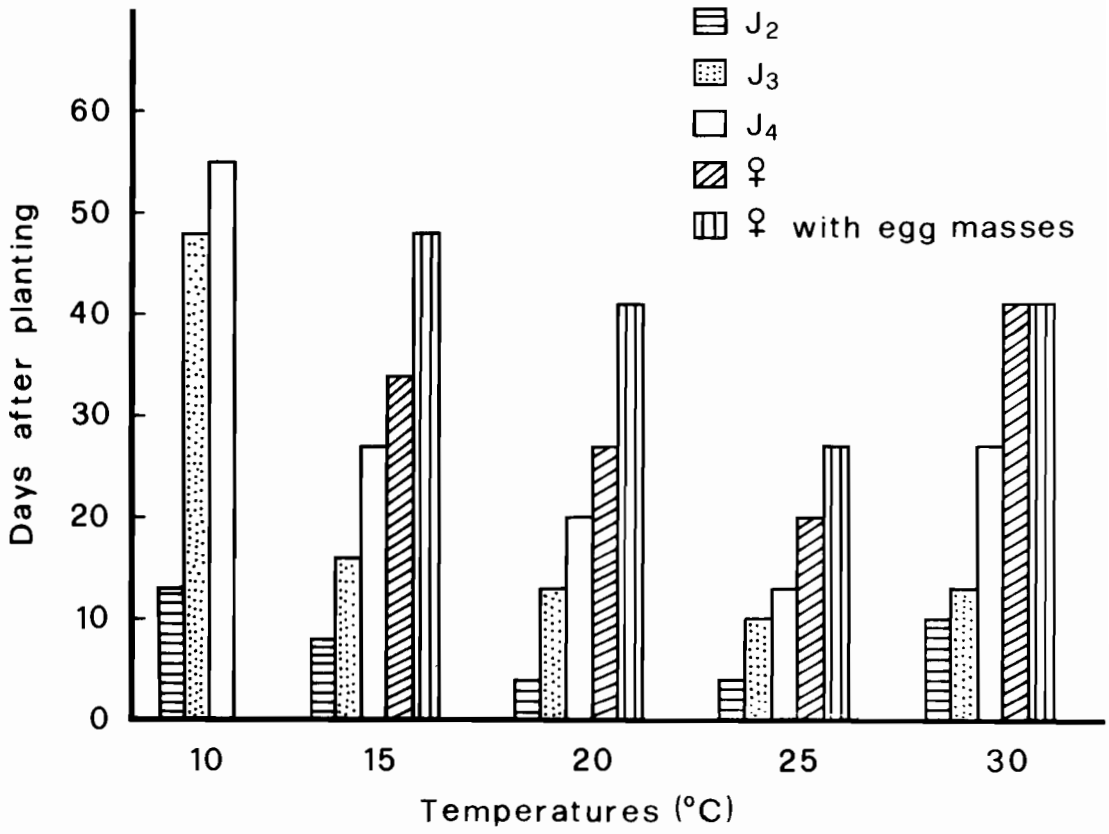

Fig. 6. Days after planting chickpea required by *Meloidogyne artiellia* to develop different life stages at various temperatures (From Di Vito *et al.*, 1988*a*).

in 1985. The nematode belongs to the *H. trifolii* group and differs from *H. trifolii* in having abundant males, different host range, and distinct morphological characteristics (Vovlas *et al.*, 1985; Sikora & Maas, 1986). The nematode has not been detected outside southern Syria.

Other hosts

The host range is confined to members of Leguminosae (Greco *et al.*, 1986*b*). The nematode reproduces well on chickpea, lentil, pea and grasspea (*Lathyrus sativus* L.) and poorly on *Vicia* spp., haricot bean, lupin and lucerne. Broad bean and several clovers are very poor or non-hosts. In tests with plants in thirteen botanical families the nematode produced a few females only on carnation.

Biology

Although the nematode invades chickpea roots at 8°C, development only occurs at temperatures of ≥ 10°C (Kaloshian *et al.*, 1986*a*). Root invasion is suppressed at 30°C. Females may protrude a small gelatinous matrix, which is void of eggs (Kaloshian *et al.*, 1986*b*). In the field large numbers of white females (Plate 4F) can be seen at the beginning of April or two weeks later on the roots of winter and spring sown chickpeas, respectively. Cysts usually appear 14 or 16 days later (Greco *et al.*, 1988*a*).

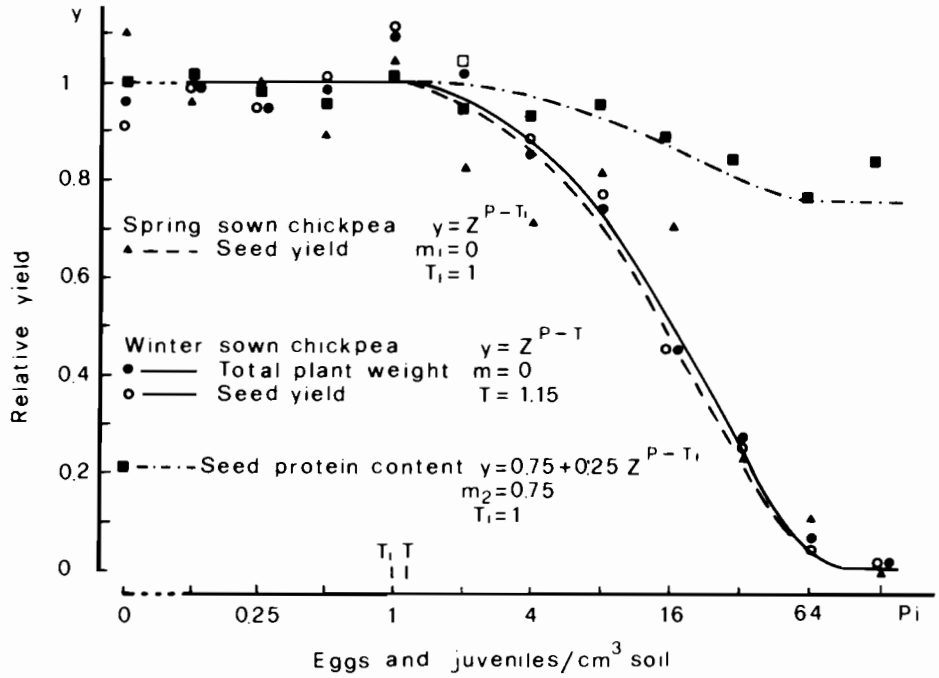

Fig. 7. Relationship between population densities of *Heterodera ciceri* at sowing and relative total plant and seed weights and grain protein content of chickpea grown in Syria, as fitted by the equation y = m + (1-m)zP-T proposed by Seinhorst (From Greco *et al.*, 1988*a*).

Economic threshold level

The tolerance limit of chickpea to *H. ciceri* is 1 egg/cm³ of soil (Fig. 7). Yield losses of 20 and 50% can be expected in fields infested with 8 or 16 eggs of the nematode/cm³ of soil, respectively. Complete crop failure occurs in fields infested with ⩾ 60 eggs/cm³ soil (Greco *et al.*, 1988*a*). Under field conditions severe chickpea decline can be observed from the end of April onwards. At harvest, protein content of chickpea grain produced in infested fields is significantly reduced, thus lowering nutritional value of the grain.

Control

Since this nematode has a rather narrow host range, it can be controlled effectively by crop rotation. An annual decline of 50% of the nematode population using non-host crops has been reported (ICARDA, 1986). These results demonstrated that short rotations are effective in reducing the nematode densities to or below the tolerance limit.

Resistance

Twenty chickpea lines out of 2001 tested had low *H. ciceri* infestation levels and were rated resistant by Di Vito *et al.* (1988). Confirmation of resistance and evaluation for yield performance, however, is required before they can be used commercially.

Pratylenchus

Root lesion nematodes cause large cavities and necrosis in the cortex of chickpea roots (Plate 4H; Fig. 8). Eggs are deposited in the cavities within the root. Several generations may develop in a

growing season, each taking about one month. Plant growth is further reduced through root damage caused by interrelationships with soil-borne root pathogens and adverse effects on *Rhizobium* nodulation. The reduced root system decreases plant resistance to drought conditions which make these nematodes important in the dry areas in both the semi-arid and dry regions of the world. In the absence of a host crop, *Pratylenchus* survive in the soil as eggs, juveniles or adults. In dry areas they survive in a anhydrobiotic condition (Glazer & Orion, 1983).

Although these nematodes are found in most fields, the damage they cause is not as severe as that caused by root-knot and cyst nematodes. Yield losses of 25 and 75% in winter and spring sown chickpea were obtained in Syria in a field infested with *P. thornei*, respectively (Greco *et al.*, 1988*b*).

The most important lesion nematode is *P. thornei* which has a cosmopolitan distribution. The nematode was detected in 74% of chickpea fields in Syria (Greco *et al.*, 1984). In India, population densities $\geq$ 0.1/g of soil were responsible for significant growth reduction while densities of $\geq$ 4/g of soil also reduced germination (Walia & Seshadri, 1985*a*). Little is known about other species of *Pratylenchus* on chickpea, undoubtedly several could infect and possibly damage this crop.

Control

Specific control measures have not been developed for lesion nematodes on chickpea. Most species of *Pratylenchus* have wide host ranges, therefore, control by rotation is problematical. This is especially true in rotations with cereals which are often good hosts for the lesion nematode.

Although chemical control is not an economically acceptable control measure, it has been demonstrated that split applications of aldicarb at 10kg a.i./ha at sowing and after seed germination, will control *P. thornei* and increase yield (Greco *et al.*, 1988*b*). Seed treatment with aldicarb, carbofuran and fensulfothion gave satisfactory control of the nematode in pot tests (Walia & Seshadri, 1985*b*) whereas under field conditions aldicarb failed to control the nematode (Greco *et al.*, 1988*b*). The lack of basipetal translocation of present day nematicides prevents extended protection of the expanding root system from nematode penetration and limits the effectiveness of seed dressing for control purposes at the present time.

Rotylenchulus

The reniform nematode, *Rotylenchulus reniformis*, a semi-endoparasite, has been found associated with chickpea mainly in India (Rashid *et al.*, 1973) and also in Ghana (Edwards, 1956). Another reniform nematode, *R. macrosoma*, occurs in chickpea fields in Syria. The nematode survives in the soil in the juvenile and adult male stages. Immature females penetrate the root and become established in the endodermis (Rebois *et al.*, 1975). The kidney shaped females produce a gelatinous matrix which covers the female body in which about 50 eggs are laid. Soil adhering to this matrix often can hamper detection of the female on the root surface.

Economic threshold level

Mahapatra and Padhi (1986) demonstrated in greenhouse tests that population densities of $\geq$ 0.5 nematodes/g of soil reduce plant growth and that growth reductions of 80% occur at 10 nematodes/g of soil.

Control

Rotations designed to reduce nematode densities are difficult to develop because of the nematode's wide host range. The only acceptable recommendation is to avoid growing chickpea in heavily infested fields and to test local crops for non-host status before suggesting alternative cropping systems. Although nematicides are effective in control of *R. reniformis*, they are not an economic alternative on chickpea.

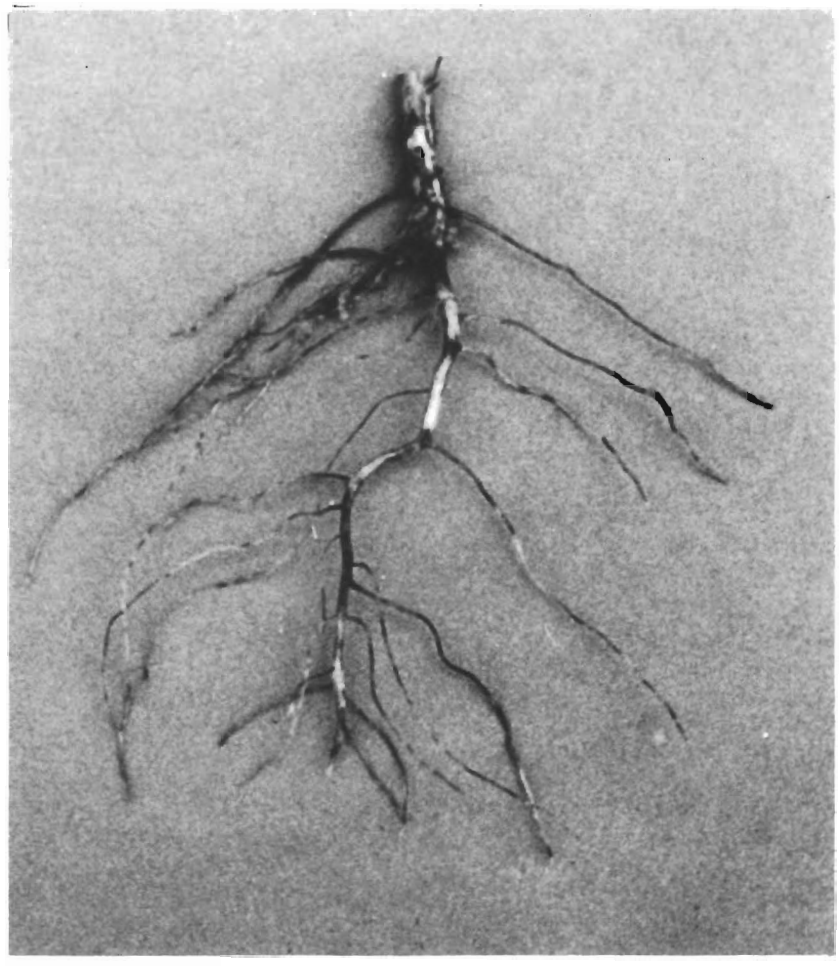

Fig. 8. Roots of chickpea exhibiting necrotic lesions caused by a lesion nematode *Pratylenchus* sp.

Other Nematodes of Chickpea

Several other nematode species have been found associated with chickpea. Species of *Pratylenchoides, Helicotylenchus, Tylenchus* and *Tylenchorhynchus* were commonly found associated with chickpea in Syria (Greco *et al.*, 1984). In India *Helicotylenchus sharafati, Hoplolaimus dimorphicus* (Mulk & Jairajpuri, 1974, 1975) and *Tylenchorhynchus vulgaris* (Gill & Swarup, 1977) were detected. Species of *Tylenchus, Scutellonema* and *Aphelenchoides* were observed in Sudan (El Tigani *et al.*, 1970) and *Tylenchorhynchus annulatus, Helicotylenchus digonicus* and *Hoplolaimus indicus* in Pakistan (Maqbool, 1986). With the exception of *Tylenchorhynchus vulgaris* the pathogenicity of these nematodes on chickpea has not been demonstrated. Gill and Swarup (1977) demostrated that densities of *T. vulgaris* ranging from 10 – 200 000/500 g of soil caused increasing reductions in plant growth.

Cowpea

Cowpea (*Vigna unguiculata* (L.) Walp. aggreg.) is known in the dry grain form as black-eyed pea, southern bean, China pea, kaffir-pea, marble pea and in the green pod form as yard-long bean, asparagus bean, Bodi bean and snake bean. It is an annual plant with a great deal of varietal variation including climbing, bushy prostrate and erect forms that probably originated in Africa or Southeast Asia. Although the plant is used mainly for dried seeds it is also used as a vegetable, pot-herb, and green manure. It is a hot weather crop well adapted to the semi-arid regions and is usually grown under rainfed conditions on well drained soil (Kay, 1979). It is usually intercropped with cereals especially sorghum and millet and can be planted without land preparation.

Meloidogyne

Root-knot nematodes are serious pests of cowpea on a worldwide basis. *M. incognita* and *M. javanica* are the major species found on cowpea in most growing regions. Other important species are *M. arenaria* reported from Brazil, Cyprus and U.S.A.; *M. hapla* from Brazil; *M. ethiopica* from Tanzania; *M. africana* from East Africa; and *M. kikuyensis* from Kenya.

Whereas *M. incognita* was widespread in Georgia cowpea fields causing an estimated 5–10% yield loss, all other species detected were sporadic in occurrence with losses estimated at below 1% (Toler *et al.*, 1963). In California *M. javanica* and *M. incognita* are considered serious pests (Thomason & McKinney, 1960). Robinson (1961) reported the common occurrence of *M. javanica* in Australia. *M. arenaria* present in soil taken from peanut fields caused severe damage to cowpea in Alabama.

Symptoms

Symptoms of damage induced by root-knot include patches of stunted and yellowed plants (Fig. 9). Severe damage can lead to reduced numbers of leaves and buds.

Economic threshold level

The threshold level, determined in glasshouse studies in sterilized soil, was 100 juveniles/500g of soil (Sharma & Sethi, 1975). Visual symptoms of damage first occurred at 1000 and 10 000 juveniles/500g of soil. *M javanica* densities of 1000 or 10 000/500g of soil caused growth reductions in pot tests (Gupta, 1979). At high densities severe root galling occurs (Fig. 10).

Disease complexes

The presence of heavy infestations of *M. javanica* on a cowpea cultivar tolerant to wilt caused by *Fusarium oxysporum* f. *tracheiphilum* caused increased wilting when compared to the susceptible cultivar (Thomason *et al.*, 1959).

High densities of *M. incognita* also have been shown to lead to poor nodulation and decreased nitrogen levels in the plant (Sharma & Sethi, 1976*a*; Abedinia, 1978; Ali *et al.*, 1981). In these studies root-knot galls were found on nodules and nodules were also produced on the surface of nematode galls. The symbiotic interrelationship was not affected at low population densities. Taha and Kassab (1980) reported that *M. javanica* when inoculated simultaneously with *Rhizobium* sp. did not affect nodulation.

Control

Crop rotation can be an efficient means of controlling root-knot nematodes in this crop. Proper selection and placement of non-host crops and resistant cultivars in rotation with susceptible cultivars can lead to control and yield increase. The wide host range of the three major species of root-knot and the poorly understood host spectrum of most other species requires careful selection and testing

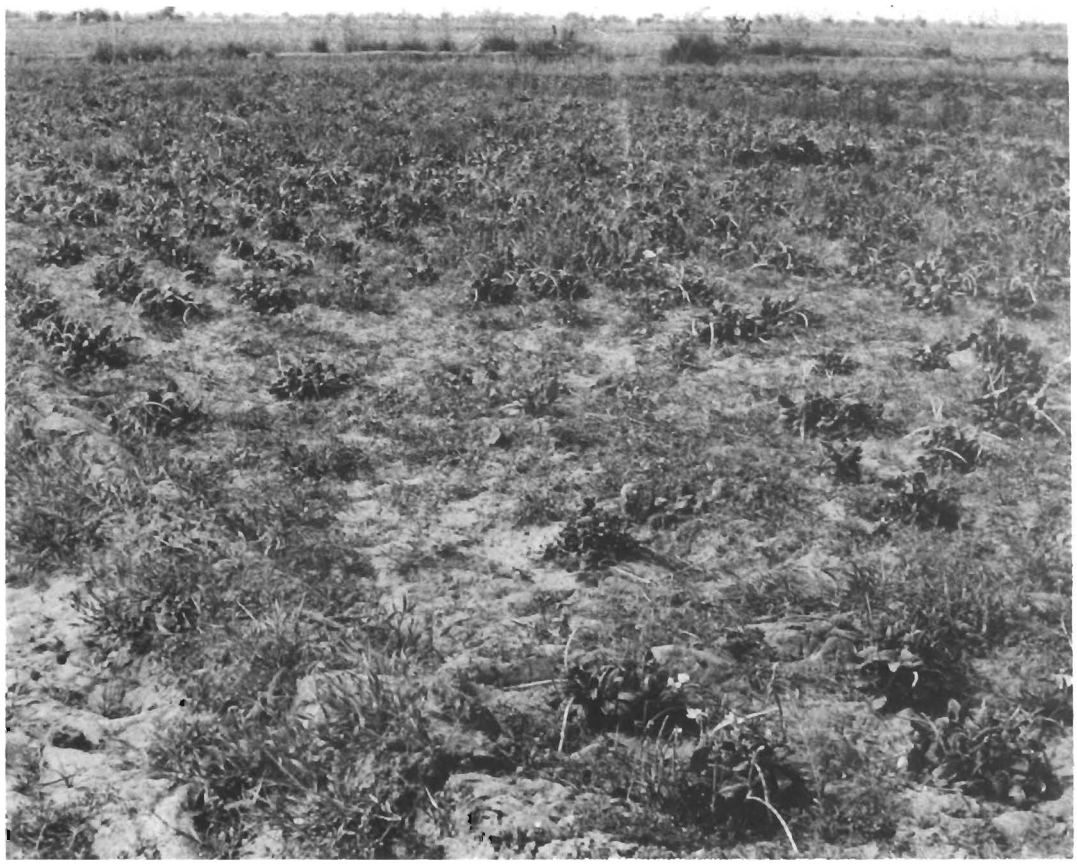

Fig. 9. Poor growth of cowpea infested with *Meloidogyne javanica* in Nigeria (Photo: J. Bridge).

prior to development of rotation schemes. Proper selection of non-hosts also is required because of the presence of races within the genus *Meloidogyne*.

Da Ponte (1972) recommended rotations with graminaceous crops or *Crotalaria*. Populations of root-knot decreased greatly when compared to fallowed plots when *C. spectabilis* Roth. was grown as a weed free cover crop (Rhoades, 1964). Mulching with cowpea foliage was also highly effective in suppressing populations (Rhoades & Forbes, 1986).

Egunjobi *et al.*, (1986) showed that *M. javanica* populations were lower when cowpea and maize were grown under mixed rather than under sole cropping systems. The results suggested that this cropping system could be used for control of the nematode. Castillo *et al.*, (1976) reported that one crop of paddy rice was sufficient to effectively reduce root-knot nematode infestations in succeeding susceptible legume crops. The reduction was greater than with rotations with non-host crops.

Dukes *et al.* (1979) demonstrated that resistant cultivars were more effective than non-fumigant nematicides in reducing root-knot damage.

Organic amendments have been used to suppress root-knot nematode populations on a number of crops (Singh & Sitaramaiah, 1966). Neem cake incorporation in the previous crop, caused reduction in the density of all nematodes in the soil on the following cowpea crop (Jain & Hasan, 1986). Cocoa pod husks incorporated at 6000 kg/ha caused 28% reductions in galling and 6.7% increases in yield (Egunjobi, 1985; Egunjobi & Olaitan, 1986).

Fig. 10. *Meloidogyne incognita* galls on cowpea in Nigeria (Photo: J. Bridge).

Although fumigant and non-fumigant nematicides reduce root-knot densities and can cause significant increases in yield, their use on cowpea is not economical. Although seed treatment with aldicarb, carbofuran and fenamiphos caused nonsignificant decreases in *M. incognita* galling, mean yield increased significantly in pot tests (Parvatha Reddy, 1984).

Resistance

Thomason and McKinney (1960) reported that all 44 cowpea cultivars and plant introductions tested showed some resistance to *M. incognita*, but were moderately to highly susceptible to *M. javanica*. Satisfactory levels of resistance to the three major root-knot species were not found in 362 lines evaluated by Caveness (1965) in Nigeria. Amosu (1974) and Ogbuji (1978) reported a number of cultivars with some resistance to *M. incognita*. Of 241 lines tested in Nigeria, four were considered resistant and 28 moderately resistant to *M. incognita* (Caveness, 1979). He considered the lack of good sources of resistance critical for crop improvement breeding programmes. Bridge (1987) listed known cultivars and breeding lines with moderate to high levels of resistance to the various root-knot species attacking the crop. Sharma and Sethi (1976*b*) reported that fifteen lines and three cultivars were resistant to *M. incognita*. In field trials with 104 lines and cultivars, eleven showed high degrees of resistance to a population mixture of *M. javanica* and *M. incognita* (Patel *et al.*, 1977). Yield increases from three cultivars resistant to *M. incognita* ranged from 19–69% (Dukes *et al.*, 1979). Hadisoeganda and Sasser (1982) reported that variability in susceptibility exists to species of root-knot and to *M. incognita* races 1, 2 and 3. All lines tested were, however, resistant to *M. incognita* race 4. Of 289 lines screened for resistance to *M. incognita* in India 93 exhibited some

degree of resistance (Singh & Reddy, 1982). Sasser and Hartman (1985) reported that of the 27 lines tested most were resistant to *M. hapla* and *M. incognita*, moderately resistant to *M. javanica* and mostly susceptible to races of *M. arenaria*. A coordinated effort is needed to evaluate these lines again for sources of resistance.

Heterodera

The cyst nematode *Heterodera cajani* has been found associated with cowpea in a number of regions of India (Koshy & Swarup, 1971*b*) and has been detected on cowpea in Egypt (Aboul-Eid & Ghorab, 1974). The host range is limited to the Leguminosae or Pedaliaceae (Sharma & Swarup, 1984). Although the nematode seems to be widespread in India, crop loss assessment data is lacking (Luc, 1985). In a glasshouse study an Egyptian population retarded emergence of leaves and retarded and reduced the number of flowering buds, flowers, growing pods and yield (Aboul-Eid & Ghorab, 1974).

Economic threshold level

Shoot length was reduced in glasshouse experiments when the population density ranged between 10–20 juveniles/100g of soil (Sharma & Sethi, 1975; Zaki & Bhatti, 1986). Both root and shoot length were reduced at nematode densities of 100/100g of soil (Sharma & Sethi, 1975).

Disease complexes

The nematode can complete its life cycle on nodular tissue and can reduce the number of *Rhizobium* nodules (Sharma & Sethi, 1975). Cowpea growth, was not affected when *Rhizoctonia bataticola* was inoculated prior to, simultaneously or after *Heterodera cajani* in glasshouse tests (Walia & Gupta, 1986).

Control

The most effective control measure for cyst nematodes is rotation with non-host crops. Cowpea rotated with paddy rice may be less affected by the nematode, because of the negative effect of flooding on nematode densities. Although nematicides have been shown to suppress nematode attack they cannot be used economically on this crop.

Resistance

Although resistance to this nematode has not been detected, the cv Barsati Mutant has been reported to be tolerant to the nematode (Sharma & Sethi, 1976*b*).

H. glycines and *H. schachtii* have been reported on cowpea but are at present of unknown economic importance on the crop. *H. vigni* reported from cowpea is now recognized as a junior synonym of *H. cajani* (Kalha & Edward, 1979). Nine cultivars of cowpea tested for susceptibility to *H. glycines* were resistant to the nematode (Epps, 1969).

Rotylenchulus

The reniform nematode, *Rotylenchulus reniformis*, has been found associated with cowpea in India and the U.S.A. Yield losses were detected when soil was treated with 1, 3-D or ultra-high frequency electromagnetic energy (Heald *et al.*, 1974). Crop loss assessment, however, is still needed to determine the true importance of the nematode on the crop, because of the broad spectrum activity of the fumigant and electromagnetic energy.

Races

The nematode has been divided into two races on their ability to parasitize cowpea, castor or cotton with race A reproducing on all three hosts and race B only on cowpea (Dasgupta & Seshadri, 1971).

Economic threshold level

The nematode reduced emergence by 7–9 days and seedling density by 6–11% at densities of 1/g soil in glasshouse studies (Nanjappa *et al.*, 1978). Significant reduction in height, and fresh shoot and root weights were observed in pot tests with 1000 juveniles/plant (Gupta & Yadav, 1980).

Control

The narrow host range of the nematode, especially that of race-B, should allow excellent control with crop rotation. For example, nematode densities were suppressed when cowpea was grown intercropped with maize (Egunjobi *et al.*, 1986). Although breeding lines have been found with resistance to the nematode commercial cultivars are not yet available (Thakar & Patel, 1984).

Although, solarization was considered an effective method for reducing nematode densities to a depth of 15 cm (Heald & Robinson, 1987) it probably can not be used economically on this crop.

Other Nematodes of Cowpea

Hoplolaimus seinhorsti, an endoparasitic nematode, was shown to cause severe damage to cowpea in Nigeria. The nematode induced marked necrosis in both the lateral and secondary lateral roots in field plot studies in Nigeria (Bridge, 1973). After nine weeks, most of the lateral feeder roots were very badly rotted or missing. The number of nematodes increased to a maximum of 1110/root system after five weeks.

Haricot Bean

Haricot bean (*Phaselous vulgaris* L.) also known as french, common, kidney, string, salad bean, runner bean, or snap bean originated in Mexico between 2300 and 4000 B.C. It is the most widely cultivated food legume (Table 3). In 1985 approximately 25.3 million hectares were in production. Among the food legumes *P. vulgaris* is the most uniformly distributed crop in the world and the main food legume in the Americas, where it is of great agricultural importance especially in Brazil, Mexico, and the U.S.A. In Asia haricot beans are extensively cultivated in India (34% of the world acreage) with extensive planting also in China, Burma, Indonesia, Iran, Japan, Thailand and Turkey. In Africa the main producers are Burundi, Cameroon, Malawi, Rwanda, Tanzania, Uganda, and Zaire, while in Europe this pulse is important only in Portugal, Rumania, Spain, and Yugoslavia. Nearly all countries in the tropics and subtropics produce *P. vulgaris* for dried grains which are eaten whole or mashed mainly in soup.

In addition to the dried grain, 0.4 million hectares are used for fresh green seeds, whole pods or are canned or frozen. In several countries beans also are cultivated in glasshouses for the high value fresh vegetable market.

Phaseolus spp. are sensitive to low temperature, therefore, in the subtropics they are cultivated during the warm seasons and sown early in the spring or in summer after the winter crop. The crop is therefore infected with many nematode species that have higher temperature optimums. The crop is grown as a sole crop, semi-climbing and as a climbing bean in relay systems with maize. Beans are often grown intercropped with maize. Maize which predominates as an intercrop, is a major constraint to increased bean production (CIAT, 1985).

Heterodera

The soybean cyst nematode *Heterodera glycines*, besides infesting soybean also attacks *Phaseolus* spp. This is important because *Phaseolus* beans are often rotated with soybean. Crop loss due to *H. glycines* infestations on haricot beans have been reported mainly in the U.S.A. (Noel, 1982).

Symptoms

Nematode attack is similar to that observed on soybean. In glasshouse tests haricot bean was less susceptible than soybean to *H. glycines* (Abawi & Jacobsen, 1984). Data on yield loss incurred in the field is lacking. The level of invasion and reproduction of *H. glycines* on haricot bean is similar to or larger than encountered on soybean (Abawi & Jacobsen, 1984; Melton *et al.*, 1985).

H. glycines must be considered a potential problem on haricot bean in areas where the nematode occurs, especially if it is rotated with soybean or other host crops. Abawi and Jacobsen (1984) postulated that because of the larger root size of haricot bean compared to that of soybean, reproduction rates of *H. glycines* on the former would be larger under field conditions and thus leading to larger soil population densities.

Control

The control measures devised for control of *H. glycines* on soybean should also be used when dealing with this nematode on haricot beans. There seems to be large variation in cultivar susceptibility to the nematode. The cultivars Kentucky Wonder Pole and Kentucky Wonder Improved Rust Resistant are resistant to *H. glycines* (Melton *et al.*, 1985) and should be recommended to avoid yield losses and reduce nematode population densities.

Meloidogyne

M.incognita and *M. javanica* appear to be the most common root-knot species of haricot beans and have been reported causing damage in the Americas, Africa and Asia. There is probably no country in the tropics and subtropics in which beans are not affected by root-knot nematodes.

Symptoms

Although symptoms of nematode attack on aerial parts are similar to those caused by these nematodes on other crops, gall size on the roots of *Phaseolus* spp. is variable and may be nearly undetectable (Blazey *et al.*, 1964). In the latter case the only visible symptom on the roots is the presence of large egg-masses. However, severe galling was observed in Brazil (Lordello & De Oliveira Santos, 1960) and in Chile (Plate 4C; Fig. 11). Due to the large number of types and cultivars of haricot bean and to the presence of root-knot races (See chapter 7.) the intensity of damage caused by *Meloidogyne* spp. varies greatly.

Disease complexes

M. incognita will reduce levels of bacterial nodulation on haricot bean (Singh & Reddy, 1981) and has been shown to increase the severity of *Macrophomina phaseolina* (Al-Hazmi, 1985). Hutton *et al.* (1972) detected increased wilting by *Fusarium solani* f.sp. *phaseoli* on beans attacked by *M. arenaria* and *M. javanica*. Extreme root rotting is often associated with root-knot damage to the root (Plate 4G).

Economic threshold level

The extent of yield loss caused by *Meloidogyne* spp. to haricot bean has not been assessed. The information available were derived from yields obtained in nematicide trials. Sharma (1981) observed significant growth reduction in soil infested with *M. javanica* at 1 egg/g of soil and a reduction of 82% at 10 eggs/g of soil in glasshouse experiments.

Control

Abiotic stress caused by adverse environmental factors and interrelationships between root-knot nematodes and other soil-borne pathogens are responsible for severe damage under field conditions. Planting time certainly plays an important role on the amount of yield losses. Most species of *Meloidogyne* found in the tropics and subtropics would be unable to initially invade bean roots if

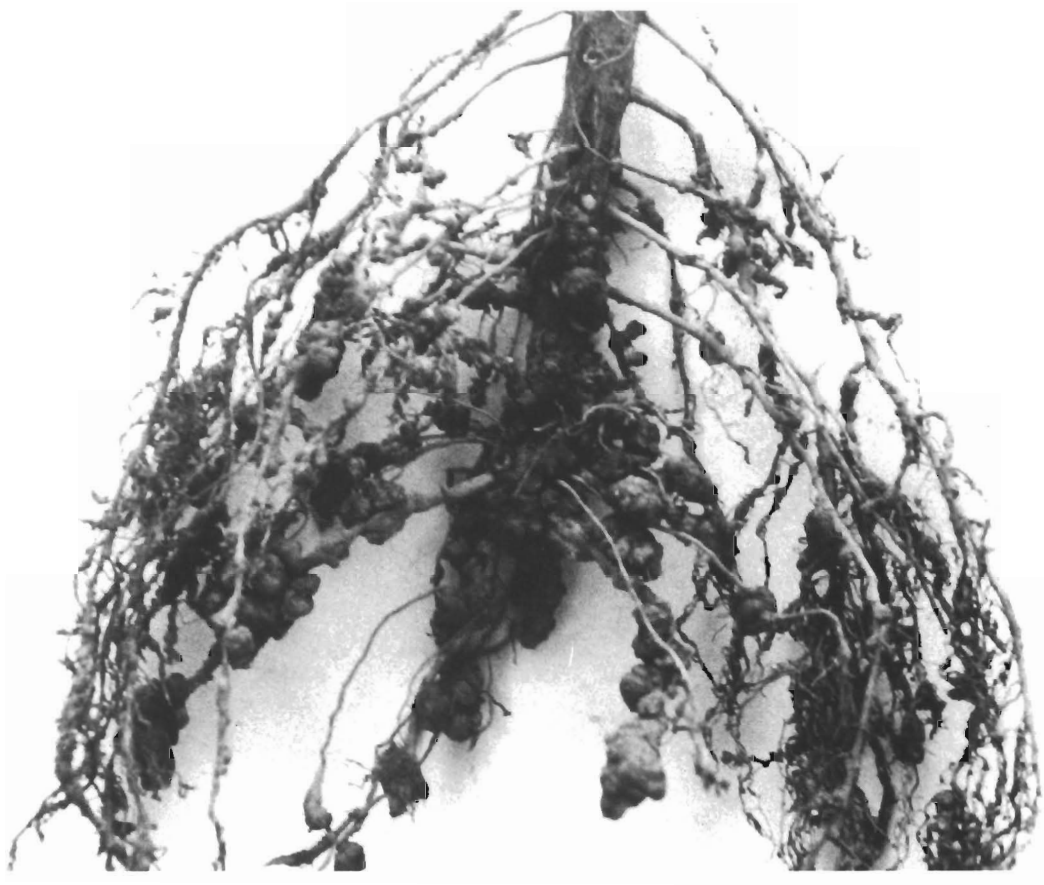

Fig. 11. Roots of haricot bean heavily galled by root-knot nematodes, *Meloidogyne* spp., in Chile.

the crop is sown at the end of winter or early in the spring, when soil temperatures are below 15°C. Escape from early root penetration would give the plant a head start. Yield would increase because the larger root system could withstand the damage caused by delayed nematode invasion. Moreover, these beans would be harvested by the end of spring or early in summer, thus limiting the number of nematode generations produced (often to only one) and overall population densities. Sowing bean late in spring or in summer would cause early nematode invasion, the development of multiple generations, severe damage and high soil densities.

Root-knot nematodes can be controlled satisfactorily with nematicides at the same rates suggested on other crops. Application of nematicides on 30–35 cm wide bands would reduce treatment costs. Seed treatment with oxamyl at 3–10% (W/V) prevented development of *M. incognita* in glasshouse tests (Rodriguez-Kabana *et al.*, 1976). Efficacy under field conditions was not determined.

Haricot beans have rather short growing seasons and therefore reduced rates of nematicides may be sufficient to give control and reduce possible environmental contamination. The use of nematicides on beans grown for the fresh vegetable market, because of the short growing season, must be closely monitored.

In countries with sufficient solar energy levels, root-knot nematodes can be effectively controlled by a 4–8 week solarization, assuming that the land will remain uncropped during summer. Control is higher when this method is used in the glasshouse. Solarization is lethal to other soil borne

pathogens and weeds but is only effective in the upper soil layers and does not reach nematodes that may migrate up to the crop. The combined use of solarization and heated water increase soil penetration and efficacy (Saleh *et al.*, 1988). The costs involved, however, may limit the use of this technology for haricot bean production.

When beans are grown for green pod or green seed production, roots should be destroyed as soon as possible after harvest to prevent further nematode development on the root tissue remaining in the soil.

Resistance

The breeding lines B–3864 (Fassuliotis *et al.*, 1967) and B–4175 (Wyatt *et al.*, 1980), both resistant to *M. incognita*, were derived from the Mexican line PI 165426. Further selection enabled Wyatt *et al.* (1983) to release the cultivar Nemasnap, the first bush snap bean cultivar resistant to *M. incognita*. More bean cultivars resistant to *M. incognita* are mentioned by Blazey *et al.* (1964). According to Hartman (1971) resistance to *M. incognita* in haricot bean is linked to three pairs of recessive genes.

In Brazil, Ribeiro and Ferraz (1983) tested 49 cultivars and lines and found that 37-R, Honduras–35, 51051, and Rajado Ag. 496 could be considered resistant to *M. javanica* although data were variable. In Kenya the cultivars Kahuti, Red Haricot, Rono, Saginaw, and Kiburn were resistant to local populations of *M. incognita* and *M. javanica* (Ngundo, 1977).

Assuming that the mentioned resistant cultivars have good agronomic attributes, they should be integrated into control systems in areas infested with root-knot nematodes.

Rotylenchulus

The reniform nematode, *Rotylenchulus reniformis*, also damages haricot bean especially, but not only, in southern U.S.A. and tropical American countries (Tarte, 1971). Investigations concerning yield loss assessment and control have been undertaken (McSorley, 1980; McSorley *et al*, 1981; McSorley & Pohronenzy, 1984). Nematode threshold levels, however, have not been determined.

Satisfactory nematode control had been obtained with six foliar sprays of oxamyl at 0.56 kg a.i./ha combined with a soil drench of 2.24 kg a.i/ha of the same chemical, furrow application of 2.5 kg a.i./ha of carbofuran (Brancalion & Lordello, 1981), and preplant fumigation with 120–240 l of DD/ha (Thames & Heald, 1974).

Rotations with cotton should be avoided because Thames and Heald (1974) demonstrated that preplant soil populations of *R. reniformis* following cotton were ten times higher than following grain sorghum.

Pratylenchus

Several lesion nematodes have been reported on haricot bean causing extensive root necrosis and yield reduction. Among them *Pratylenchus scribneri* (Thomason *et al.*, 1976), and *P. penetrans* (Elliot & Bird, 1985) have been shown to reduce plant growth when soil populations exceed 0.5 nematodes/cm^3 of soil. The cultivars Saginaw, Gratiot, and Kentwood were tolerant to *P. penetrans*. It should be noted that *P. penetrans* reduced vesicular-arbuscular mycorrhiza *Glomus fasciculatum* levels, the latter is important in phosphorous uptake by bean roots. Although *P. penetrans* reproduction was not affected by mycorrhiza, the presence of the fungus symbiont reduced the severity of nematode damage. This indicates that mycorrhizal fungi are important in regulating nematode populations in haricot bean (Elliott *et al.*, 1984).

The cosmopolitan species *P. alleni, P. brachyurus*, and *P. thornei* infect haricot bean. Their importance in crop production is unknown.

Other Nematodes of Haricot Bean

The false root-knot nematode, *Nacobbus aberrans*, another sedentary endoparasitic nematode, is found in the Americas and damages bean in Mexico (Lehman, 1985). Infected roots show large galls similar to those of *Meloidogyne* spp.. Therefore, close observation is required for correct diagnosis. *Nacobbus aberrans* seems to be less pathogenic than root-knot. One generation requires 36 days at 25 °C. The nematode has a wide host range including sugar beet, tomato, potato, pepper, and many cruciferous plants and a variety of weeds. The wide host range complicates the development of effective rotation systems for control purposes. The nematode reproduces well on a number of different soil types and damage is not restricted to sandy soils as is the case with most root-knot species. Nematode populations from different areas may have different host ranges indicating the possible existence of races or pathotypes.

Belonolaimus longicaudatus, B. gracilis, Hoplolaimus galeatus, Zygotylenchus guevarai, Helicotylenchus dihystera, Tylenchorhynchus acutus and *Dolichodorus heterocephalus* have also been reported from haricot bean. Yield increases have been obtained following the application of nematicides in infested fields. Studies on their threshold levels and the exact extent of yield loss associated with these nematodes have not been conducted. These nematodes often occur concomitantly with economically important species e.g. *Heterodera glycines, Rotylenchulus reniformis* and species of *Meloidogyne* and *Pratylenchus*. Nematicides suggested for the control of the latter are usually effective against those nematodes of lesser importance.

Lentil

Lens culinaris Medic., is a small seeded legume that has been cultivated since ancient times in the Mediterranean region and more recently in Asia. Turkey with 34% and India with 33% of total world production are the largest growers of lentil. The crop also is important in Syria, Bangladesh, Iran, Pakistan, Ethiopia, Morocco, Spain and Chile. Lentil is a winter crop normally rotated with cereals and cultivated from sea level to more than 3000 m elevation. It is moderately resistant to low temperature and drought, but yields poorly in wet soils. Lentil is mainly used for human consumption in soup, roasted as a snack and for baking flour. The straw has a high nutritional value and is commonly used as animal fodder.

Heterodera

H. ciceri is a major limiting factor affecting lentil production in North Syria and is the only cyst nematode known to damage lentil in the field. The nematode causes severe stunting and yellowing which can be observed early in April (Plate 4A).

Economic threshold level

Lentil is less susceptible than chickpea to this cyst nematode. The tolerance limit (Greco *et al.*, 1988*a*) on lentil was 2.5 eggs/cm^3 of soil (Fig. 12) compared to 1 egg/cm^3 for chickpea (Fig. 7). Yield losses of 20% occurred in fields infested with 20 eggs/cm^3 of soil, but up to 50% when population densities exceeded 64 eggs/cm^3. Lentil produced on fields infested with *H. ciceri* also contained less protein. *H. ciceri* reproduction in the field was similar to that on chickpea at low population densities. Lower reproductive rates, however, were obtained at $\geqslant$ 2 eggs/cm^3 of soil, due to lower numbers of new cysts produced and reduced number of eggs/cyst (Greco *et al.*, 1988*a*).

Ditylenchus

Ditylenchus dipsaci, the stem nematode, has been reported on lentil in Syria (Greco & Di Vito, 1987) and isolated from the base of the stems showing brownish necrotic lesions. Although the

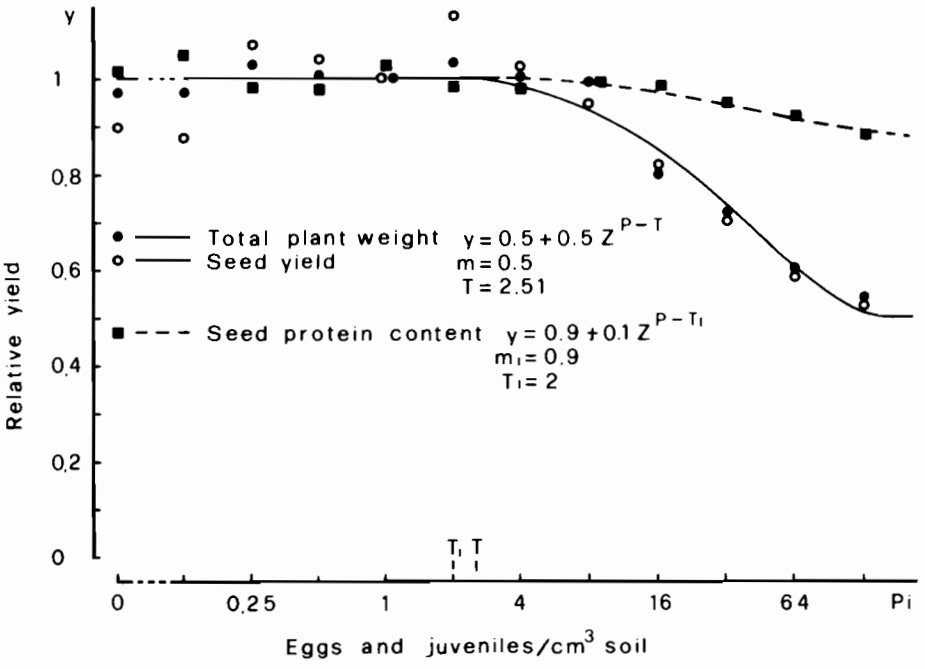

Fig. 12. Relationship between population densities of *Heterodera ciceri* at sowing and relative total plant and seed weights and grain protein content of lentil in Syria, as fitted by the equation y = m + (1-m)zP-T proposed by Seinhorst (From Greco *et al.*, 1988*a*).

impact of the nematode on crop growth has not been measured it can be assumed that *D. dipsaci* could damage lentil if late winters and early springs are cool and moisture levels are high.

Avoiding rotations with other host plants for the nematode, wider row spacing and proper weed control should be adequate to limit damage caused by the stem nematode. Augustin and Sikora (1989*a*) reported on the importance of weeds in Syria on population dynamics of the 'giant race' of *D. dipsaci*.

Other Nematodes of Lentil

Other nematodes occasionally found in the rhizosphere of lentil are *Helicotylenchus mucronatus* (Mulk & Jairajpuri, 1974) and *Meloidogyne javanica* (Prakash, 1981) in India and *M. incognita* in Pakistan (Maqbool, 1986). The root-knot nematode species should not constitute a problem, because lentil is a winter crop and low temperatures are unfavourable for the development of these two species.

Moth Bean

Moth bean (*Phaseolus aconitifolius* Jacq. syn. *P. trilobus* Ait.) is also known as dew and mat bean. It is a perennial or annual creeping legume native to India, Pakistan and Burma. It is of importance in the semi-arid regions where it is eaten whole after frying, split as dhal or used for flour. It has also been planted in California and Texas.

The crop has been reported to be a host of *Heterodera glycines* (Riggs & Hamblen, 1962) and attacked by root-knot nematodes (Bessey, 1911) in the U.S.A. *M. incognita* and *R. reniformis* have been shown to cause significant reductions in plant growth in glasshouse pot tests at levels ≤ 1

juvenile/g of soil (Mishra & Gaur, 1981). In similar tests Zaki and Bhatti (1986) detected reduction in growth caused by *H. cajani* when plants were inoculated with 10 juveniles/kg of soil.

Resistance was detected in two lines tested in microplots (Hasan & Jain, 1986).

Mung Bean

Mung bean (*Phaseolus aureus* Roxb, syn. *Vigna radiata* (L.) Wilczek var. *radiata*), also known as green or golden gram, probably originated in India. It is an annual, warm temperature crop that can be grown in both main growing seasons or as a mid-season crop. It is an important grain crop and is probably best known when used as a vegetable in the form of bean sprouts. It is often rotated with rice where it is planted directly into the stubble by broadcasting or it is intercropped with cereals. Mung bean is tolerant of alkaline and saline growing conditions.

Meloidogyne

All four major species of root-knot nematodes have been shown to parasitize mung bean. Species of *Meloidogyne* are a serious problem in India, Thailand, Philippines, and the U.S.A (Bridge, 1981). *M. javanica* has been shown to cause damage to the crop in the Philippines (Castillo, 1975).

Prasad *et al.* (1971) evaluated field damage and noted that the nematode had a greater impact on grain formation than on pod setting. Root-knot nematodes caused severe galling of the root system, chlorosis and stunting. *M. incognita* caused significant reductions in plant growth, nodulation and nitrogen content of the shoot and root (Hussaini & Seshadri, 1975; Inderjit Singh *et al.*, 1977).

Although no apparent differences in shoot growth were noticed after two months, when 14 day old plants were inoculated with 0, 10, 25, 50 or 100 *M. javanica* egg-masses (Catibog & Castillo, 1975) the severe root galling produced indicated that inoculation at planting would have resulted in greater losses. Losses of 28% were measured in a field infested with a mixed population of *M. incognita* and *Rotylenchulus reniformis* (Castillo *et al.*, 1977).

Control

Standard rotations, especially those including paddy rice, probably limit the degree of damage caused by nematodes on this crop. The extent to which root-knot nematodes affect the crop in multiple cropping situations is not known.

Yield increases of 68% were obtained in field trials when aldicarb was applied at 1.5 kg a.i./ha (Yein *et al.*, 1977; Sultan *et al.*, 1985). Seed treatment with neem cake and neem oil reduced *M. incognita* penetration 75 and 64%, respectively (Vijayalakshmi & Goswami, 1986). Neither treatment was shown to be an economically feasible approach to control.

Although a number of breeding lines have been shown to be moderately resistant to *M. incognita* in India (Mathur *et al.*, 1973; Hussaini & Seshadri, 1976), cultivars with good agronomic characteristics are not available.

Rotylenchulus

Rotylenchulus reniformis is considered to be an important pest of mung bean in the Philippines (Bajet & Castillo, 1974; Castillo, 1975). In pot tests, inoculation with 20 000 juveniles caused 30.5, 48.9 and 41.5% reductions in shoot weight, root weight and yield, respectively (Bajet & Castillo, 1974).

Control measures have not been developed for the nematode. Patel and Thakar (1985) reported that two breeding lines were moderately resistant to the nematode. Castillo *et al.* (1978) showed flooding for 30 days effectively reduced population levels in pot tests.

Other Nematodes of Mung Bean

Mung bean has been reported to be a suitable host for the soybean cyst nematode *Heterodera glycines* (Epps & Chambers, 1959). The nematode caused severe stunting on two cultivars, but did not affect a type breeding line.

Pea

Pisum sativum L., is a food legume used both as a dried grain and fresh vegetable. Pea was originally cultivated for grain, and only in the 16th century did the use of fresh seeds become popular. In the last few decades pea has probably become the most common frozen vegetable in the U.S.A. and in Europe. The U.S.S.R. alone accounts for 61% of the world pea acreage, China (15%) and India (5%). Small amounts are grown in Burundi, Ethiopia, U.S.A., Columbia, Peru, Iran, Pakistan, Denmark, France, Hungary, United Kingdom, and Australia. Only 0.8 million hectares is devoted to the production of green peas for the frozen food industry. Pea straw is also used for livestock feeding.

Heterodera

The cyst nematodes *Heterodera goettingiana, H. trifolii* (Mulvey & Anderson, 1974) and *H. ciceri* (Greco *et al.*, 1986*b*) reproduce well on garden pea. No damage by the latter two species has been reported on pea in the subtropical regions of the Mediterranean where both species occur. The most noxious cyst nematode affecting pea is *H. goettingiana*.

Infested fields show patches in which peas are stunted, chlorotic (Fig. 13) and have few flowers which produce small and often empty pods. Symptoms of nematode infestations are very evident at flowering. Heavily infected plants have large numbers of swollen females on the surface of roots (Fig. 14). The root systems are reduced in size, and exhibit poor nodulation. Additional applications of fertilizer may not lessen damage. Damage is amplified by an interrelationship of *H. goettingiana* with the soil-borne fungus *Fusarium oxysporum* f.sp. *pisi* (Garofalo, 1964). In dry areas peas suffer greatly from drought due to the reduced size and efficiency of the root system. Senescence also tends to occur earlier.

Economic threshold level

Although the extent of damage caused by the nematode may vary with cultivar and environmental conditions, yield losses can be expected when peas are sown in soil infested with more than 3–5 eggs/cm^3 of soil (Di Vito *et al.*, 1978). The tolerance limit of pea to *H. goettingiana* is 0.5 eggs/cm^3 of soil, with 20 to 50% yield losses expected at between 3–8 eggs/cm^3 of soil. Complete crop failure occurs at densities of $\geqslant$ 32 eggs/cm^3 of soil (Greco, unpubl.).

Other hosts

H. goettingiana reproduces well on garden pea (*P. sativum*), field pea (*P. arvense* L.), broad bean (*Vicia faba* L.), vetch (*Vicia* spp.) and grass pea (*Lathyrus sativus* L.). Reproduction on other cultivated leguminous species is negligible. Several wild species of *Vicia* and *Lathyrus* (Jones, 1950; Winslow, 1954) are also hosts and are responsible for maintaining high soil densities even in the absence of host crops.

Biology

The time required by juveniles to reach the adult stage is strongly influenced by temperature and can take seven weeks in winter and only two weeks in spring (Greco *et al.*, 1986*a*). *H. goettingiana*, having a minimum temperature for development of 4.4 °C, can penetrate and develop on pea during the winter season (Beane & Perry, 1984). On pea sown in mid-autumn, females are formed by the

Fig. 13. Patch of stunted and yellow peas in a field heavily infested with *Heterodera goettingiana*.

end of autumn or in early winter. In this season, soil temperature is below 15 °C and the females protrude egg-masses containing 100–150 eggs. When peas are sown from late autumn throughout early spring, females occur in the spring. Soil temperature may exceed 15 °C and low moisture availability is common. Egg-masses will not be protruded, or they will be small and empty. While eggs in egg-masses hatch promptly when suitable environmental conditions exist (15–20 °C and adequate soil moisture), no substantial hatch occurs in new cysts during the first two months. Egg hatch is suppressed at 25 °C and therefore no root invasion would occur during the warm season. In England, one generation per year was reported on pea and two on broad bean (Jones, 1950). In the subtropical climate of the Mediterranean region only one generation is completed on pea sown from late autumn onwards, but two to three generations if pea is sown in early autumn. In the latter case, egg-masses could be produced and a high reproduction rate expected (Greco *et al.*, 1986*a*).

Control

Control of *H. goettingiana* varies with crop type. Cultivation of early pea for green pod production usually gives high return and therefore the use of nematicides is economical. Nematode control can be obtained by fumigating the soil 3–4 weeks before sowing, with DD or a mixture of DD and methyl isothiocyanate at 100–300 l/ha, depending on degree of soil infestation (Di Vito *et al.*, 1973). Granular nematicides, such as aldicarb, fenamiphos, oxamyl and carbofuran at 5–10 kg a.i./ha also give satisfactory nematode control and increased yield (Di Vito *et al.*, 1973; Whitehead *et al.*, 1979).

Fig. 14. Roots of peas heavily infested with white females of *Heterodera goettingiana*.

Improved control is achieved by incorporating these non-fumigant nematicides into the top 10–15 cm of soil at sowing only or at sowing and again after emergence. Granular nematicides must enter the soil solution to become effective and therefore irrigation may be required prior to and/or after treating the soil in semi-arid areas.

Soil solarization could be an alternative method for cyst nematode control on high value crops (Greco *et al.*, 1985). Mulching irrigated soil with thin (30–50 μm) polyethylene sheets for 4–8 weeks can reduce *H. goettingiana* in regions with sufficient solar energy assuming that the field can remain free of crops for the required time. However, solarization and non-fumigant nematicides usually are less effective than fumigants.

None of the above methods are economically acceptable when peas are grown for the production of dried grain. Rotating pea with non-host crops for a 3–6 year period will reduce nematode densities to non-damaging levels, assuming an annual population decline of 50% (Di Vito & Greco, 1986).

Meloidogyne

Pea is a good host for root-knot nematodes even though reports on infestations are limited. *Meloidogyne incognita* was reported on pea in India (Reddy, 1985). There is little doubt that this nematode is an important parasite of peas in the tropics. In the subtropics, pea is mostly grown as a winter crop and therefore damage caused by root-knot nematodes would be negligible. Unless, however, pea is sown early in autumn after a summer host crop, in which case pea growth would be suppressed

at early stage. Aboveground symptoms of nematode attack are similar to those outlined for *H. goettingiana*. The roots exhibit large galls, are reduced in size and *Rhizobia* nodulation is reduced.

Peas escape nematode attack, in the subtropics when sowing is postponed to mid-autumn, when temperatures drop. In other areas seed treatment with 1% aldicarb, fenamiphos, and carbofuran, has been shown to increase yield (Mani & Sethi, 1984). Soil treatment with fumigant and non-fumigant nematicides, although uneconomical on this crop, also limit yield losses in fields infested with *Meloidogyne*.

Other Nematodes of Pea

Ditylenchus dipsaci damages pea in several countries (Hooper, 1972). Infected plants show extensive brownish and necrotic lesion on the stems (Fig. 15) and leaf chlorosis. These symptoms can be confused with those produced by other nematodes and diseases. *D. dipsaci* damages epidermal, cortical parenchyma and external phloem tissue, thereby adversely affecting translocation processes. Infected pods are distorted, contain few seeds, which in turn may also be infected. However, it is not known whether the nematode can survive within grains as is typical on other crops.

In the subtropics, attacks of *D. dipsaci* are more severe on peas sown in autumn and symptoms become more obvious throughout late winter and early spring. The same control measures suggested for this nematode on broad bean should also be adopted on pea. The root-lesion nematodes, *Pratylenchus crenatus* and *P. penetrans* have been found in association with pea decline. Symptoms caused by these nematodes are similar to those observed on other crops. *Pratylenchus* spp. also are known to break down plant resistance to *Fusarium* wilt (Oyekan & Mitchell, 1971).

Pigeonpea

Pigeonpea (*Cajanus cajan* (L.) Mill.) also known as red gram, Congo pea and no-eyes pea originated in Africa around 2000 B.C. Pigeonpea is a woody, short-lived perennial shrub that reaches a height of up to 3.5 m. It is grown in both the tropics and subtropics and is very common in India where over 80% of the world crop is grown and consumed. The drought resistant crop is often intercropped with cereals in India and Africa especially in semi-arid regions. The crop, which is usually planted as an annual and grown for dried grain, is used for dhal (decorticated split seed) in a variety of foods. In other countries the green seeds are eaten as a substitute, or in preference, to green peas.

A large number of plant parasitic nematode species have been found associated with pigeonpea on a worldwide basis (Sharma, 1985). The vast majority are of limited economic importance.

Heterodera

The cyst nematode *Heterodera cajani* described by Koshy (1967) was first recorded on pigeonpea in India by Swarup *et al.* (1964). The nematode has subsequently been reported attacking the crop in a number of states in India (Sharma & Swarup, 1984). The exact distribution and frequency of occurrence within the country, however, has not been determined. The nematode was detected in only 7 out of 471 fields examined by Koshy and Swarup (1971*a*) and more recently has been detected in a large number of experimental fields in central India. In the latter case the nematode was more prevalent on vertisol rather than alfisol soils (S. B. Sharma, unpubl.). Although the nematode seems to be widespread in India, studies on crop losses have not been conducted.

Symptoms

In the field, yellowing and stunting have been observed, the former may vary with plant genotype. In glasshouse tests, plants infected with 1000 or 5000 juveniles/500 cm^3 of sterilized soil were stunted with smaller internodes and leaves. Chlorosis, however, was not very apparent. Stunting was directly related to initial nematode density (Sharma, pers. comm.).

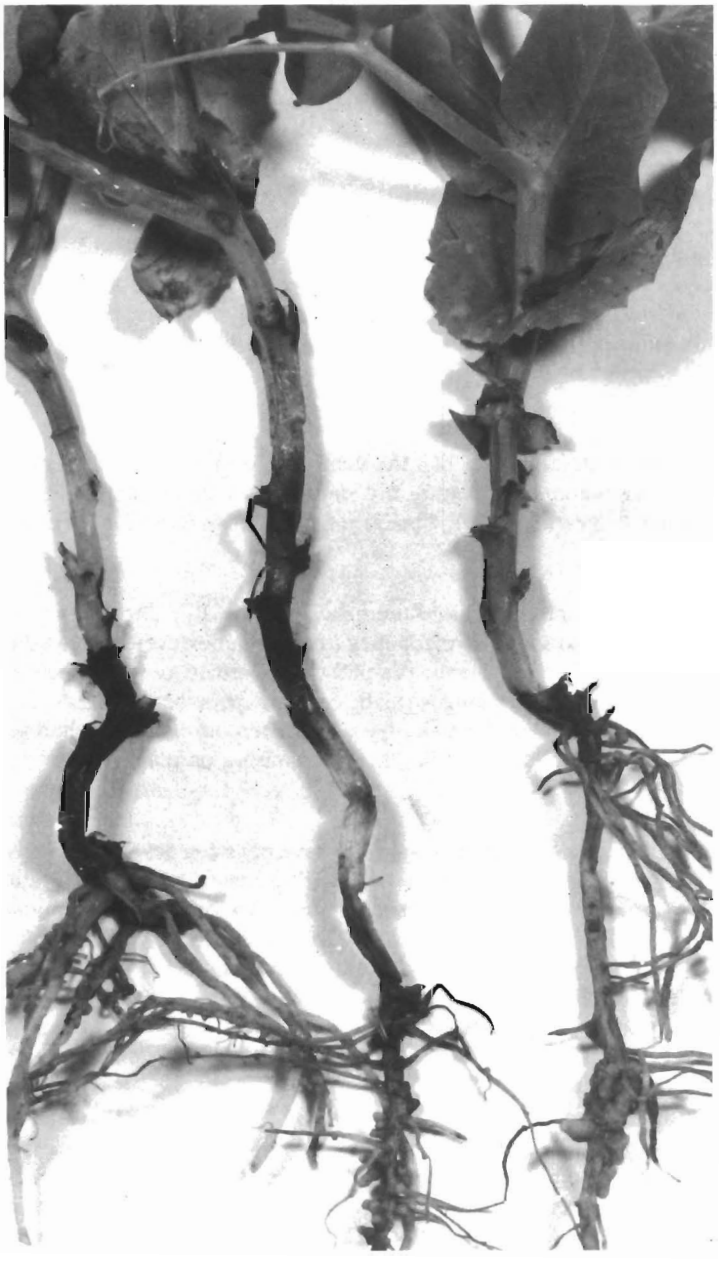

Fig. 15. Peas showing stem necrosis caused by infestation of *Ditylenchus dipsaci* in Italy (Photo: N. Vovlas).

Other hosts

More than 105 plant species belonging to 58 genera in the families Leguminosae and Pedaliaceae are known hosts (Koshy & Swarup, 1972). Important hosts are chickpea, horse gram, hyacinth bean, soybean, tepary bean, moth bean, and a number of species in the genera *Phaseolus* and *Vicia*.

Economic threshold level

Field densities have been shown to range from 2–130 cysts/500 cm^3 of soil. The highest numbers were detected on perennial plants or in fields cropped successively for 3–4 years (S. B. Sharma, unpubl.). Plants associated with high cyst densities growing in vertisol soils were stunted and frequently chlorotic. Symptoms of damage seemed to be more prevalent in the Kharif crop planted in the autumn. Initial populations of 5 juveniles/100 cm^3 of soil were found to affect plant growth. Zaki and Bhatti (1986) reported that 100 juveniles/kg of soil caused significant reductions in growth in pot trials.

Biology

At a soil temperature of 29°C, the nematode completes one generation in 16 days (Koshy & Swarup, 1971*a*). Optimum temperature for emergence is 28°C with distinct reductions in emergence at 25°C (Sharma & Swarup, 1984). The largest number of juveniles emerged between August and October.

Disease complexes

Wilt intensity caused by *Fusarium udum* increased significantly when combined with *H. cajani* in pot tests in sterilized soil. The pigeonpea lines used, however, reacted differently to the nematode/fungus combination. In one instance the pathogenic effects of the nematode on plant growth were negated in the presence of the fungus (S. B. Sharma, pers. comm.).

Although *H. cajani* females have also been observed attached to *Rhizobium* nodules, nothing is known about the effects of the interrelationship on plant health.

Control

Strategies for control of the nematode have not been developed. Rotation with cereal crops especially millet probably limit nematode damage in most established rotation schemes. *Echinocloa colona* (barnyard millet), *Paspalum scorbiculatum* (Kodo millet), *Setaria italica* (Italian millet), *Chionachne* spp., *Trilobachne* spp. and *Zea mexicana* (teosinte) were shown to be non-hosts (Sharma & Swarup, 1984) and could be used effectively in crop rotation patterns.

Zaki and Bhatti (1986) attempted control using seed treatment with non-fumigant nematicides. Although they were effective in reducing nematode populations, plant growth was also suppressed. Solarization has also been shown to reduce nematode densities. Neither control measure, however, can be used on this crop on an economic basis.

Resistance

Many of the pigeonpea types and genotypes grown are unimproved landraces. This germplasm should serve as a basis for the development of nematode resistant cultivars with good agronomic characteristics. A large number of lines have been reported resistant to the nematode, however, retesting has not always substantiated the results. Variation in testing techniques and in reporting the degree of resistance must be more closely monitored to avoid improper designation of the level of resistance.

Meloidogyne

M. javanica was found on pigeonpea in Puerto Rico (Ayala, 1962*a*) and Brazil (Lordello & Arruda, 1956). Pigeonpea was shown to be highly susceptible to a population of *M. arenaria* taken from

peanut fields in Alabama (Rodriguez-Kabana & Ingram, 1978). Plant growth was significantly reduced in pot tests at initial densities of 100 juveniles/500 g of soil (Pathak *et al.*, 1985).

Salam and Khan (1986) reported that *M. javanica* caused increased wilt in plants affected by *Fusarium udum*.

Although a number of breeding lines have been shown to be highly resistant to both *M. incognita* and *M. javanica*, the lines with resistance to *Fusarium udum* were all susceptible (Patel *et al.*, 1987). Acosta *et al.* (1986) reported that all cultivars tested were susceptible to *M. javanica*.

Rotylenchulus

Linford and Oliveira (1940) in Hawaii were the first to report *Rotylenchulus reniformis* on pigeonpea. It has since been reported attacking the crop in Puerto Rico, Jamaica, and India. The nematode causes yellowing of new leaves, progressive dieback of twigs and main stems and premature death of many plants in Jamaica (Hutton & Hammerton, 1975). Although the root system was reduced in size extensive necrosis was not observed. Root death seemed to be caused by excessive infection of the root tip (Ayala, 1962*b*).

Thakar and Yadav (1985*a*) reported significant reductions in plant weight at 1000 or 10 000 nematodes/700 g of soil in pot tests on susceptible or resistant cultivars, respectively. Suppression of growth was also detected at densities of 100 nematodes/500 g of soil (Pathak *et al.*, 1985). The nematode, in concomitant inoculations with *M. incognita*, consistently suppressed root-knot density.

The nematode also reproduced on *Rhizobium* nodules (Ayala, 1962*c*). In a glasshouse experiment race A caused marked reductions in total plant fresh weight after 30 days at a density of 142 nematodes/100 g of soil (Thakar & Yadav, 1985*a*).

Pigeonpea lines have been shown to be moderately resistant to the nematode (Patel *et al.*, 1987; Thakar & Yadav, 1985*b*).

Other Nematodes of Pigeonpea

Germani (1972) reported that *Aphasmatylenchus straturatus* was associated with stunted and chlorotic pigeonpea in Upper Volta. *Hoplolaimus seinhorsti* has been found associated with poor plant growth in India.

In pot experiments wilt caused by *Fusarium udum* was not affected by simultaneous or sequential inoculation of *Tylenchorhynchus vulgaris, Helicotylenchus indicus* or *Hoplolaimus indicus* (Hasan, 1984).

Soybean

Glycine max (L.) Merr., originally confined to temperate zones, is becoming more important in many tropical and subtropical regions, especially in Brazil, South America, the Far East and more recently Africa. Whole soybeans have not always been accepted as a food legume in many countries, because of the development of an objectionable flavour during processing. Technology now exists that allows use of the whole bean in many foods (Hinson & Hartwig, 1977). Most soybean, however, is still processed for oil, high protein meal animal supplement, soy flour, soybean milk and curd. The average cultivar grown in north America contains 40% protein and 21% oil on a dry weight basis.

The crop can be grown successfully under a wide range of temperature conditions as long as adequate amounts of moisture are available during the seed development period (Hinson & Hartwig, 1977). A growing season with little or no moisture stress for about a 120 day period produces near maximum yields. Although soybean is usually drilled in rows, it probably can be successfully intercropped with cereals. In Asia the seed is often inserted into the hills remaining after the rice harvest. Minimum tillage is effective, but requires heavy equipment and liberal herbicide appli-

Fig. 16. Soybean plants exhibiting chlorosis and early senescence caused by *Meloidogyne arenaria* in North Carolina, U.S.A. (Photo: D. Schmitt).

cations. A major factor limiting adaptation to the humid and subhumid tropics is that seeds lose their viability and rapidly degrade in storage.

Meloidogyne

Root-knot nematodes *M. incognita, M. javanica*, and *M. arenaria* are important factors limiting soybean production. According to Schmitt and Noel (1984) the latter two species are becoming more important in warmer climatic regions. This is probably related to the introduction of the crop into new growing regions where cropping patterns have favoured these two species. They are likely to become important pests wherever soybean is grown.

Root-knot nematodes cause varying degrees of stunting, chlorosis and in some cases early senescence, depending on the initial population density (Fig. 16). Losses can often be related to intensity of galling which is also dependent on initial population densities. Galls on the root system are typical of root-knot infection, but can be confused with *Rhizobium* nodules by unexperienced observers.

Losses of 90% due to *M. incognita* have been reported from Florida (Kinloch, 1974). The level of damage is lower in North Carolina when compared to Florida indicating that temperature affects crop loss intensity (Schmitt & Noel, 1984).

Economic threshold level

Kinloch (1982) showed that plant growth is inversely proportional to initial population density. Environmental factors especially moisture have a strong influence on the level of crop loss, with higher yield associated with increased moisture availability (Barker, 1982). Losses incurred at a specific threshold level are therefore highly variable.

Disease complexes

Goswami and Agarwal (1978) in pot tests showed yield reductions were greater when *M. incognita* was present with *Fusarium oxysporum* or *F. solani* than when inoculated singly.

Control

The use of crop rotation is hampered by the wide host range of all three root-knot species. With the exception of grasses, few alternative non-host crops exist. The use of nematicides is not an economically acceptable means of controlling this nematode, even though good control can be obtained with low dosages of non-fumigant nematicides.

Resistance

A number of cultivars are available that are moderately resistant to *M. incognita, M. javanica* and *M. arenaria* (Armstrong & Jensen, 1978; Sasser & Kirby, 1979).

Heterodera

The soybean cyst nematode *H. glycines* is a major limiting factor in semi-arid regions of the U.S.A and has been reported to occur in China, Soviet Union, Colombia, Korea, Indonesia, Egypt and parts of Argentina and Brazil (Noel, 1985). The nematode causes severe stunting and yellowing of the foliage and, in extreme cases, plant death (Plate 4B). Yield losses can range from 10 to 80% depending on rainfall, soil fertility, presence of other diseases and nematode density (Jacobsen *et al.*, 1983).

Races

Five races have been identified (Table 4) using host differentials suggested by Golden *et al.* (1970) and Inagaki (1979). However, the variation in reactions of many populations to this set of differentials indicates that other races probably exist (Riggs *et al.*, 1981). The problems associated with race designation have been discussed elsewhere (Schmitt & Noel, 1984; Noel, 1985).

TABLE 4. Bioassay for races of *Heterodera glycines*; Reaction/Reproduction on cultivar or line

Race	Pickett	Peking	PI88788	PI90763	Lee
1	−	−	+	−	*s/c*
2	+	+	+	−	*s/c*
3	−	−	−	−	*s/c*
4	+	+	+	−	*s/c*
5	+	−	+	−	*s/c*

Reproduction of *Heterodera glycines* less than 10% of the susceptible control cv Lee (s/c) is considered negative and above 10% positive.

Biology

Optimum temperature for emergence and penetration is 24°C and for development 28–31°C. There is little or no development at $\leq$ 15°C or $\geq$ 33°C (Schmitt & Noel, 1984). The nematode is reported to have a diapause stage (Ross, 1963) which may reduce spontaneous emergence at a given time of

year. The nematode is susceptible to desiccation (Slack & Hamblen, 1961). Percent survival of eggs and juveniles decreases with increasing temperature from northern to southern growing regions of the USA (Noel, 1985). The reduction is considered to be due to the influence of temperature on nematode activity and increased biological control through soil pathogens and parasites.

The nematode will complete six to seven generations per season in temperate growing areas with the greatest increase in density occurring in the first generation (Lawn & Noel, 1986).

Economic threshold level

Noel (1984) reported that, on silt loam soils with 2% organic matter, economic losses were incurred when densities were $\geqslant$ 699 eggs and juveniles or 12 cysts containing viable eggs/250 cm^3 of soil.

Other hosts

Noel (1985) reported that other hosts of economic importance were: adzuki bean (*Phaseolus angularis* Wright), haricot bean (*Phaseolus vulgaris* L.), and some species of *Lespedeza* and *Melilotus*. Monocotyledonous species have not been reported to be hosts.

Disease complexes

The nematode will severely reduce *Rhizobium* nodule weight and the level of nitrogen fixation (Lehman *et al.*, 1971).

Control

Rotation with non-host crops for two years will reduce populations sufficiently to allow planting of susceptible cultivars (Fig. 17) (Schmitt & Noel, 1984). Resistant cultivars are effective against some races of the nematode (Fig. 18). The use of resistant cultivars (Wrather *et al.*, 1984) and possibly tolerant cultivars (Boerma & Hussey, 1984) in the rotation would increase the effectiveness of integrated control programmes. Problems associated with rotation management have been discussed by Noel (1985). Nematicides are not used for control of this nematode on a field scale. Sources of resistance have been given by Tisselli *et al.* (1980).

Other Nematodes of Soybean

Rotylenchulus reniformis can cause stunting and chlorosis on soybean. The nematode has been found attacking soybean in a number of tropical and subtropical countries (Schmitt & Noel, 1984). Rotation with non-host crops of two or more years is an effective control measure. The wide host range of this nematode requires careful selection of rotation crops. Resistant cultivars are available (Birchfield *et al.*, 1971; Lim & Castillo, 1979).

Hoplolaimus columbus has been shown to cause damage in the southeastern U.S.A. High densities of a *Hoplolaimus* sp. were also detected in the rhizosphere of soybean in India (Sikora, 1972). *Belonolaimus longicaudatus* which is also limited to the southeastern U.S.A. will cause stunting chlorosis and wilting. The nematode is usually controlled with crop rotation. Non-fumigant nematicides are also effective and may be used depending on the value of other crops in the rotation.

Pratylenchus brachyurus and other *Pratylenchus* species have been found attacking soybean in most growing regions. They can cause stunting, leaf yellowing and yield loss depending on soil densities at planting. Yield losses are linearly related to *P. brachyurus* densities in a sandy-clay loam soil (Schmitt & Barker, 1981). Control of these nematodes is hampered by wide host ranges and the presence of multiple species in a field. The lesion nematodes are also known to increase damage caused by root-rotting fungi which may further reduce yield.

Fig. 17. Effect of rotation with maize-peanut-soybean (right) verses monoculture of soybean (left) on soybean growth in a field infested with the soybean cyst nematode *Heterodera glycines* (Photo: D. Schmitt).

Winged Bean

Winged bean (*Psophocarpus tetragonolobus* (L.) D. C.) also known as Goa bean, asparagus pea, four-angled bean, Manila bean and princess pea, originated in Asia or Africa. It is a perennial crop grown as an annual for green immature pods, seeds, tubers and leaves in the humid tropics. The crop is resistant to high temperatures and is often intercropped with sweet potato, taro, banana, sugarcane and vegetables. It can be grown as a dry season crop with irrigation, but is not drought resistant.

Meloidogyne

Root-knot nematodes have been shown to cause serious damage to winged bean in a number of tropical countries. *Meloidogyne incognita* has been reported on the crop in Papua New Guinea (Price & Linge, 1979), India (Singh *et al.*, 1979), Okinawa (Teruya *et al.*, 1984), and Nigeria (Whitehead, 1969). *M. javanica* caused damage in Papua New Guinea (Price & Linge, 1979), Brazil (Lordello & Almeida, 1979), and Okinawa (Teruya *et al.*, 1984). Root-knot nematodes are considered the most widely distributed of winged bean pests in Papua New Guinea.

Fig. 18. Growth differences between soybean cultivars Clark-63 (susceptible, left) and Custer (resistant, right) to soybean cyst nematode, *Heterodera glycines*.

A "*Meloidogyne-javanica-incognita-arenaria* species complex" was responsible for severe galling to roots and tubers in the Ivory Coast (Fortuner *et al.*, 1979). Species of *Meloidogyne* have also been reported from Mauritius (de Sorney, 1913) and the Philippines (Fajardo & Palo, 1933).

The distribution of the two major species attacking winged bean is influenced by temperature. *M. incognita* seems to be more predominant in the warmer coastal regions of Papua New Guinea and at lower altitudes in East Africa, whereas, *M. javanica* is common in the highlands and higher altitudes, respectively (Whitehead, 1969; Price & Linge, 1979). These observations are supported by the fact that hatching of local populations occurs in a temperature range of 25–30°C for *M. incognita* and at 20–30°C for *M. javanica* (Price & Linge, 1979). In the field the juveniles penetrate the root within one week and females and galls develop after 4 weeks (Linge, 1976).

In the Ivory Coast, the root-knot nematode species complex caused heavy root galling and tuber galling so severe that they were unsuitable for consumption. An estimated 50–70% of the tubers failed to develop. Damage to the tubers was observed even at very low initial infestation levels (Fortuner *et al.*, 1979). Damage seems to be more severe on winged bean grown in the dry season (Khan, 1976; Price & Linge, 1979).

No attempts have been made to develop control measures for root-knot nematodes on this crop. Resistance to *M. incognita* has not been detected in the lines screened to date (Duncan *et al.*, 1979; Singh *et al.*, 1979; Valdez, 1981; Phukan & Hazarika, 1985). Breeding lines with resistance to *M. javanica* have been found (Valdez, 1981).

Other Nematodes of Winged Bean

A number of plant parasitic nematodes of unknown importance have been found associated with winged bean (Teruya *et al.*, 1984; Bridge, 1987).

Nematode Parasites of other Food Legumes

A large number of food legumes have not been discussed in detail in this chapter. Most of these crops were considered to be of local importance. In some cases only a few reports of nematodes associated with the crop were found. The common and botanical names of these legumes are given in Table 5.

TABLE 5. Common and botanical names of food legumes of local importance (Uphof, 1968; Purseglove, 1983).

Common	Botanical	Common	Botanical
Adzuki bean	*Vigna angularis* (Willd.) Ohwi & Ohashi syn. *Phaseolus angularis* (Willd.) Wight	Lupin, pearl	*Lupinus mutabilis* Sweet
		Lupin, white	*Lupinus albus* L. syn. *Lupinus termis* Fors
Catjang bean	*Vigna cylindrica* L., syn. *Vigna catjang* Walp. *Vigna catjang* Walp. v. Iron	Moth bean	*Phaseolus aconitifolius* Jacq. syn. *P. trilobus* Ait.
Cluster bean	*Cyamopsis tetragonoloba* (L.) Taub. syn. *C. psoralioides* DC.	Rice bean	*Vigna umbellata* (Thunb.) Ohwi & Ohashi syn. *Phaseolus calcaratus* Roxb.
Grass Pea	*Lathyrus sativus* L.	Runner bean	*Phaseolus cocceneus* L. syn. *P. multiflorus* Willd.
Horsegram	*Dolichos uniflorus* Lam. syn. *D. biflorus* auct. non L.	Sword bean	*Canavalia gladiata* (Jacq.) DC.
Hyacinth bean	*Lablab niger* Medik. syn. *Dolichos lablab* L.	Tepary bean	*Phaseolus acutifolius* Gray var. *latifolius* Freem.
Jack bean	*Canavalia ensiformis* (L.) DC.	Velvet bean	*Mucuna pruriens* (L.) DC. var. *utilis* (Wall, ex Wight) Baker ex. Burck
Lima bean	*Phaseolus lunatus* L. syn. *P. limensis* Macf.		

The plant parasitic nematodes that have been found associated with these food legumes have been compiled from major lists (Table 6) and are not considered complete. Species of root-knot nematodes, *Meloidogyne*, cyst nematodes, *Heterodera*, lesion nematodes, *Pratylenchus*, parasitize many of these crops. The stem and bulb nematode, *Ditylenchus dipsaci*, the reniform nematode, *Rotylenchulus reniformis*, and *Belonolaimus* cause severe damage on many food legumes and are most probably important on the crops listed. The species that have been reported to attack a number of these crops and may be economically important are *H. glycines, M. arenaria, M. incognita* and *M. javanica*, and *R. reniformis*.

Conclusions and Future Prospects

On many of the food legumes discussed there is a definite lack of information on the presence and distribution of plant parasitic nematodes within the major growing regions. In some cases survey work has only been conducted near nematology stations with a complete lack of survey data on nematode distribution and frequency of occurrence in the major growing regions. Crop loss assessment has not been conducted in the majority of cases where important plant parasitic nematodes are known to occur.

Food legumes are not high value cash crops, therefore, control is often limited to rotation with non-host crops. Resistance in many crops is not known or has not been transferred to cultivars suitable for farmer use.

The development of rotations for nematode management in temperate regions, where one crop per year is grown, are reasonably easy to formulate. In the tropics and subtropics, however, intercropping, and sequential and relay cropping, involving the production of two to four crops in one year is common practice (Steiner, 1982; Ruthenberg, 1983). Designing rotations for nematode

TABLE 6. Plant parasitic nematodes associated with food legumes of local or limited importance in tropical and subtropical climatic areas (Goodey *et al.*, 1965; Sitaramaiah, 1984; Mani *et al.*, 1982; Saka & Carter, 1987).

	Food legumes															
Nematode	Adzuki bean	Catjang bean	Cluster bean	Grass pea	Horse gram	Hyacinth bean	Jack bean	Lima bean	Lupin, pearl	Lupin, white	Moth bean	Rice bean	Runner bean	Sword bean	Tepary bean	Velvet bean
Belonolaimus spp.								•								
Ditylenchus dispsaci			•										•			
Helicotylenchus spp.				•			•									
Hemicycliophora spp.		•														
Heterodera cajani			•		•	•	•					•			•	
Heterodera glycines	•	•		•		•	•	•	•	•	•	•			•	
Heterodera goettingiana				•						•						
Heterodera lespedezae	•															
Heterodera schachtii	•	•		•												
Heterodera trifolii				•												
Hirschmanniella mucronata					•											
Hoplolaimus spp.		•	•	•		•					•					
Longidorus spp.							•									
Meloidogyne spp.	•		•	•	•	•	•	•	•	•	•	•	•	•	•	
Meloidogyne arenaria		•				•				•			•			
Meloidogyne hapla		•														
Meloidogyne incognita		•	•	•	•	•	•	•		•		•	•	•		
Meloidogyne javanica			•		•	•		•		•	•	•	•			•
Pratylenchus spp.				•		•										
Pratylenchus brachyurus						•	•	•			•					
Pratylenchus coffeae				•				•								
Pratylenchus pratensis											•					
Pratylenchus scribneri				•				•								
Pratylenchus vulnus								•			•					
Radopholus similis			•	•						•		•	•	•	•	
Rotylenchulus reniformis						•		•		•						
Scutellonema spp.						•										
Trichodorus spp.											•					
Tylenchorhynchus spp.			•	•	•	•					•				•	
Xiphinema spp.						•										

management under these conditions is a challenge to nematology. Bridge (1987) suggested a number of approaches to nematode control in cropping systems.

Research on the influence of different cropping systems and the long term effects of crop rotations on nematode population dynamics and yield loss has not been conducted. Whereas data on intercropping systems have demonstrated that crop yield can be increased in legume/cereal intercrop situations, the effects of intercropping on damage caused by plant parasitic nematodes have not been ascertained.

Rotation especially with non-host crops and where possible in a paddy rice cropping system could be an efficient method of controlling nematodes in the following legume crop. Dry fallow in the semi-arid subtropics is also effective in reducing population densities. Research, however, is needed to determine if these observations are valid in all situations. The use of trap crops, that act as green

manures and control components, should be looked at as an alternative control measure.

Nematicides are still too costly for the vast majority of food legumes. The development of a new generation of nematicides that are safe and effective and that could be used as seed dressing could allow their incorporation into nematode management systems.

There are a number of publications that list resistant cultivars and lines to food legumes (Sasser & Kirby, 1979; Bridge, 1981; Armstrong & Jensen, 1978; Tisselli *et al.*, 1980). In many instances, however, screening for resistance or tolerance has not been initiated. In other cases known sources of resistance, because of inadequate methodology, has led to false interpretation of results. Coordination of the screening process is needed if good resistance or tolerance is to be developed in many of the important food legumes.

Diagnosis

Root-knot nematodes

Species of root-knot nematodes can usually be recognized by the presence of root galls, which with most species affecting food legumes in tropical and subtropical climates, are large. To the untrained eye, root-knot galls often resemble *Rhizobium* nodules. The latter, however, are distinct knots of root tissue attached to the surface of the root which can be easily detached from the root surface, whereas galls are swellings arising on all sides of the root.

Above ground symptoms vary from stunting to chlorosis. Plants may wilt when exposed to moisture stress and in cases involving interrelationships with fungal wilt diseases. In some plants early senescence has been reported.

Cyst forming nematodes

The presence of white lemon-shaped or round females, 0.4–0.8 mm in length, attached to the root surface is the most characteristic symptom of this group of nematodes. Knowledge of the day/degree (the sum of temperature above the minimum temperature needed for activity) that coincides with appearance of adult females on the root surface can be used to simplify detection in field survey work. The presence of white females on the root surface is simultaneous verification of parasitism.

The presence of cysts in soil samples is an indication that a cyst nematode problem is present in the cropping system, it does not indicate which crop or weed is being parasitized. Cyst colour varies greatly from white to dark brown. Colour can be species specific, but usually indicates cyst ages with dark brown an indication of an old cyst.

The extraction of cysts from a predetermined quantity of soil and determination of the total number of eggs and juveniles found in the extracted cysts is the most exact measure used to determine nematode densites and to study population dynamics. The criteria is used in most countries for glasshouse and field studies.

Stem and bulb nematode

Wallace (1962) demonstrated that the stem nematode migrates to the soil surface after rain. The date selected for soil sampling and the depth of sampling, therefore, is important in determining nematode densities when only looking at nematodes in the upper soil layers.

On broad bean, leaf spot symptoms caused by fungal diseases can be confused with necrosis induced by the stem nematode. The spots on infested seed cannot be used as a diagnostic characteristic, because they can be caused by insect damage and water spotting.

For routine studies and experimentation Hooper (1983*a*) suggested soaking 150 g of seed in 500 ml of water overnight. To prevent introduction of the nematode into nematode-free areas a high level of nematode extraction accuracy from seed is necessary. Augustin and Sikora (1989*b*) suggested first soaking and then maceration of the seed and extraction on a modified Baermann tray (see Chapter 2).

Lesion nematodes

Species of *Pratylenchus* cause distinct small brown to black lesions on the root surface of many food legumes (Plate 4H). They can often be seen with a simple magnifying glass in the field or with the field microscope. In extreme cases the lesions coalesce to form large necrotic lesions. The nematodes can be extracted as outlined in Chapter 2.

Acknowledgements

The authors would like to thank Dr. Suebsak Sontirat, Kasetsart University, Bangkok, Thailand for reviewing the manuscript.

References

Abawi, G. S. & Jacobsen, B. J. (1984). Effect of initial inoculum densities of *Heterodera glycines* on growth of soybean and kidney bean and their efficiency as host under greenhouse conditions. *Phytopathology*, 74:1470–1474.

Abedinia, M. (1978). *Host-parasite relationships of the root-knot nematode*, Meloidogyne incognita and *cowpea*. Ph.D. Thesis. University of Reading, 218 p.

Aboul-Eid, H. Z. & Ghorab, A. I. (1974). Pathological effects of *Heterodera cajani* on cowpea. *Plant Disease Reporter*, 58:1130–1133.

Acosta, N., Vicente, N. & Toro, J. (1986). Susceptibility of pigeon pea (*Cajanus cajan*) cultivars and lines to *Meloidogyne javanica*. *Nematropica*, 16:1–10.

Ahmad, S. & Husain, S. I. (1988). Effect of root-knot nematodes on qualitative and quantitative characters of chickpea. *International Nematology Network Newsletter*, 5:12–13.

Al-Hazmi, A. S. (1985). Interaction of *Meloidogyne incognita* and *Macrophomia phaseolina* in a root-rot disease complex of french bean. *Phytopathologische Zeitschrift*, 113:311–316.

Ali, M. A., Trabulsi, I. Y. & Abd-Elsamea, M. E. (1981). Antagonistic interaction between *Meloidogyne incognita* and *Rhizobium leguminosarum* on cowpea. *Plant Disease*, 65:432–435.

Amosu, J. O. (1974). The reaction of cowpea (*Vigna unguiculata* L. Walp) to the root-knot nematode (*Meloidogyne incognita*) in Western Nigeria. *Nigerian Agricultural Journal*, 11:165–169.

Armstrong, J. M. & Jensen, H. J. (1978). *Indexed bibliography of nematode-resistance in plants*. Station Bulletin 639, Agricultural Experiment Station Oregon State University, Corvallis, Unnumbered.

Augustin, B. (1985). *Biologie, Verbreitung und Bekämpfung des Stengelälchens, Ditylenchus dipsaci (Kühn), Filipjev and Vicia faba L. in Syrien und anderen Ländern des Nahen Ostens und Vorderafrikas*. Ph.D. Thesis, University of Bonn, Fed. Rep. Germany, 160 p.

Augustin, B. & Sikora, R. A. (1984). Influence of aldicarb and fenamiphos on the population dynamics of soil or seed-borne *Ditylenchus dipsaci* and yield of *Vicia faba*. *Proceedings International Congress of Nematology*, Guelph, Canada, August 5–10, 1984: 7 [Abstr.].

Augustin, B. & Sikora, R. A. (1989*a*). Studies on the host range of the normal and giant faba bean race of *Ditylenchus dipsaci*. *Nematologia mediterranea*, 17: 63–66.

Augustin, B. & Sikora, R. A. (1989*b*). Zur Methodik des Nachweises von *Ditylenchus dipsaci* in Körnerlegumenosen-saatgut. *Gesunde Pflanzen*, 5:189–192.

Ayala, A. (1962*a*). Occurrence of the nematode *Meloidogyne javanica* on pigeonpea roots in Puerto Rico. *Journal of Agriculture, University of Puerto Rico*, 46:154–156.

Ayala, A. (1962*b*). Pathogenicity of the reniform nematode on various hosts. *Journal of Agriculture, University of Puerto Rico*, 46:73–82.

Ayala, A. (1962*c*). Parasitism of bacterial nodules by the reniform nematode. *Journal of Agriculture, University of Puerto Rico*, 46:67–69.

Ayala, A. & Ramirez, C. T. (1964). Host range, distribution and bibliography of the reniform nematode, *Rotylenchulus reniformis* with special reference to Puerto Rico. *Journal of Agriculture, University of Puerto Rico*, 48:142–161.

Bajet, N. B. & Castillo, M. B. (1974). Effects of *Rotylenchulus reniformis* inoculations on mung bean, soybean and peanut. *Philippine Phytopathology*, 1:50–55.

Barker, K. (1982). Influence of soil moisture, cultivar, and population density of *Meloidogyne incognita* on soybean yield in microplots. *Journal of Nematology*, 14:429 [Abstr.].

Beane, J. & Perry, R. N. (1984). Observation on the invasion and development of the pea cyst-nematode *Heterodera goettingiana* in winter field beans (*Vicia faba*), *Annals of applied Biology*, 105:503–508.

Bessey, E. A. (1911). Root-knot and its control. *Bulletin Bureau Plant Industry U.S. Department Agriculture*, No. 217, 89 p.

Birchfield, W., Williams, C., Hartwig, E. E. & Brister, L. R. (1971). Reniform nematode resistance in soybeans. *Plant Disease Reporter*, 55:1043–1045.

Blazey, D. A., Smith, P. G., Gentile, A. G. & Miyagawa, S. T. (1964). Nematode resistance in the common bean. *Journal of Heredity*, 55:20–22.

Boerma, H. R. & Hussey, R. S. (1984). Tolerance to *Heterodera glycines* in soybean, *Journal of Nematology*, 16:289–296

Brancalion, A. M. & Lordello, L. G. E. (1981). Controle quimico de *Rotylenchulus reniformis* em algodeiro. *Sociedade Brasilieira de Nematologica*, 5:191–195.

Bridge, J. (1973). *Hoplolaimus seinhorsti*, an endoparasitic nematode of cowpea in Nigeria. *Plant Disease Reporter*, 57:798–799.

Bridge, J. (1981). Nematodes. In: Ward, A., Mercer, S. L. & Howe, V. (Eds). *Pest control in tropical grain legumes*. Centre for Overseas Pest Research, London: 111–125.

Bridge, J. (1987). Control strategies in subsistence agriculture. In: Brown, J. & Kerry, B. (Eds). *Principles and practice of nematode control in crops*. Academic Press, Australia: 389–420.

Brothwell, D. R. & Brothwell, P. (1969). *Food in Antiquity*. London, Thames and Hudson Publishing Company. 316 p.

Brown, E. B. (1958). Pea root eelworm in the eastern counties of England. *Nematologica*, 3:257–268.

Caveness, F. E. (1965). End of tour progress report on nematology project. *Ministry of Agriculture and Natural Resources*, Western Region, Nigeria, 137 p.

Caveness, F. E. (1979). Cowpea, lima bean, cassava, yams and *Meloidogyne* spp. in Nigeria. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes*. New York, Academic Press: 295–300.

Castillo, M. B. (1975). Plant parasitic nematodes associated with mung bean, soybean and peanut in the Philippines. *Philippine Agriculturist*, 59:91–99.

Castillo, M. B., Arceo, M. B. & Litsinger, J. A. (1976). Nematodes in cropping patterns. IV. Populations of plant parasitic nematodes associated with cropping patterns under different rice-growing environments in Manaoag, Pangasinan. *Philippine Phytopathology*, 12:24–29.

Castillo, M. B., Alejar, M. S. & Litsinger, J. A. (1977). Pathological reactions and yield loss of mung bean to known populations of *Rotylenchulus reniformis* and *Meloidogyne acrita*. *Philippine Agriculturist*, 61:12–24.

Castillo, M. B., Alegar, M. S. & Harwood, R. R. (1978). Effect of flooding on pot populations of *Rotylenchulus reniformis* and *Meloidogyne incognita*. *Philippine Phytopathology*, 12:11–16.

Catibog, C. S. & Castillo, M. B. (1975). Pathogenicity of *Meloidogyne javanica* on mung bean *Phaseolus aureus* Roxb. *Philippine Agriculturist*, 59:189–195.

Centro Internacional de Agricultura Tropical (CIAT). (1985). *CIAT in the 1980's revisited. A mid-term plan for 1986–1990*. Cali, Colombia. 216 p.

Chahal, P. P. K. & Chahal, V. P. S. (1987). Adverse effect of *Meloidogyne incognita* on the functioning of nodules of mungbean (*Vigna radiata*). *Nematologia mediterranea*, 15:13–19.

Dasgupta, D. R. & Seshadri, A. R. (1971). Races of the reniform nematode, *Rotylenchulus reniformis* Linford and Oliveira, 1940. *Indian Journal of Nematology*, 1:21–24.

Datta, S., Trivedi, P. C. & Tiagi, B. (1987). Nematodes of guar and mung in some areas of Rajasthan, India. *International Nematology Network Newsletter*, 4:12–16.

Decker, H. (1969). *Phytonematologie*. Berlin, VEB Deutscher Landwirtschaftsverlag, 526 p.

Dehne, W.-W. (1987). Zur Nutzung der VA Mykorrhiza als Antistreßfaktor. *Angewandte Botanik*, 61:135–143.

Di Vito, M., Lamberti, F. & Inserra, R. (1973). Prove preliminari di lotta chimica contro *Heterodera goettingiana* Liebscher, grave parassita del pisello nell 'Italia Meridionale. *Nematologia mediterranea*, 1:125–138.

Di Vito, M., Lamberti, F. & Inserra, R. N. (1978). Effects of *Heterodera goettingiana* on weight of foliage of pea plants in pots. *Nematologica*, 24:209–212.

Di Vito, M., Greco, N. & Lamberti, F. (1980). Comportamento di popolazione di *Heterodera goettingiana* su specie diverse di leguminose. *Informatore Fitopotologico*, 30(5):7–10.

Di Vito, M., Greco, N. & Zaccheo, G. (1985). On the host range of *Meloidogyne artiellia. Nematologia mediterranea*, 13:207–212.

Di Vito, M. & Greco, N. (1986). The pea cyst nematode. In: Lamberti, F. & C. E. Taylor, (Eds.) *Cyst Nematodes*. New York & London, Plenum Publishing Co.: 321–332.

Di Vito, M. & Greco, N. (1988*a*). Investigation on the biology of *Meloidogyne artiellia. Revue de Nématologie*, 11:221–225.

Di Vito, M. & Greco, N. (1988*b*). The relationship between initial population densities of *Meloidogyne artiellia* and yield of winter and spring chickpea.*Nematologia mediterranea*, 16:163–166.

Di Vito, M., Greco, N., Singh, K. B. & Saxena, M. C. (1988). Response of chickpea germplasm lines to *Heterodera Ciceri* attack. *Nematoligia mediterranea*, 16:17–18.

Dukes, P. D., Fery, R. L. & Hamilton, M. G. (1979). Comparison of plant resistance and a nematicide for control of southern root-knot nematodes in southernpeas, *Vigna unguiculata. Phytopathology*, 69:1A3–1A4.

Duncan, L. W., Caveness, F. E., & Perez, A. T. (1979) The susceptibility of winged bean (*Psophocarpus tetragonolobus*) to the root-knot nematodes, *Meloidogyne incognita*, race 2, and *M. javanica. Tropical Grain Legume Bulletin, IITA*, 15:30–34.

Edwards, E. E. (1956). Studies on resistance to root-knot nematode of the genus *Meloidogyne* Goeldi, 1887. *Proceedings of the helminthological Society of Washington*, 23:112–118.

Egunjobi, O. A. (1985). Effects of cocoa pod husks soil amendment on cowpea infestation by *Meloidogyne* spp. *Pakistan Journal of Nematology*, 3:99–103.

Egunjobi, O. A. & Olaitan, J. O. (1986). Response of *Meloidogyne incognita*-infected cowpea to some agro-waste soil amendments. *Nematropica*, 16:33–34.

Egunjobi, O. A., Akonde, P. T. & Caveness, F. E. (1986). Interaction between *Pratylenchus sefaensis, Meloidogyne javanica* and *Rotylenchulus reniformis* in sole and mixed crops of maize and cowpea. *Revue de Nématologie*, 9:61–70.

Elliot, A. P., Bird, G. W. & Safir, G. R. (1984). Joint influence of *Pratylenchus penetrans* and *Glomus fasciculatum* (Phycomyceta) on the ontogeny of *Phaseolus vulgaris. Nematropica*, 14:111–119.

Elliot, A. P. & Bird, G. W. (1985). Pathogenicity of *Pratylenchus penetrans* to navy bean (*Phaseolus vulgaris* L.). *Journal of Nematology*, 17:81–85.

El Tigani, M., El-Amin, M. & Siddiqi, M. R. (1970). Incidence of plant parasitic nematodes in the Northern Fung Area, The Sudan. *FAO Plant Protection Bulletin*, 18: 102–106.

Epps, J. M. & Chambers, A. Y. (1959). Mung bean (*Phaseolus aureus*), a host of the soybean cyst nematode (*Heterodera glycines*). *Plant Disease Reporter*, 43:981–982.

Epps, J. M. (1969). Nine varieties of southern peas resistant to the soybean cyst nematode. *Plant Disease Reporter*, 53:245

Eriksson, K. B. (1972). Nematode Diseases of pasture legumes and turf grasses. In: Webster, J. M. (Ed). *Economic Nematology*. London, Academic Press, 66–96.

Fajardo, R. G. & Palo, M. A. (1933). The root-knot nematode, *Heterodera radicicola* (Greef) Müller, of tomato and other plants in the Philippine Islands. *Philippine Journal of Science*, 51:457–484.

FAO. (1974). *FAO Production Yearbook*. Rome, 28:290

FAO. (1985). *FAO Production Yearbook*. Rome, 39:289.

Fassuliotis, G., Hoffman, J. C. & Deakin, J. R. (1967). A new source of root-knot nematode resistance in snap bean. *Nematologica*, 13:141.

Fortuner, R., Fauquet, C. & Lourd, M. (1979). Diseases of the winged bean in Ivory Coast. *Plant Disease Reporter*, 63:194–199.

Franklin, M. T. (1961). A British root-knot nematode, *Meloidogyne artiellia* n. sp. *Journal of Helminthology*, R. T. Leiper supp.: 85–92.

Freire, F. C. das O., Diógenes, A. M. & da Ponte, J. J. (1972). Nematodes das galhas *Meloidogyne javanica* e *M. incognita*, parasitando leguminosas forrageiras. *Revista da Sociedade Brasileira de Fitopatologia*, 5:27–32.

Garofalo, F. (1964). Fenomeni di correlazione tra *Heterodera goettingiana* e *Fusarium oxysporum* (Schl.) Snyd. *et* Hans. nell'avvizzimento delle piante di pisello e di lupino. *Bollettino del Laboratorio Sperimentale dell'Osservatorio Fitopatologico, Torino*. 27:33–48.

Gaur, H. S., Mishra, S. D. & Sud, U. C. (1979). Effect of date of sowing on the relation between the population density of the root-knot nematode, *Meloidogyne incognita* and the growth of three varieties of chickpea, *Cicer arietinum*. *Indian Journal of Nematology*, 9:152–159.

Germani, G. (1972). Une chlorose des légumineuses de Haute-Volta liée à la présence d'un nématode. *Comptes Rendus des Séances hebdomadaires de l'Académie d'Agriculture de France*, 58:202–204.

Gill, J. S. & Swarup, G., (1977). Pathogenic effect of *Tylenchorynchus vulgaris* on gram. *Indian Journal of Nematology*, 7:155–156.

Glazer, I. & Orion, D. (1983). Studies on anhydrobiosis of *Pratylenchus thornei*. *Journal of Nematology*, 15:333–338.

Golden, A. M., Epps, J. M., Riggs, R. D., Duclos, L. A., Fox, J. A. & Bernard, R. L. (1970). Terminology and identity of infraspecific forms of the soybean cyst nematode (*Heterodera glycines*), *Plant Disease Reporter*, 54:544–546.

Goodey, J. B., Franklin, M. T. & Hooper, D. J. (1965). *The Nematode parasites of plants catalogued under their hosts*. C. A. B. Farnham Royal, Bucks, England. 214 p.

Goswami, B. K. & Agarqwal, D. K. (1978). Interrelationships between species of *Fusarium* and root-knot nematodes, *Meloidogyne incognita* in soybean. *Nematologia mediterranea*, 6:125–128.

Greco, N. (1984). Presenza di *Meloidogyne artiellia* su cece in Italia. *Nematologia mediterranea*, 12:235–238.

Greco, N., Di Vito, M., Reddy, M. V. & Saxena, M. C. (1984). A preliminary report of survey of plant parasitic nematodes of leguminous crops in Syria. *Nematologia mediterranea*, 12:87–93.

Greco, N., Brandonisio, A. & Ellia, F. (1985). Control of *Ditylenchus dipsaci, Heterodera carotae* and *Meloidogyne javanica* by solarization. *Nematologia mediterranea*, 13:191–197.

Greco, N., Di Vito, M. & Lamberti, F. (1986*a*). Studies on the biology of *Heterodera goettingiana* in Southern Italy. *Nematologia mediterranea*, 14:23–39.

Greco, N., Di Vito, M., Reddy, M. V. & Saxena, M. C. (1986*b*). Effect of mediterranean cultivated plants on the reproduction of *Heterodera ciceri*. *Nematologia mediterranea*, 14:193–200.

Greco, N. & Di Vito, M. (1987). The importance of plant parasitic nematodes in food legume production in the Mediterranean Region. In: Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (Eds). *Proceedings of a Workshop on nematodes parasitic to Cereals and Legumes in Temperate Semi-Arid Regions, Larnaca, Cyprus, 1–5 March 1987:* 29–45.

Greco, N., Di Vito. M., Saxena, M. C. & Reddy, M. V. (1988*a*). Effect of *Heterodera ciceri* on yield of chickpea and lentil and development of this nematode on chickpea in Syria. *Nematologica*, 34:98–114.

Greco, N., Di Vito, M., Saxena, M. C. & Reddy, M. V. (1988*b*). Investigation on the root lesion, nematode, *Pratylenchus thornei*, in Syria. *Nematologia mediterranea*, 16:101–105.

Green, C. D. (1981). The effects of weeds and wild plants on the reinfestation of land by *Ditylenchus dipsaci* (stem and bulb nematode) and on the stability of its populations. In: Thresh, J. M. (Ed). *Pests, Pathogens and Vegetation*. London, Pitman: 217–224.

Green, C. D., Williamson, K., Dennis, E. B. & McBurney, T. (1981). The effect of oxamyl on the growth of peas attacked by the pea cyst nematode. *Annals of applied Biology*, 97:303–309.

Griffin, G. D. (1984). Nematode parasites of alfalfa, cereals, and grasses. In: Nickle, W. R. (Ed). *Plant and Insect Nematodes*. New York, Marcel Dekker Inc.: 243–323.

Gupta, D. C. (1979). Studies on the pathogenicity and relative susceptibility of some varieties of cowpea [*Vigna unguiculata* (L.) Walp.] against *Meloidogyne javanica*. *Forage Research*, 5:141–145.

Gupta, D. C. & Yadav, B. S. (1979). Studies on the pathogenicity of reniform nematode, *Rotylenchulus reniformis* to urd, *Vigna mungo* (L.) Wilczek. *Indian Journal of Nematology*, 9:48–50.

Gupta, D. C. & Yadav, B. S. (1980). Pathogenicity of *Rotylenchulus reniformis* on cowpea. *Nematologia mediterranea*, 8:91–93.

Hadisoeganda, W. W. & Sasser, J. N. (1982). Resistance of tomato, bean, southern pea, and garden pea cultivars to root-knot nematodes based on host suitability. *Plant Disease*, 66:145–150.

Hanounik, S. B., Halila, H. & Harrabi, M. (1986). Resistance in *Vicia faba* to stem nematodes (*Ditylenchus dipsaci*). *FABIS Newsletter* (*Faba Bean Information Service, ICARDA*), 16:37–39.

Hartman, R. W. (1971). Inheritance of resistance to root-knot nematodes (*Meloidogyne incognita*) in beans (*Phaseolus vulgaris* L.). *Journal of the American Society of horticultural Sciences*, 96:344–347.

Hasan, A. (1984). Synergism between *Heterodera cajani* and *Fusarium udum* attacking *Cajanus cajan*. *Nematologia mediterranea*, 12:159–162.

Hasan, N. & Jain, R. K.(1986). Screening mothbean (*Vigna aconitifolius* Jacq) germplasm for resistance to root-knot nematode (*Meloidogyne incognita*). *Agricultural Science Digest, India*, 4:198–199.

Heald, C. M., Menges, R. M. & Wayland, J. R. (1974). Efficacy of ultra-high frequency (UHF) electromagnetic energy and soil fumigation on the control of the reniform nematode and common purslane among southern peas. *Plant Disease Reporter*, 58:985–987.

Heald, C. M. & Robinson, A. F. (1987). Effects of soil solarization on *Rotylenchulus reniformis* in the lower Rio Grande Valley of Texas. *Journal of Nematology*, 19:93–103.

Hinson, K. & Hartwig, E. E. (1977). Soybean production in the tropics. *FAO Plant Production and Protection Paper*, No. 4, 92 p.

Hooper, D. J. (1972). *Ditylenchus dipsaci*. Description of Plant Parasitic Nematodes, Set 1, No. 14. St. Albans UK) C. I. H. 4p.

Hooper, D. J. (1983*a*). Observations on stem nematode, *Ditylenchus dipsaci*, attacking field beans, *Vicia faba*. *Rothamsted Report for 1983*, 2:239–260.

Hooper, D. J. (1983*b*). Nematode pests of *Vicia faba* L. In: Hebblethwaite, P. D. (Ed). *The Faba Bean* (Vicia faba L.) London, Butterworths: 347–370.

Hussaini, S. S. & Seshadri, A. R. (1975). Interrelationships between *Meloidogyne incognita* and *Rhizobium* sp. on mung bean (*Phaseolus aureus*). *Indian Journal of Nematology*, 5:189–199.

Hussaini, S. S. & Seshardri, A. R. (1976). Resistance in some mung bean (*Vigna radiata*) varieties and breeding lines to the root-knot nematode, *Meloidogyne incognita*. *Indian Journal of Nematology*, 6:131–137.

Hussey, R. S. & Roncadori, R. W. (1982). Vesicular-arbuscular mycorrhizae may limit nematode activity and improve plant growth. *Plant Disease*, 66:9–14.

Hutton, D. G., Wilkinson, R. E. & Mai, W. F. (1972). Effect of two plant-parasitic nematodes on *Fusarium* dry root rot of beans. *Phytopathology*, 63:749–751.

Hutton, D. G. & Hammerton, J. L. (1975). Investigating the role of *Rotylenchulus reniformis* in a decline of pigeon pea. *Nematropica*, 5:24. [Abstr.]

ICARDA (*International Centre for Agricultural Research in the Dry Areas*). (1986). Studies on nematodes of food legumes. *Progress Report, 1986/87*, Aleppo, Syria 32 p.

Inagaki, H. (1979). Race status of five Japanese populations of *Heterodera glycines*. *Japanese Journal of Nematology*, 9:1–4.

Inderjit Singh, V. P. S., Chahal, P. K., Sakhuja, P. K. & Chohan, J. S. (1977). Effect of different levels of *Meloidogyne incognita* in the presence or absence of *Rhizobium phaseoli* on *Phaseolus aureus*. *Indian Journal of Nematology*, 7:172–174.

Jacobsen, B. J., Edwards, D. I., Noel, G. R., & Shurtleff, M. C. (1983). The soybean cyst nematode problem. *Report on Plant Diseases, University of Illinois Cooperative Extension Service*, No. 501, 12 p.

Jain, R. K. & Hasan, N. (1986). Efficacy of "Neem" cake on fodder production, photosynthetic pigments and

nematodes associated with oats and its residual effect on cowpea. *Indian Journal of Nematology*, 16:98–100.

Jones, F. G. W. (1950). Observations on the beet eelworm and other cyst forming species of *Heterodera*. *Annals of applied Biology*, 37:304–440.

Kalha, C. S. & Edward, J. C. (1979). *Heterodera vigni* Edward & Misra, 1968, a synonym of *H. cajani* Koshy, 1967. *Allahabad Farmer*, 50:143.

Kaliram, D. C. & Gupta, D. C. (1982). Efficacy of plant leaves, nematicides and fertilizer alone and in combination against *Meloidogyne javanica* infecting chickpea (*Cicer arietinum* L.). *Indian Journal of Nematology*, 12:221–225.

Kaloshian, I., Greco, M. & Saad, A. T. (1986*a*). Hatching of cysts and infectivity of *Heterodera ciceri* on chickpea. *Nematologia mediterranea*, 14:129–133.

Kaloshian, I., Greco, M., Saad, A. T. & Volvas, N. (1986*b*). Life cycle of *Heterodera ciceri* on chickpea. *Nematologia mediterranea*, 14: 135–145.

Kay, D. E. (1979). *Food Legumes*. TPI Crop and Product Digest No. 3. Tropical Pest Institute, London, 435 p.

Khan, T. N. (1976). Papua New Guinea: a centre of genetic diversity in winged bean (*Psophocarpus tetragonolobus* (L.) D. C. *Euphytica*, 25:693–706.

Kinloch, R. A. (1974). Response of soybean cultivars to nematicidal treatments of soil infested with *Meloidogyne incognita*. *Journal of Nematology*, 6:7–11.

Kinloch, R. A. (1982). The relationship between soil populations of *Meloidogyne incognita* and yield reduction of soybean in the coastal plain. *Journal of Nematology*, 14:162–167.

Koshy, P. K. (1967). A new species of *Heterodera* from India. *Indian Phytopathology*, 20:272–274.

Koshy, P. K. & Swarup, G. (1971*a*). Investigations on the life history of the pigeon-pea cyst nematode, *Heterodera cajani*. *Indian Journal of Nematology*, 1:44–51.

Koshy, P. K. & Swarup, G. (1971*b*). Distribution of *Heterodera avenae, H. zeae, H. cajani*, and *Anguina tritici* in India. *Indian Journal of Nematology*, 1:106–111.

Koshy, P. K. & Swarup, G. (1972). Susceptibility of plants to pigeon-pea cyst nematode, *Heterodera cajani*. *Indian Journal of Nematology*, 2: 1–6.

Lamberti, F. (1981). Plant nematode problems in the Mediterranean region. *Helminthological Abstracts*, Series B, Plant Nematology, 50:145–166.

Lawn, D. A. & Noel, G. R. (1986). Field interrelationships among *Heterodera glycines, Pratylenchus scribneri* and three other nematode species associated with soybean, *Journal of Nematology*, 18:98–106.

Lehman, P. S., Huisingh, D. & Barker, K. R. (1971). The influence of races of *Heterodera glycines* on nodulation and nitrogen-fixing capacity of soybean. *Phytopathology*, 61:1239–1244.

Lehman, P. S. (1985). *Nacobbus*, the false root-knot nematode. *Florida Department of Agriculture & Consumer Services, Division of Plant Industry. Nematology Circular*, No. 119, 4 p.

Lim, B. K. & Castillo, M. B. (1979). Screening soybeans for resistance to reniform nematode disease in the Philippines. *Journal of Nematology*, 11:275–282.

Linford, M. B. & Oliveira, J. M. (1940). *Rotylenchulus reniformis* nov. gen., n. sp., a nematode parasite of roots. *Proceedings helminthological Society of Washington*, 7:35–42.

Linge, D. S. (1976). *Studies on the root-knot of winged-bean (Psophocarpus tetragonolobus (L) DC.) in Papua New Guinea*. Thesis, Department of Agriculture, University of Papua New Guinea, 46 p.

Lordello, L. G. E. & Arruda H. V. (1956). Nematoídes parasitando Guandu. *Bragantia*, 15:5–6.

Lordello. L. G. E. & de Oliveira Santos, C. F. (1960). Incidencia de nematodes en cultura de feijao. *O Biologico*, 26: 213–217.

Lordello, R. R. A., & Almeida, L. D. de. (1979). Feijáo alado, novo hospedeiro de *Meloidogyne javanica*. *Revista Agricultura, Piracicaba.*, 54:136.

Luc, M. (1985). Cyst nematodes in equatorial and hot tropical regions, In: Lamberti, F. & Taylor, C. E. (Eds). *Cyst Nematodes*. New York, Plenum Press, :355–372.

Mahapatra, B. C. & Pahdi, N. N. (1986). Pathogenicity and control of *Rotylenchulus reniformis* on *Cicer arietinum*. *Nematologia mediterranea*, 14:287–290.

Mamluk, O. F., Augustin, B. & Bellar, M. (1983). New records of cyst and root-knot nematodes on legume crops in the dry areas of Syria. *Phytopathologia mediterranea*, 22: 80.

Mani, A., Koshy, P. K. & Swarup, G. (1982). Nematodes associated with grain and forage legumes. *FAO Technical Document*, No. 129, 75 p.

Mani, A. & Sethi, C. L. (1984). Plant growth of chickpea as influenced by initial inoculum levels of *Meloidogyne incognita*. *Indian Journal of Nematology*, 14: 41–44.

Mathur, B. N., Handa, D. K. & Singh, H. G. (1969) Note on the occurrence of *Meloidogyne arenaria* as a serious pest of *Cicer arietinum*. *Madras agricultural Journal*, 56: 744.

Mathur, R. L., Handa, D. K. & Mathur, B. N. (1973). Resistance of varieties of cowpea, green gram and guar to root knot nematodes (*Meloidogyne javanica* and *M. incognita*). *Indian Journal of Mycology and Plant Pathology*, 3: 182–183.

Maqbool, M. A. (1986). *Classification and distribution of plant parasitic nematodes in Pakistan*. National Nematological Research Centre, University of Karachi, Pakistan, 58 p.

McSorley, R. (1980). Effect of *Rotylenchulus reniformis* on snap bean and methods for control by oxamyl. *Nematropica*, 10: 89–95.

McSorley, R., Pohronezny, K. & Stall, W. M. (1981). Aspects of nematode control in snap bean with emphasis on the relationship between nematode density and plant damage.*Proceedings of the Florida State horticultural Society*, 94: 134–136.

McSorley, R. & Pohronezny, K. (1984). Cost-effectiveness of nematode control by fumigation with SMDC on Rockdale soils. *Proceedings of Soil and Crop Science Society of Florida*, 43: 188–192.

Melton, T. A., Jacobsen, B. J. & Hagedorn, S. J. & Noel, G. R. (1985). Comparative host suitabilities of snap bean to soybean cyst nematode (*Heterodera glycines*). *Plant Disease*, 69: 119–122.

Midha, R. L. & Trivedi, P. C. (1988). Reaction of some black-gram varieties to the reniform nematode *Rotylenchulus reniformis*. *International Nematology Network Newsletter*, 5:18–19.

Mishra, S. D. & Gaur, H. S. (1981). Pathogenicity of *Meloidogyne incognita* and *Rotylenchulus reniformis* to mothbean, *Vigna aconitifolius* Jacq. *Indian Journal of Nematology*, 11: 228–230.

Mulk, M. M. & Jairajpuri, M. S. (1974). Nematodes of leguminous crops in India. II. Five new species of *Helicotylenchus* Steiner, 1945 (Hoplolaimidae). *Indian Journal of Nematology*, 4: 212–221.

Mulk, M. M. & Jairajpuri, M. S. (1975). Nematodes of leguminous crop in India. III. Three new species of *Hoplolaimus* Daday, 1905 (Hoplolaimidae). *Indian Journal of Nematology*, 5: 1–8.

Mulvey, R. H. & Anderson, R. V. (1974). *Heterodera trifolii*. Description of Plant Parasitic Nematodes. Set 4, No. 46, St. Albans, UK, C. H. I., 4 p.

Nadakal, A. M. (1964). Studies on plant parasitic nematodes of Kerala. III. An additional list of plants attacked by root-knot nematode, *Meloidogyne* sp. (Tylenchoidea:Heteroderidae). *Journal of Bombay Natural History Society*, 61: 467–469.

Nanjappa, C. K., Panda, M. & Seshadri, A. R. (1978). Effects of *Meloidogyne incognita* and *Rotylenchulus reniformis* on the emergence and survival of seedlings. *Abstract of Third International Congress of Plant Pathology. München, Germany*, : 150.

NAS, (National Acadamy of Science) *ad hoc* panel of the Advisory Committee on Technology innovation. (1979). *Tropical Legumes: Resources for the Future*. National Academy of Sciences, Washington, D. C. 332 p.

Nath, R. P., Banerjee, A. K., Haider, M. G. I. & Singh, B. K. (1979). Studies on the nematodes of pulse crops in India. I. Pathogenicity of *Meloidogyne incognita* on gram. *Indian Phytopathology*, 32: 28–31.

Ngundo, B. W. (1977). Screening of bean cultivars for resistance to *Meloidogyne* spp. in Kenia. *Plant Disease Reporter*, 61: 991–993.

Noel, G. R. (1982). Soybean cyst nematode in commercial snap beans, *Plant Disease*, 66: 520–522.

Noel, G. R. (1984). Relating numbers of soybean cyst nematodes to crop damage.*Proceedings 5th Cyst Nematode Workshop*, p. 17.

Noel, G. R. (1985). The soybean cyst nematode. In: Lamberti F. & Taylor C. E. (Eds.) *Cyst nematodes*. New York, Plenum Press. 257–268.

Ogbuji, R. O. (1978). Reactions of cowpea to *Meloidogyne incognita* in eastern Nigeria. *PANS*, 24: 32–34.

Oyekan, P. O. & Mitchell, J. E. (1971). Effect of *Pratylenchus penetrans* on the resistance of pea variety to *Fusarium* wilt. *Plant Disease Reporter*, 55: 1032–1035.

Palmisano, A. M., Tacconi, R. & Trotti, G. C. (1971). Sopravvivenza di *Ditylenchus dipsaci* (Kühn) Filipjev (Nematoda: Tylenchidae) al processo digestivo nei suini, equini e bovini. *Redia*, 52: 725–737.

Parvatha Reddy, P. (1984). Efficacy of seed treatment with three nematicides for the control of *Meloidogyne incognita* infecting cowpea, french bean and peas. *Indian Journal of Nematology*, 14: 39–40.

Patel, B. A., Chavda, J. C., Patel, S. T. & Patel, D. J. (1987). Reaction of some pigeonpea lines to reniform nematode (*Rotylenchulus reniformis*). *International Pigeonpea Newsletter*, 6: 57–59.

Patel, D. S. & Thakar, N. A. (1985). Reaction of some mungbean varieties to the reniform nematode, *Rotylenchulus reniformis* Linford and Oliveira, 1940. *Indian Journal of Nematology*, 15: 239.

Patel, G. J., Shah, H. M. & Patel, D. J. (1977). Screening of cowpea cultivars against root-knot nematodes. *Indian Journal of Nematology*, 7: 169–170.

Pathak, K. N., Nath, R. P. & Gaider, M. G. (1985). Effect of initial inoculum levels of *Meloidogyne incognita* and *Rotylenchulus reniformis* on pigeonpea and their interrelationship. *Indian Journal of Nematology*, 15:177–179.

Phukan, P. N. & Hazarika, M. H. (1985). Reaction of some winged bean varieties to root-knot nematode, *Meloidogyne incognita. Indian Journal of Nematology*, 15:246.

da Ponte, J. J. (1972). Doencas do feijoeiro macássar, *Vigna sinensis* Endl. no nordest Brasileiro. *Boletim da Sociedad e Cearense de Agronomia*, 13:1–12.

Powell, D. F. (1974). Fumigation of field beans against *Ditylenchus dipsaci. Plant Pathology*, 23:110–113.

Prakash, A. (1981). *Lens culinaris* – a new host for root-knot nematode, *Meloidogyne javanica* in India. *National Academic Science Letters*, 4: 459.

Prasad, S. K., Chawla, M. L., Kumar S. & Saxena, H. P. (1971). Root-knot nematode, *Meloidogyne javanica* (Treub, 1885) Chitwood, 1949 and stem borer, *Stomopteryx nertaria* Meyrick affecting green gram, *Phaseolus aureus. Indian Journal of Entomology*, 33:55–60.

Price, T., V. & Linge, D. S. (1979). Studies on the root-knot nematodes of winged bean (*Psophocarpus tetragonolobus*) in Papua New Guinea. *Tropical Agriculture*, 56:345–352.

Purseglove, J. W. (1983). *Tropical Crops – Dicotyledons*. London, Longman Group Limited, 717 p.

Rashid, A., Khan, F. A, & Khan, A. M. (1973). Plant parasitic nematodes associated with vegetables, fruits, cereals and crops in North India. *Indian Journal of Nematology*, 3: 8–23.

Rebois, R. V., Madden, P. A., & Eldridge, B. J. (1975). Some ultrastructural changes induced in resistant and susceptible soybean roots following infection by *Rotylenchulus reniformis. Journal of Nematology*, 7: 122–139.

Reddy, P. P. (1985). Estimation of crop losses in peas due to *Meloidogyne incognita. Indian Journal of Nematology*, 15: 226.

Rehm, S. & Eslpig, G. (1976). *Die Kulturpflanzen der Tropen und Subtropen*. Stuttgart Verlag Eugen Ulmers. 496 p.

Rhoades, H. L. (1964). Effect of *Crotalaria spectabilis* and *Sesbania exaltata* on plant nematode populations and subsequent yield of snap beans and cabbage. *Proceedings of the Florida State horticultural Society*, 77:233–237.

Rhoades, H. L. & Forbes, R. B. (1986). Effects of fallow, cover crops, organic mulches, and fenamiphos on nematode populations, soil nutrients, and subsequent crop growth. *Nematropica*, 16: 141–151.

Ribeiro, C. A. & Ferraz, S. (1983). Resistencia varietal do feijoerio (*Phaseolus vulgaris* L.) a *Meloidogyne javanica. Sociedade Brasileira de Nematologia*, 7: 261–270.

Riggs, R. D. & Hamblen, M. L. (1962). Soybean-cyst nematode host studies in the family Leguminosae. *Report Arkansas Agricultural Experiment Station, University of Arkansas*, Serial 110:1–18.

Riggs, R. D., Hamblen, M. L. & Rakes, L. (1981). Infra-species variation in reactions to hosts in *Heterodera glycines* populations. *Journal of Nematology*, 13:171–179.

Roberts, P. A., Van Gundy, S. D. & McKinney, H. E. (1981). Effect of soil temperature and planting date of wheat on *Meloidogyne incognita* reproduction, soil population, and grain yield. *Journal of Nematology*, 13: 378–345.

Robinson, P. E. (1961). Root-knot nematodes and legume nodules. *Nature*, 189: 506–507.
Rodriguez-Kabana, R., King, P. S. & Truelove, B. (1976). A seed treatment method for control of plant parasitic nematodes. *Proceedings of the American Phytopathological Society*, 3: 297.
Rodriguez-Kabana, R. & Ingram, E. G. (1978). Susceptibilidad del gandul a especies de fitonematodos en Alabama. *Nematropica*, 8:32–34.
Routaray, B. N., Sahoo, H. & Das, S. N. (1986). Evaluation of green gram and black gram varieties against reniform nematode, *Rotylenchulus reniformis*. *Indian Journal of Nematology*, 16: 27–29.
Ross, J. P. (1963). Seasonal variation of larval emergence from cysts of the soybean cyst nematode. *Phytopathology*, 53:608–609.
Ruthenberg, H. (1983). *Farming systems in the tropics*. Third Edition, Oxford Clarendon Press, 180 p.
Saka, V. E. & Carter, C. C. (1987). Hosts and nonhosts of the root-knot nematode *Meloidogyne incognita*. Cooperative Publication of the Department of Plant Pathology, North Carolina State University and the United States Agency for International Development, Raleigh, 62 p.
Salam, M. A. & Khan, M. W. (1986). Reaction of some cultivars of pigeon pea against *Fusarium udum* and *Melodogyne javanica*. *International Nematology Network Newsletter*, 3:16–17.
Saleh, H., Abu-Gharbieh, W. I. & Al-Banan, L. (1988). Effect of solarization combined with solar-heated water on *Meloidogyne javanica*. *Nematologica*, 34:290–291.
Sasser, J. N. & Kirby, M. F. (1979). *Crop Cultivars Resistant to Root-knot Nematodes, Meloidogyne Species*. Department of Plant Pathology, North Carolina State University, Raleigh, USA, 24 p.
Sasser, J. N. & Hartman, K. M. (1985). Evaluation of some pigeonpea lines for resistance to the root-knot nematodes, *Meloidogyne* spp. *International Pigeonpea Newsletter*, 4:44–45.
Saxena, M. C. (1987). *Agronomy of chickpea*. In: Saxena, M. C. & Singh, K. B. (Eds.) *The Chickpea*. Wallingford, C. A. B. International: 207–232.
Schmitt, D. P. & Barker, K. R. (1981). Damage and reproduction potentials of *Pratylenchus brachyurus* and *P. penetrans* on soybean. *Journal of Nematology*, 13: 327–332.
Schmitt, D. P. & Noel, G. R. (1984). Nematode parasites of soybeans. In: Nickel, W. R. (Ed). *Plant and insect nematodes*. New York, Marcel Dekker: 13–59.
Schreiber, E. R. (1977). Lebensweise, Bedeutung und Bekämpfungsmöglichkeiten von *Ditylenchus dipsaci* (Kühn) Filipjev an Ackerbohne (*Vicia faba* L.) In Marokko. *Dissertation der Technischen Universität, Berlin*, D83 No. 79, 150 p.
Seinhorst, J. W. (1956*a*). Population studies on stem eelworms (*Ditylenchus dipsaci*) *Nematologica*, 1:159–164.
Seinhorst, J. W. (1956*b*). Biologische Rassen van het stengelaaltje *Ditylenchus dipsaci* (Kühn) Filipjev en hun Waardplaten. *Tijdskrift voor Plantenziekten*, 62:179–188.
Sharma, R. D. (1981). Pathogenicity of *Meloidogyne javanica* to bean (*Phaseolus vulgaris* L.) *Sociedade Brasilerira de Nematologia*, 5: 137–144.
Sharma, S. B. (1985). *A world list of nematode pathogens associated with chickpea, groundnut, pearl millet, pigeon pea, and sorghum*. Patancheru, Andhra Pradesh, India ICRISAT. 36 p.
Sharma, N. K. & Sethi, C. L. (1975). Effects of initial inoculum levels of *Meloidogyne incognita* and *Heterodera cajani* on cowpea and on their population development. *Indian Journal of Nematology*, 5: 148–154.
Sharma, N. K. & Sethi, C. L. (1976*a*). Interrelationship between *Meloidogyne incognita, Heterodera cajani* and *Rhizobium* sp. on cowpea (*Vigna sinensis* (L.) Savi). *Indian Journal of Nematology*, 6:117–123.
Sharma, N. K. & Sethi, C. L. (1976*b*). Reaction of certain cowpea varieties to *Meloidogyne incognita* and *Heterodera cajani*. *Indian Journal of Nematology*, 6:99–102.
Sharma, S. B. & Swarup, G. (1984). *Cyst forming nematodes of India*. New Delhi, Cosmo Publications, 149 p.
Sikora, R. A. (1972). Plant parasitic nematodes associated with sugarbeet and soybean in India. *Indian Journal of Nematology*, 2:200–201.
Sikora, R. A. (1981). Interaction between plant parasitic nematodes, plant roots, and vesicular arbuscular mycorrhizae. *Proceedings of Symposium on Biological and Chemical Interactions in the Rhizosphere*, Stockholm: 115–135.
Sikora, R. A. & Maas Ph. (1986). An analysis of the *Heterodera trifolii* complex and other species in the *schachtii*

group attacking legumes. In: Lamberti, F. & Taylor, C. E. (Eds.). *Cyst Nematodes*. New York & London Plenum Press: 293–313.

Sikora, R. A. (1987). Analysis of plant parasitic nematodes affecting pasture and forage legumes in temperate semiarid regions. In: Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (Eds). *Nematodes parasitic to cereals and legumes in temperate semi-arid regions*. Proceedings of a Workshop, Larnaca, Cyprus. International Centre for Agricultural Research in Dry Areas, (ICARDA). Aleppo, Syria, 13–28.

Singh, R. S. & Sitaramaiah, K. (1966). Incidence of root knot of okra and tomato in oil-cake amended soil. *Plant Disease Reporter*, 5:668–672.

Singh, R. S. & Sitaramaiah, K. (1971). Control of root-knot through organic and inorganic amendments of soil: Effect of sawdust and inorganic nitrogen. *Indian Journal of Nematology*, 1: 80–84.

Singh, D. B., Parvatha, R. & Rajendran, R. (1979). Reaction of certain winged bean varieties to the root-knot nematode, *Meloidogyne incognita. Indian Journal of Nematology*, 9:43–45.

Singh, D. B. & Reddy, P. P. (1981). Influence of *Meloidogyne incognita* infestation on *Rhizobium* nodule formation in french bean. *Nematologia mediterranea*, 9: 1–5.

Singh, D. B. & Reddy, P. P. (1982). Cultivars of cowpea resistant to root-knot nematode in India. *Tropical Pest Management*, 28:185–186.

Sitaramaiah, K., Singh, R. A., Singh, K. P. & Sikora, R. A. (1971). *Plant parasitic and soil nematodes of India*. U. P. Agriculture, University Experiment Station Bulletin, No. 3, 70 p.

Sitaramaiah, K. (1984). *Plant parasitic nematodes of India*, New Delhi Today & Tomorrow's Printers & Publishers, 292 p.

Slack, D. A. & Hamblen, M. L. (1961). The effect of various factors on larval emergence from cysts of *Heterodera glycines*. *Phytopathology*, 51: 350.

Sorney, P. de (1913). *Les Plantes Tropicales Alimentaires et Industrielles de la Famille des Légumineuses*. P. 3. Paris Challamel.

Sosamma, V. K. & Koshy, P. K. (1977). Additional hosts of the burrowing nematode, *Radopholus similis*, infesting coconut palm in South India. *Plant Disease Reporter*, 61: 760–761.

Srivastava, A. S., Upadhyay, K. D. & Singh, G. (1974). Effect of root-knot nematode, *Meloidogyne javanica*, on gram crop. *Indian Journal of Nematology*, 4: 248–251.

Steiner, K. G. (1982). *Intercropping in Tropical Smallholder Agriculture with Special Reference to West Africa*. Gesellschaft für Technische Zusammenarbeit (GTZ) Publication No. 137, 303 p.

Stone, A. R. & Course J. A. (1974). *Heterodera goettingiana*. Commonwealth Institute of Helminthology. Descriptions of Plant-Parasitic Nematodes. Set 4, No. 47, UK, C.I.H. 4 p.

Sultan, M. S., Singh, I. & Sharma, S. K. (1985). Efficacy of some nematicides for the control of root-knot nematode infesting mung. *Nematologia mediterranea*, 13:257–259.

Swarup, G., Prasad, S. K. & Raski, D. J. (1964). Some *Heterodera* species from India. *Plant Disease Reporter*, 48:235.

Taha, A. H. Y. & Kassab, A. S. (1980). Interrelations between *Meloidogyne javanica, Rotylenchulus reniformis* and *Rhizobium* sp. on *Vigna sinensis*. *Journal of Nematology*, 12:57–62.

Tarte, R. (1971). Estudios sobre la distribution y poblationes de nematodes en fincas hortalizas intensamente cultivades. *Turrialba*, 21: 34–37.

Teruya, R., Abe, J., Nagamine, M. & Nakamura, H. (1984). Nematological survey on winged bean fields in Okinawa with special reference to varietal difference in susceptibility to root-knot nematodes. *Japan agricultural Research Quarterly*, 18: 142–157.

Thakar, N. A. & Patel, C. C. (1984). Screening of few cowpea varieties against reniform nematode, *Rotylenchulus reniformis* Linford and Oliveira, 1940. *Indian Journal of Nematology*, 14:204.

Thakar, N. A. & Yadav, B. S. (1985*a*). Comparative pathogenicity of the reniform nematode *Rotylenchulus reniformis* on a susceptible and a resistant variety of pigeonpea. *Indian Journal of Nematology*, 15: 167–169.

Thakar, N. A. & Yadav, B. S. (1985*b*). Screening pigeonpeas for their resistance to reniform nematodes. *International Pigeonpea Newsletter*, 4: 42–43.

Thames, W. H. & Heald, C. M. (1974). Chemical and cultural control of *Rotylenchulus reniformis* on cotton. *Plant Disease Reporter*, 58: 337–341.

Thomason, I. J., Erwin, D. C. & Garber, M. J. (1959). The relationship of the root-knot nematode, *Meloidogyne javanica*, to Fusarium wilt of cowpea. *Phytopathology*, 49:602–606.

Thomason, I. J. & McKinney, H. E. (1960). Reaction of cowpeas, *Vigna sinensis*, to root-knot nematodes, *Meloidogyne* spp. *Plant Disease Reporter*, 44:51–53.

Thomason, I. J., Rich, J. R. & Omelia, F. C. (1976). Pathology and histopathology of *Pratylenchus scribneri* infecting snap bean and lima bean. *Journal of Nematology*, 8: 347–352.

Timm, R. W. (1956). The reniform nematode, a root parasite of *Vicia faba*. *Pakistan Review of Agriculture*, 2:135.

Tisselli, I., Sinclair, J. B. & Hymowitz, T. (1980). Sources of resistance to selected fungal, bacterial, viral and nematode disease of soybeans. *International agricultural publications INTSOY*, Series No. 18:134 p.

Tobar Jimenez, A. (1973). Nematodes de los "secanos" de la comarca de Alhama. I. Niveles de poblacion y cultivos hospedadores. *Revista Iberica de Parasitologia*, 33: 525–556.

Toler, R. W., Tompson, S. S. & Barber, J. M. (1963). Cowpea (Southern pea) diseases in Georgia, 1961–1962. *Plant Disease Reporter*, 47: 746–747.

Uphof, J. C. Th. (1968). *Dictionary of Economic Plants*. New York, Verlag von J. Cramer, 591 p.

Upadhyay, K. D. & Dwivedi, K. (1987). Analysis of crop losses in pea and gram due to *Meloidogyne incognita*. *International Nematology Network Newsletter*, 4:6–7.

Valdez, R. B. (1981). Screening tomato, eggplant and winged bean for resistance to *Meloidogyne incognita* and *M. javanica*. *Proceedings of the 3rd research planning conference on root-knot nematodes, Meloidogyne spp. July 1981, Jakarta, Indonesia. Raleigh, North Carolina State Univeristy*, 82–88.

Vijayalakshmi, K. & Goswami. B. K. (1986). Effect of seed treatments with neem cake and neem oil on the germination of moong (green gram) and its vulnerability to root-knot nematodes. *International Nematology Network Newsletter*, 3:8–9.

Vovlas, N., Greco, N., & Di Vito, M. (1985). *Heterodera ciceri* sp. n. (Nematoda: Heteroderidae) on *Cicer arietinum* L. from northern Syria. *Nematologia mediterranea*, 13: 239–252.

Walia, K. K. & Gupta, D. C. (1986). Effect of the fungus, *Rhizoctonia bataticola* on the population development of pigeon-pea cyst nematode, *Heterodera cajani* on cowpea (*Vigna unguiculata*). *Indian Journal of Nematology*, 16:131–132.

Walia, R. K. & Seshadri, A. R. (1985*a*). Pathogenicity of the root-lesion nematode *Pratylenchus thornei* on chickpea. *International Chickpea Newsletter*, 12: 31.

Walia, R. K. & Seshadri, A. R. (1985*b*). Chemical control of *Pratylenchus thornei* on chickpea through seed treatment. *International Chickpea Newsletter*, 13: 32–34.

Wallace, H. R. (1962). Observations on the behaviour of *Ditylenchus dipsaci* in soil. *Nematologica*, 7:91–101.

Ward, A., Mercer, S. L. & Howe, V. Editors. (1981). *Pest control in tropical grain legumes*. Centre for Oversea Pest Research, London 206 p.

Whitehead, A. G. (1969). The distribution of root-knot nematodes (*Meloidogyne* spp.) in tropical Africa. *Nematologica*, 15: 315–333.

Whitehead, A. G., Bromilow, R. H., Tite, D. J., Finch, P. H., Fraser, J. E. & French, E. M. (1979). Incorporation of granular nematicides in soil to control pea cyst-nematode, *Heterodera goettingiana*. *Annals of applied Biology*, 92: 81–91.

Wilson, W. R. & French, N. (1975). Population studies of stem eelworm (*Ditylenchus dipsaci*) in microplots, field plots and fields in north of England under different crop rotations. *Plant Pathology*, 24:176–183.

Winslow, R. D. (1954). Provisional lists of host plants of some root eelworm. (*Heterodera* spp). *Annals of applied Biology*, 41: 591–605.

Wrather, J. A., Anand, S. C. & Dropkin, V. H. (1984). Soybean cyst nematode control. *Plant Disease*, 68:829–833.

Wyatt, J. E., Fassuliotis, G., Johnson, A. W., Hoffman, J. C. & Deakin, J. R. (1980). B4175 root-knot nematode resistant snap bean breeding line. *Hort Science*, 15: 530.

Wyatt. J. E., Fassuliotis, G., Hoffman, J. C. & Deakin, J. R. (1983). "Nemasnap" snap bean. *Hort Science*, 18: 776.

Yein, B. R., Singh Harcharan & Chhabra, H. K. (1977). Effect of pesticides and fertilizers singly and in combination on the root-knot nematode infesting mung. *Indian Journal of Nematology*, 7:117–122.

Zaki, F. A. & Bhatti, D. S. (1986), Pathogenicity of pigeon-pea cyst nematode, *Heterodera cajani*, Koshy, 1967 on some pulse crops. *Indian Journal Nematology*, 16:30–35.

Chapter 7

Nematode Parasites of Vegetables

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Vegetables are an extremely important component of our daily diet as well as a high value cash crop for small and large growers alike. Vegetables, especially the leaf vegetables, are rich in protein, vitamins, minerals and fibre. Leaf vegetables, for example, are a major source of protein in the humid tropics (Rhem & Espig, 1976). Mass transportation and modern processing has made many of these often highly perishable foods – which were previously only available on a seasonable basis in local markets or in restricted growing regions – more readily available both nationally and internationally. Many vegetables that were once only of local or regional importance are now standard produce on markets throughout the world. The major vegetables common to the subtropics and tropics are given in Table 1.

In most areas of the world vegetable consumption and production is expanding rapidly. This is especially evident in countries with rapidly expanding populations, where large amounts of land near urban centres have been devoted to vegetable production. Large scale vegetable production has been further stimulated by advances made in the processing industry.

The rapid development of vegetable production in the tropics is illustrated by an 18% increase in production between 1981 and 1985. Conversely, in the more developed countries, vegetable production only expanded 7.7% in the same time span (FAO, 1985). Production figures for some typical subtropical and tropical vegetable crops are given by region in Table 2. The major producers of vegetables in the tropics in order of importance are: Asia, Africa, South America and Central America.

The types of vegetables grown are numerous and full coverage is beyond the scope of this chapter. Many of the important crops that can be used as vegetables, for example the leaves of cassava, and taro, have been discussed under root and tuber crops (Chapter 5). Similarly, many of the crops covered under food legumes (Chapter 6), such as peas and haricot beans, which are considered vegetables, will not be dealt with here.

Cultivation techniques

Depending on demographic structure and economic development of a region, vegetable growing in the subtropics and tropics varies from gathering of fruits, leaves and tubers found amongst the natural vegetation and various forms of multiple cropping to large scale commercial production (Kassam, 1976).

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

TABLE 1. Common name, botanical name, use, economic importance and origin of the most common subtropical and tropical vegetables (Zeven & de Wet, 1982).

Common name	Botanical name	Use	Economical importance	Origin
Beetroot	*Beta vulgaris* L.	Roots	S	S. Europe, India
Black mustard	*Brassica nigra* L.	Leaves	S	Europe
Broccoli	*Brassica oleracea* L. v. *botrytis*	Flower	S	Europe
Carrot	*Daucus carota* L.	Roots	S	Europe, N. Africa
Calabash	*Lagenaria vulgaris* Ser.	Fruits	S	Africa, Asia, Trop. Aus.
Cabbage	*Brassica oleracea* L. v. *capitata*	Leaves	I	Europe
Cauliflower	*Brassica oleracea* v. *botrytis* L.	Flower	M	Europe
Celery	*Apium graveolens* L.	Leaves	S	S. Europe
Chayotte	*Sechium edulis* Schwartz	Fruits	S	C. America
Chilli	*Capsicum annuum* L.	Fruits	I	S. America
Chinese cabbage	*Brassica chinensis* L.	Leaves	M	East China
Cucumber	*Cucumis sativus* L.	Fruits	M	N. India
Eggplant	*Solanum melongen* L.	Fruits	I	India
Garlic	*Allium sativum* L.	Bulbs	M	C. Asia
Kale	*Brassica oleracea* L. v. *acephale*	Leaves	S	Europe
Leek	*Allium porrum* L.	Leaves	M	Middle East
Lettuce	*Lactuca sativa* L.	Leaves	M	N. Africa
Sponge gourd	*Luffa cylindrica*	Fruits	S	India
Melon	*Cucumis melo* L.	Fruits	M	Africa
Okra	*Abelmoschus esculentus* (L.) Moench	Fruits	I	India
Onion	*Allium cepa* L.	Bulbs	I	C. Asia
Parsley	*Petroselinum crispum* Nym. ex A. W. Hill	Leaves	S	S. Europe
Pumpkin	*Cucurbita pepo* L.	Fruits	S	S. America
Radish	*Brassica sativus* L.	Roots	S	Japan
"Spinach"	*Amaranthus hybridus* L.	Leaves	M	N. Africa
	Amaranthus viridis L.	Leaves	M	S. America
	Basella alba L.	Leaves	S	S. E. Asia
	Ipomoea reptans Poir	Leaves	S	Tropics
	Solanum nigrum L.	Leaves	S	W. Africa
Sweet pepper	*Capsicum annuum* L. v. *grossum*	Fruits	M	S. America
Tomato	*Lycopersicon esculentum* Mill.	Fruits	I	S. America
Watermelon	*Citrullus vulgaris* Schrad.	Fruits	M	Africa

S = Small, locally produced in home and small market gardens. M = More important production often near big centres. I = Important, generally produced throughout the tropics, major vegetables.

In humid tropical forests, shifting cultivation, where forests are cleared and burned, cropped, then abandoned again for up to 30 years, was the prevalent system. In most tropical areas today, however, a multiple cropping system is now practised with up to twenty different plant species grown simultaneously on a small plot of land. Shifting cultivation has been gradually replaced in many areas by different forms of multiple crop farming systems (Norman *et al.*, 1981). In many of these situations, survival of the subsistence farm family is governed by the quantity and quality of the crops produced.

Large scale vegetable production is more input orientated than traditional methods and is dependent on higher levels of mechanization, a secure water supply, effective and safe pesticides, and high quality seed or planting material.

TABLE 2. Area, yield and total production of different vegetables in tropical regions in 1985 (FAO, 1985).*

	Africa			*C. America*			*S. America*			*Asia*		
	Area	Yield	Prod.	Area	Yield	Prod.	Area	Yield	Prod.	Area	Yield	Prod.
Cabbage	30	25.7	767	27	15.7	424	21	21.6	460	796	20.3	161
Cantaloupes and other melons	48	15.9	756	34	12.5	425	26	13.6	351	317	12.9	4083
Cauliflower	7	22.2	185	1	13.0	13	5	15.8	72	195	10.8	2105
Chillies, pepper, green	170	7.2	1221	69	8.2	566	20	8.5	172	608	5.7	3468
Cucumber and gherkin	23	16.2	368	36	7.3	262	3	16.6	47	420	15.5	6512
Eggplant	378	14.0	5293	–	–	–	1	13.1	9	328	13.0	4257
Garlic	8	24.2	195	7	7.4	52	26	4.7	124	382	5.0	1928
Onions	157	13.1	1974	12	7.2	86	111	14.7	1635	950	12.1	11524
Pumpkins, squashes and gourds	69	14.9	984	41	7.0	288	75	9.8	741	202	12.4	2498
Tomato	445	13.6	6042	154	19.3	2974	133	25.7	3426	798	19.0	15183
Watermelon	120	18.4	2200	34	13.2	449	120	9.3	1118	970	16.6	16125

*Area in 1000 ha, Yield in MT/ha, Production (Total) in 1000 MT

Nematodes of Vegetables

The role plant parasitic nematodes play in limiting vegetable production depends to a large extent on the farming system employed. In general, nematodes will be less important under more extensive and varied growing systems typical of shifting cultivation and multiple-crop farming in subsistence agriculture or in widely spaced rotations of commercial farming systems than in more intensive production where monocropping and narrow rotations are practiced. This was observed in Senegal where crops grown under local cropping conditions were not parasitized by root-knot while neighbouring irrigated vegetable fields were heavily infested (Netscher, 1978).

The crops grown in shifting cultivation and in the other multiple-crop systems common to subtropical and tropical areas still have much in common with the natural flora from an ecological standpoint. The distribution of important plant parasitic nematodes associated with the natural vegetation is clustered, and so the distribution of the species which survive the drastic shift to multiple cropping will also be heterogeneous even if polyphagous species are present. Extensive damage by nematodes, therefore, is extremely rare in the crops produced directly after clearing. Exceptions to the rule occur in those instances where nematode infested planting material in the forms of seedlings or tubers are used for planting (Bridge, 1987).

Multiple cropping systems, although initially reflecting the natural flora, will promote nematode population build-up with time. The extent of the increase will depend on the nematodes initially present and on the percentage of susceptible plants per unit area. Damage intensity usually increases slowly with time in the multiple cropping system, as compared to the rapid increase in damage encountered in large scale vegetable production where near monoculture is practiced.

Great differences exist between the plant parasitic nematode communities of tropical and temperate regions. Most vegetable crops have been recorded as a host for at least one of the most frequently occurring species of root-knot nematodes, *M. incognita, M. javanica* and *M. arenaria*. Important temperate parasites like *Ditylenchus dipsaci* and species of *Heterodera* are only of local importance in the warm tropics. Conversely root-knot nematodes that predominate in tropical regions are uncommon in temperate regions (Taylor, 1976).

Root-knot nematodes, which increase to damaging levels within a few seasons under susceptible crops, are so common in subtropical and tropical vegetable production that frequently they are taken

to represent "nematodes" in general. Other economically important nematode species are often overlooked, because of a lack of distinct symptoms and are often neglected by plant protection agencies. This has been particularly true for cyst nematodes.

Research has shown that a number of other parasites frequently encountered in vegetable production such as *Rotylenchulus reniformis* and *Paratrichodorus minor* are of economic importance in vegetable production. Other nematodes like *Heterodera schachtii, Nacobbus aberrans, Belonolaimus longicaudatus* and *Tylenchorhynchus brassicae* have also been shown to be serious pests of local importance.

Meloidogyne

Initially, all root-knot nematodes were considered to belong to one extremely polyphagous species, *Heterodera marioni* (Cornu 1887) Goodey, 1932, until Chitwood (1949) re-established the genus *Meloidogyne* Goeldi, 1987. Although 51 species of *Meloidogyne* have been described to date (Jepson, 1987), four species are of particular economic importance to vegetable production, *M incognita, M. javanica, M. arenaria*, and *M. hapla*. Out of 1000 root-knot populations collected in 75 countries, 53% were identified as *M. incognita*, 30% as *M. javanica*, 8% as *M. arenaria*, 8% as *M. hapla* and 2% *M. exigua* or other species (Johnson & Fassuliotis, 1984).

M. incognita, M. javanica, M. arenaria and *M. hapla* have the widest host ranges. *M. incognita* and *M. javanica* are commonly found in the tropics, whereas *M. arenaria* which is also found sporadically in the tropics, is more common in the subtropics. *M. hapla*, a species common in the temperate regions, can occasionally be found in the cooler upland tropics. *M. incognita* var. *acrita* Chitwood, 1949, later promoted to specific rank (Esser *et al.*, 1976; Jepson, 1987), is synonymized in this chapter with *M. incognita* (Triantaphyllou & Sasser, 1960).

In Table 3 the main species of *Meloidogyne* found parasitizing vegetables are listed by crops and their relative level of importance noted.

Symptoms of damage

The presence of galls on the root system is the primary symptom associated with *Meloidogyne* infection. In galls formed by one female a swelling of the central cylinder, highly deformed vascular elements and the spherical part of the female surrounded by the cortical parenchyma can be easily observed at low magnification in stained roots (Plate 5H).

The size and form of the gall depends on the species involved, number of nematodes in the tissue, host and plant age. In cucurbits, the roots react to the presence of *Meloidogyne* by the formation of large, fleshy galls (Fig. 1), whereas in most other vegetables, galls are large and firm (Plate 5D). Occasionally very small galls develop (Plate 5E) and in some cases galls are not visible. Symptoms of root-knot on monocotyledonous crops like onion and leek are very discrete, the main symptom being the presence of the protruding egg masses. Galls on sweet and chilli pepper, for example, are also frequently small. The symptoms caused by *M. hapla* differ from those produced by most other species in that only small, more or less spherical galls are produced with profuse root branching originating from the gall tissue causing a "bearded root" system (Plate 5F).

When plants are severely infected by *Meloidogyne* the normal root system is reduced to a limited number of severely galled roots with a completely disorganized vascular system. Rootlets are almost completely absent (Plate 5D). The roots are seriously hampered in their main functions of uptake and transport of water and nutrients. Plants wilt rapidly, especially under dry growing conditions, and are often stunted. Growth is retarded and leaves may be chlorotic (Plate 5A,B). In Thailand, wilting often occurs in non-chlorotic plants and has given rise to the term "Green wilt disease" (S. Sontirat, pers. comm.). In cases where seedling infection has taken place, numerous plants die in the seedbed and seedlings do not survive transplanting. In those plants that do survive, flowering and fruit production is strongly reduced. The losses caused by *Meloidogyne* on root and tuber crops like carrot, are both quantitative and qualitative, because nematode galling affects marketability

TABLE 3. Root-knot nematodes, *Meloidogyne* spp., associated with major vegetable crops in the subtropics and tropics and their relative economic or potential importance.

Botanical Name	Common Name	*Meloidogyne arenaria*	*Meloidogyne acronea*	*Meloidogyne cruciani*	*Meloidogyne ethiopica*	*Meloidogyne exigua*	*Meloidogyne hapla*	*Meloidogyne incognita*	*Meloidogyne javanica*	*Meloidogyne thamesi*
Abelmoschus esculentus	Okra	V							V	V
Allium asacolonium	Shallot							U	U	
A. cepa	Onion	L				U			L	U
A. porrum	Leek							U	L	
A. sativum	Garlic							U		
A. schocnoprasum	Chives								U	
Amaranthus hybridus	Spinach (bajem)							M	M	
A. viridis	African spinach								M	
Apium graveolens	Celery							V	V	V
Basella alba	Spinach							M	M	
Beta vulgaris	Beetroot	L					L			
Brassica chinensis	Chinese cabbage							M		
B. nigra	Black mustard	U								
B. oleracea v *acephale*	Kale	U							U	
B. oleracea v. *botrytis*	Cauliflower	L							L	
B. oleracea v. *capitata*	Cabbage	L					L	L	L	
Capsicum annuum	Sweet pepper, chilli	L				L		M		
C. frutescens	Cayenne pepper	L						M	L	
Celosia argentea	African spinach	L					L	M	M	
Citrullis vulgaris	Watermelon	V						V	V	
Cucumis melo	Melon	L						V	V	
C. sativus	Cucumber	V						V	V	
Cucurbita maxima	Squash	V						V	V	
C. pepo	Pumpkin	V						V	V	
Daucus carota	Carrot	L					L	V	V	
Ipomea reptans	"Spinach" (kangkung)						U			
Lactuca sativus	Lettuce	L					U	V	V	L
Lagenaria siceraria	Bottle gourd	M							V	
L. vulgaris	Calabash	M						V	V	
Luffa cylindrica	Sponge gourd							V	V	
Lycopersicon esculentum	Tomato	V	U	U	U			V	V	L
Momordica charantia	Balsam pear							U		
Petroselinum crispum	Parsley	L					L	V		U
Sechium edule	Chayotte								V	
Solanum melongena	Eggplant	V						V	V	
S. nigrum	Black nightshade	U						U	U	

V = Very important. M = Moderately important. L = Limited or of local importance and U = Unknown importance.

Fig. 1. Massive galls produced by *Meloidogyne javanica* on cucurbit roots in India.

(Fig. 2; Plate 5F). As the season advances the galls are often invaded by fungi and bacteria that induce rotting (Fig. 3; Plate 5D). In severe cases the firm stele of the primary root is the only remnant of the original intact root system.

Biology and life cycle

There are optimum temperatures for different phases of the life cycle of *M. javanica* (Ferris & Van Gundy, 1979). Optimum temperature range for an Australian population was 25–30°C and those for a California population between 32–34°C. Dao (1970) demonstrated that populations adapt to local climatic conditions. Optimum temperatures, for nematode development correspond to those found in tropical vegetable growing regions, a factor insuring serious root-knot infestations. Survival of eggs and juveniles of *M. javanica* decreased strongly when submitted to a temperature of 45°C for three hours (Demeure, 1978). Temperature optimums for *M. hapla* are at least 5°C lower than for the other major species in the tropics. *M. hapla* is therefore limited to the upland tropics and temperate growing regions. *M. incognita, M. javanica* and *M. arenaria* occur in areas with an average temperature of 36°C or lower in the warmest month. *M. hapla* conversely, occurs in areas having a

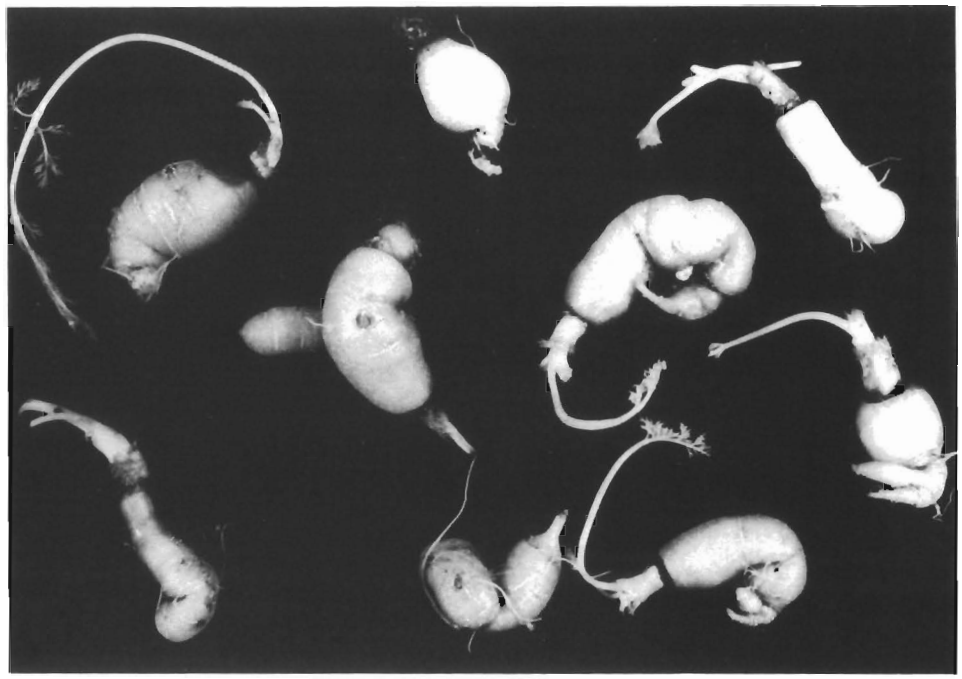

Fig. 2. Deformed carrots caused by *Meloidogyne* sp. in Tonga.

temperature as low as –15°C during the coldest month, but is limited to regions with an average high of less than 27°C during the warmest month (Taylor *et al.*, 1982).

Soil texture and structure are directly related to water holding capacity and aeration and influence nematode survival, emergence, and disease severity. Sikora (1989), studying paddy rice – vegetable cropping systems, detected severe root-knot damage on vegetables grown in sandy soils after paddy but a total absence in clay soils. Soil type and soil pH has also been shown to influence nematode distribution (Taylor *et al.*, 1982). Soil type may also influence the types of crops grown, thereby affecting nematode distribution, population buildup and damage intensity. Juveniles in sandy soils are able to move horizontally and vertically over distances of up to 75 cm in 9 days (Prot, 1977). Prot and Van Gundy (1981) found that migration decreased with increasing clay content of the soil with no migration in soils with more than 30% of clay. The effect of soil pH on root-knot varies greatly. *Meloidogyne* species survive and reproduce at pH levels ranging from 4.0–8.0 (Ferris & Van Gundy, 1979). Emergence of *M. javanica* was greatest between 6.4 and 7.0 and inhibited below pH 5.2 (Wallace, 1966). Many tropical soils are very acid (pH of 4.5 is rather common), a fact that does not seem to prevent *Meloidogyne* buildup to extremely high densities.

Races

Sasser (1954) proposed a method for the identification of the four major species, *M. incognita, M. javanica, M. arenaria* and *M. hapla*, based on the reaction of four hosts. The host differentials were expanded to include a tobacco cultivar with resistance to many *M. incognita* populations following the discovery of physiological races within *Meloidogyne* species (Taylor & Sasser, 1978).

It soon became evident that within species great physiological variability existed. Riggs and Winstead (1959) demonstrated that when populations of *M. incognita* and *M. arenaria* were inoculated to resistant cultivars of tomato, enough selection pressure was exerted by the cultivar that within a short time resistant breaking populations called "B races" were created. Sasser (1966) found

that when different populations of the same species were inoculated to certain hosts, they often reacted differently. Thus certain populations of *M. incognita* parasitized cotton while others did not. In the same way, two categories of *M. arenaria* populations could be distinguished using peanut as a differential host. When a resistant cultivar of tobacco, NC 95, was included in the host range, the situation became still more complicated, according to the reactions on the two differential hosts, cotton and tobacco, *M. incognita* populations could be split into four races. From these and other observations (Southards & Priest, 1973) it became evident that in contrast to other genera of parasitic nematodes, like *Heterodera*, the identification of root-knot did not automatically give exact indications of the host range of that population.

The use of host differentials allows determination of the four main species and races of *Meloidogyne* (Table 4). Based on the results obtained with several hundred *Meloidogyne* populations, Sasser (1979*a*) concluded that there is considerable uniformity in host response and that resistance breaking races are not common. However, Southards and Priest (1973) demonstrated that host differentials can react differently to populations of the same species.

Fig. 3. Root degradation in tomato caused by the concomitant infestation of *Meloidogyne incognita* and root-rotting fungi in the Philippines.

TABLE 4. Differential host test identification of the most common *Meloidogyne* species and races (Hartman & Sasser, 1985).

	Tobacco	Cotton	Pepper	Watermelon	Peanut	Tomato
M. incognita						
Race 1	−	−	+	+	−	+
Race 2	+	−	+	+	−	+
Race 3	−	+	+	+	−	+
Race 4	+	+	+	+	−	+
M.arenaria						
Race 1	+	−	+	+	+	+
Race 2	+	−	−	+	−	+
M.javanica	+	−	−	+	−	+
M.hapla	+	−	+	−	+	+

Cotton: cv Deltapine; tobacco: cv N.C.95; pepper: cv Early California Wonder; watermelon: cv Charleston Gray; peanut: cv Florunner; tomato: cv Rutgers. (−) indicates a resistant host, (+), a susceptible host.

Further complicating identification is the fact that many populations are composed of more than one species (Netscher, 1978; Fargette, 1987). From one point of view, identification of *Meloidogyne* to species has little practical importance to vegetable growers, since most vegetables are susceptible to the major species encountered in the tropics. Amaranthus, celosia, beetroot, swiss chard, lettuce, most cabbages, cauliflower, most cucurbits, beans, peas, tomato, potato, eggplant, okra, carrot and many other vegetables have all been reported to be hosts of *M. arenaria, M. incognita* and *M. javanica* (see also Chapter 4 Food Legumes for other hosts). Correct species identification of *Meloidogyne* is important, however, in the correct selection of non-host crops for rotation purposes or a resistant cultivar.

Survival and means of dissemination

Root-knot nematodes are obligate parasites, therefore, the absence of suitable host plants for prolonged periods ultimately leads to their disappearance. In the absence of susceptible crops, however, they often survive on weed hosts. In general, conditions favourable for plant growth will also be favourable for *Meloidogyne* reproduction. De Guiran and Demeure (1978) found that the optimum moisture levels for emergence of *M. incognita* juveniles was slightly above field capacity. If, under conditions optimum for emergence, host plants are absent, juveniles will deplete their energy reserves in the soil and eventually die. Although nematode populations rapidly decline, a proportion of the eggs in the eggmass are in diapause and assure perpetuation of the species (de Guiran, 1979; de Guiran & Villemin, 1980).

Under adverse environmental conditions, emergence and juvenile activity is reduced, thus, increasing the chances of survival. Survival is mainly influenced by moisture content of the soil and to a lesser extent by temperature. High temperatures are often associated with low soil moisture content, whereas in the cases of waterlogged or inundated soils, high temperatures rarely occur. Juveniles and eggs survive periods of moisture stress in a state of anhydrobiosis. Egg masses collected from dry soils will contain empty eggs and anhydrobiotic eggs with second stage juveniles in diapause.

In field soil, the number of juveniles decreased from an initial infestation of approximately 10 000 nematodes/dm^3 of soil to zero after 12 weeks, when the soil was gradually dried (de Guiran, 1979). Similar effects were found in the dry season in Senegal (Demeure, 1977). Nematodes could not be detected in the top twenty cm of the soil at the end of the dry season. The number of nematodes in the 20 – 40 cm horizon, where available soil moisture was slightly higher, reached 0.9% of the initial population.

Dissemination takes place when juveniles or eggs are transported from infested to uninfested

areas. Wind-borne dissemination of root-knot nematodes has been reported (Orr & Newton, 1971) and may occur in regions where wind storms occur. Spread with irrigation water has been demonstrated in the U.S.A. (Faulkner & Bolander, 1970) and in Spain (Tobar & Palacios, 1974). Dispersal in runoff water produced during rain storms is another source of spread. Soil adhering to animals, foot wear and agricultural implements also spread infestations. Dispersal over great distances and over international borders occurs by movement of infested plants. Farms are often infested and damage maintained and intensified by growers using infested planting material.

Disease complexes

Many examples of disease complexes are known (Pitcher, 1963; Powell, 1971*a, b*; Taylor, 1979; Webster, 1985). Tomato plants wilt more quickly and can be killed when *Fusarium oxysporum* is simultaneously present (Plate 5C). Resistance in tomato cultivars to fungal wilt caused by *Fusarium oxysporum* f. sp. *lycopersici* was reduced in the presence of *Meloidogyne* (Jenkins & Coursen, 1957; Sidhu & Webster, 1977). Conversely, Abawi and Barker (1984) did not detect any synergistic effect of *M. incognita* or *Fusarium* wilt on either resistant or susceptible tomato. Field studies on the importance of complex disease interrelationships to crop production are scarce and many of the experimental techniques used in the past are considered inadequate (Wallace, 1983; Sikora & Carter, 1987).

Damage to the root system caused by root-knot nematode attack has been considered responsible for increases in the intensity of bacterial wilt caused by *Pseudomonas solanacearum* (Valdez, 1978) and bacterial canker caused by *Corynebacterium michiganense* (Moura *et al.*, 1975). The interrelationship between pathogenic bacteria and root-knot have not been studied in detail and are probably highly complex (Taylor, 1979). Many plants are susceptible to weak fungal pathogens only in the seedling stage. However, when simultaneously present with *Meloidogyne*, these fungi may increase damage to mature plants.

The weight of the roots and shoots of tomato plants was more strongly reduced when secondary microbial invasion existed following inoculation with *M. incognita* than when aseptic juveniles were added (Mayol & Bergeson, 1970). Van Gundy *et al.* (1977) demonstrated that leachings of nematode infected plants, applied to tomato inoculated with *Rhizoctonia* resulted in the appearance of severe rot, when compared to the controls. Suppression of this disease complex, which is very common in the tropics, by the control of *Meloidogyne*, could increase yields significantly.

Economic importance

Estimations of vegetable crop losses in the tropics (Sasser, 1979*b*) ranged from 17–20% on eggplant; 18–33% on melon and 24–38% on tomato. The role *Meloidogyne* plays in total crop loss is difficult to ascertain in cases where crops are suffering from simultaneous attack by fungi, viruses, insects and other nematodes, a situation, very common in tropical countries. Nematicide trials have been used to demonstrate losses associated with *M. incognita* infestations on a number of crops (Lamberti, 1979*b*). Crop loss due to this nematode ranged from 30–60% on eggplant and 50% on cantaloupe and watermelon. In the United States, yield on plots infested with *M. incognita* and treated with DD-MENCS and planted with beans, summer squash, okra or cucumber, increased 128, 180, 507 and 1175%, respectively (Johnson, 1985). These figures must be used with caution because nematicides affect other soil organisms and indirectly stimulate plant growth. Proper crop loss assessment trials, especially under multiple cropping systems, are lacking and are needed to demonstrate the true impact of nematodes on vegetable production in small scale subsistence farming systems.

Economic threshold level

In Table 5, *M. arenaria* and *M. incognita* tolerance limits (T), or the population density at which damage is first observed, are given for a number of vegetables (Seinhorst, 1965; Barker & Olthof, 1976; Barker *et al.*, 1985; Di Vito *et al.*, 1986; Ferris *et al.*, 1986). The wide variation in tolerance

limits reflects the great difference in plant response to nematode infection as well as the influence of soil type and environmental conditions on disease development and severity (Ferris *et al.*, 1986).

TABLE 5. Tolerance limit of some vegetables to *Meloidogyne* species.

	Meloidogyne species*	
Crops	*M. arenaria*	*M. incognita*
Bell pepper	–	65
Cabbage	–	150–1000
Cantaloupe	–	20
Chilli pepper	–	39
Eggplant	–	5.4
Lettuce	–	60
Tomato	2–100	2–100
Watermelon	2–50	2–50

*Number of juveniles/100 cm^3 of soil

In the San Joaquin Valley of California, U.S.A., the number of juveniles in samples taken from sandy loam soils has been used for estimating potential yield loss in processing tomato production areas (Table 6). These figures are given here to be used as guidelines for estimating possible loss in other growing regions. Environmental factors, soil types and cropping sequences will affect damage threshold levels, therefore, caution should be used when using these figures.

TABLE 6. Effect of root-knot nematode populations on processing tomato yield in San Joaquin Valley sandy loam soil (Anon., 1985).

Number of Root-knot Juveniles Per Kilogram in Soil Samples		Percent of Normal Yield
Autumn Samples	Spring Samples	
0 to 160	0 to 25	100
310	50	98
620	100	95
940	150	91
1250	200	88
1560	250	85
1870	300	82
2190	350	79
2500	400	77
2810	450	74
3120	500	72
3440	550	69
3750	600	67
4060	650	65
4370	700	63
4690	750	61
5000	800	60
5310	850	58
5620	900	56
5920	950	55
6250	1000	53

Control

The variation in vegetable growing techniques that range from shifting cultivation to large scale commercial production systems prevents the development of one control strategy applicable to all situations. For example, the subsistence farmer frequently utilizes a mixture of local cultivars of a crop to assure himself a minimum yield and will usually not follow recommendations to grow an unfamiliar nematode resistant cultivar. On the other hand, a commercial plantation manager will not hesitate to utilize resistant cultivars or expensive nematicides to protect a crop (Radewald *et al.*, 1987). In the first case, crop improvement is more difficult.

Control strategies should be preventative rather than curative in nature and aimed from the onset at preventing the buildup of high population densities. It should be noted that many of the techniques used for control of *Meloidogyne* on vegetables simultaneously control other plant parasitic nematodes affecting the crop. This is especially important where multiple species of economically important nematodes affect crop growth (IFAS, 1989).

Once high populations of *Meloidogyne* have developed in a field, it is virtually impossible to suppress and maintain populations at sufficiently low levels without repeated treatment, regardless of the control method practiced. For example, although *M. javanica* densities were reduced to low levels (following either two non-hosts, or a resistant cultivar, or a poor host) and eggplant yield increased significantly, nematode population density rose to high levels at season end (Netscher, 1981*a*).

Cultural practices

Root-knot free nurseries

Only seedlings with roots free of galls should be selected for transplanting. Nurseries must be free of root-knot nematodes in order to reduce dissemination into root-knot free production areas on contaminated transplants. All the techniques described below can aid in maintaining nematode free nursery areas and in some cases to eradicate the nematode from the soil. Seedbeds should be selected on sites which previously were not planted to host plants. To reduce contamination, seedbeds should be planted for dry season crops on land normally flooded during the wet season e.g. in previous paddy fields (Bridge, 1987; Sikora, 1988).

Chemical disinfestation is a common and effective practice in large production operations, whereas, other methods must be considered for subsistence farming. Fumigant nematicides could be used in nurseries even in the case of traditional farming systems, because of the small amount needed and low impact on the environment.

Soil can be heated in drums or on old sheets of metal before being added to trays or plastic bags for seedling production. Solarization of small quantities of soil may also prove feasible. The burning of straw, paddy husks or sawdust on land to be used for seedbeds has been suggested (Choudhury, 1981). Although this method reduces populations, quantities of 20 kg paddy husk per m^2 must be burned to obtain control (Krishnamurthy & Elias, 1969).

Rotation

Page (1979) and Sikora *et al.*, (1988) suggested rotations designed to reduce the impact of root-knot nematodes in tropical vegetable cropping systems in Bangladesh and Niger, respectively. A number of rotations exist in the tropics, especially in Asia, which are predominantly composed of cruciferous crops moderately resistant or tolerant to root-knot nematodes, together with a small number of highly susceptible crops (Fig. 4). Rotations of this design can be effectively used to reduce root-knot nematode densities.

Vegetables can be classified according to their susceptibility to root-knot nematodes e.g.: *very susceptible:* tomato, eggplant, lettuce, melon etc.; *moderately susceptible:* cabbage, cauliflower; *slightly susceptible:* onion; *resistant:* mint, (Netscher & Luc, 1974). These reactions seem to be

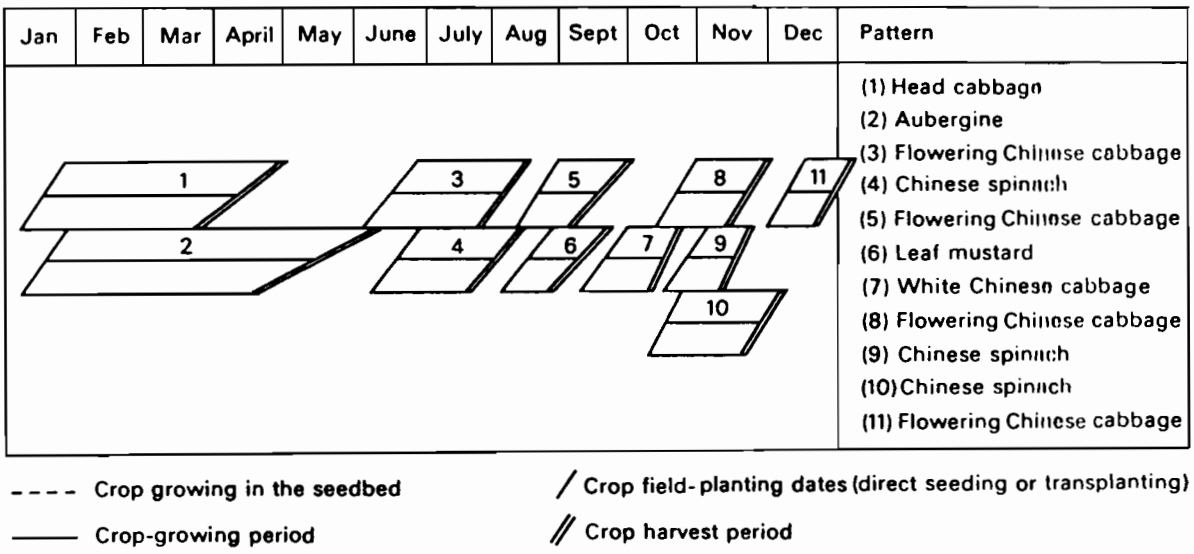

Fig. 4. Rotation with relay-planting and intercropping in Taiwan and China (Ruthenberg, 1983).

independent of the *Meloidogyne* species concerned but vary from one population to another (Netscher, 1970).

Similar classifications have been made for vegetable crops in Mauritania, Malawi, Bangladesh and Niger and have been used to formulate new crop rotations for control of root-knot nematodes. Vegetables considered moderately susceptible or tolerant to root-knot were: cabbage, cauliflower and onion in Mauritania (Netscher & Luc, 1974) all cruciferous crops, onion and leek in Malawi (Bridge & Page, 1977) and broccoli, cauliflower, cabbage and onion in Bangladesh. Amaranthus and chilli were considered resistant in Bangladesh (Page, 1979) onion and amaranthus were resistant in Niger (Sikora *et al.*, 1988).

Caution must be taken with regards to variation in nematode populations and to the composition of root-knot species present in a field. Often the *Meloidogyne* populations are composed of several species. Detection of species that make up less than five percent of the population is difficult. The fact that the minimum temperature required for *M. incognita* development in the root is significantly lower than the minimum "activity threshold" of 18°C for *M. incognita* second stage juveniles (Roberts *et al.*, 1981) has been used to alter date of planting for control of root-knot. Changing the normal date of planting to coincide with low soil temperature was considered an important control tactic on carrots (Roberts, 1987) and could be used to limit nematode damage on vegetables in cool upland tropical regions.

In areas where the climate is characterized by a prolonged and severe hot dry season, fallow during the dry season followed by non-hosts during the wet season for a period of two to three years, may result in the reduction of *Meloidogyne* populations (Duc, 1980).

The effect of crop rotations may be seriously compromised, however, if susceptible weeds are present. Proper weed control can be a vital factor in nematode control, reducing multiplication of *Meloidogyne* on weed hosts.

Root destruction

Galled roots remaining in the field after harvest, should be eliminated by uprooting and destruction. The spread of the nematode will be retarded and the initial population density reduced because the nematode can survive and reproduce on the roots in the soil after harvest. It has been estimated

that, when soil temperatures are high, each month that the root system survives causes a 10-fold increase in root-knot nematode densities (IFAS, 1989).

Organic amendments

The incorporation of organic material into the soil reduces root-knot densities (Muller & Gooch, 1982). Oil cakes, sawdust, urea and bagasse have been used with some success (Singh & Sitaramaiah, 1966, 1967; Sikora *et al.*, 1973*a*). Chitin in combination with waste products from the paper industry has been used to reduce root-knot nematodes (Culbreath *et al.*, 1985). Although the use of organic amendments for effective nematode control is often limited by the large quantities needed, they will reduce nematode population densities to different degrees. In addition to their suppressive effects on nematode density, organic amendments improve soil structure and waterholding capacity.

Physical

Flooding

Meloidogyne densities drop significantly when soils are flooded for prolonged periods of time and are, therefore, often not considered severe problems in the dry season in tropical regions where paddy rice is a normal component of the rotation system. Thames and Stoner (1953) demonstrated that flooding of rice fields for three months gives acceptable control of root-knot nematode for two succeeding vegetable crops. Root-knot nematode densities were lower on susceptible dry season crops in paddy rice rotations than in upland areas in the Philippines (Castillo *et al.*, 1976*b*).

Sikora (1989) showed that the degree of root-knot damage in Philippine vegetable production was less severe in cropping systems based on paddy rice – vegetable rotations than in rotations without paddy rice when flooding was maintained for at least 4 months. The level of galling decreased significantly with increasing clay content of the soil, indicating that soil type plays an active role in population reduction under flooded conditions. Similar effects of paddy rice cropping patterns were noted in northern Java, Indonesia (C. Netscher, unpub.). In Florida, flooding alternated with drying during the summer is recommended for vegetables grown on muck soils to reduce root-knot nematode densities (IFAS, 1989). Crops grown in fields not flooded were frequently severely damaged. Working the soil during the dry cycle is also recommended to prevent weed growth that could harbour other hosts.

Solarization

Soil solarization with clear plastic tarps has been attempted as a means of raising temperatures to lethal levels to control soil-borne diseases (Katan, 1980). The technique, however, is only adaptable to regions where sufficient solar energy is available for long periods of time. In many climatic regions and in subsistence agriculture the costs of using transparent plastic can be a factor limiting application. Solarization has been shown to have a potential in the subtropical climate of Florida where it reduced root-knot, *Verticillium* wilt, and weeds in the autumn crops, even though climatic conditions are not considered ideal for soil solarization (Overman & Jones, 1986). The techniques may, however, have application as a means of eliminating nematodes from seedbeds. Black plastic (Abu-Gharbieh *et al.*, 1987) with the simultaneous use of solar heated water applied by drip irrigation, increases hot water penetration into deeper soil horizons, and may be promising for high value crops (Saleh *et al.*, 1988).

Resistance and tolerance

Non-host crops

Root-knot nematodes are extremely polyphagous, therefore, relatively few non-host plants are available for control through crop rotation. Unfortunately, there are many reports of *Meloidogyne* populations parasitizing plants which have been reported non-hosts, an important factor in developing rotation based control systems (Netscher & Taylor, 1979). Peanut, for example, is often considered

a non-host of *M. incognita*, and *M. javanica* (Netscher, 1975). However, it is attacked by *M. javanica* in Zimbabwe (Martin, 1956), Egypt (Ibrahim & El Saedy, 1976) and USA (Minton *et al.*, 1969) and is tolerant to *M. javanica* in Bangladesh (Page, 1979).

Fodder and green manure crops considered to be non-hosts to species of *Meloidogyne*, which could be used in developing rotations, are listed in Table 7. Differences, however, in susceptibility between cultivars of the fodder grass *Panicum maximum*, considered a non-host of the more common tropical root-knot nematodes, has been detected in South African populations of *M. incognita* (van der Linde, 1956). Therefore these crops should be used for control only after testing with local populations.

TABLE 7. Fodder crops and green manures considered non-hosts of *Meloidogyne* species.

Plant	*M. arenaria*	*M. javanica*	*M. incognita*
Aeschynome	–	–	+
Arachis hypogaea	+*	+	+
Crotalaria fulva	–	+	+
Crotalaria grahamiana	–	+	+
Crotalaria retusa	–	+	+
Crotalaria usaramoensis	–	–	+
Eragrostis curvula	–	+	+
Glycine javanica	–	–	+
Indigofera hirsuta	–	–	+
Panicum maximum	–	+	+
Stylosanthes gracilis	–	+	+

+ = Resistant, – = not tested, * = Susceptible to many populations.

Plants considered good host plants of a *Meloidogyne* species in one part of the world are not necessarily hosts to all populations of that species (Southards & Priest, 1973). Two races of *M. arenaria* were identified using peanut, previously considered a non-host, as a differential host (Sasser, 1966). Netscher (1970) showed that different populations within a species can be characterized by differences in virulence to a host. Lamberti (1979*a*) obtained similar results on tomato with 12 populations of *M. incognita* in southern Italy (Table 8). Because of this large variation in host status within species of root-knot, all crops being considered for rotation must be tested for host status to local populations before rotation schemes are recommended for the field.

TABLE 8. Differences in virulence of *Meloidogyne incognita* populations to tomato expressed as severity of galling (Lamberti, 1979).

Origin of population	Degree of galling (scale 0–5)
Control	0.0
Altomonte, Cosenza (Tomato)	1.1
Monopoli Bari (Lettuce)	1.3
Vicio Equense, Napoli (Squash)	2.6
Lecce (Tobacco)	2.8
Torino (Celery)	2.9
Margherita di S, Foggia (Tomato)	2.9
Bari (Tomato)	3.0
Fondi, Latina (Eggplant)	3.3
Ragusa (Tomato)	3.4
Casterlamare di S, Napoli (Tomato)	4.1
Scafati, Salerno (Anemone)	4.5

Local shade trees as well as plants being selected for wind-breaks, e.g. the baobab tree, *Adansonia digitata* (Taylor *et al.*, 1978) or *Prosopis juliflora* (Netscher & Luc, 1974), can be good hosts. Conversely, neem (*Azadirachta indica*), cashew nut (*Anacardium occidentale*) and *Eucalyptus camaldulensis* may be resistant to *Meloidogyne* (Netscher, 1981*b*). Fruit trees like papaya are also good hosts (Chapter 10).

Furthermore, roots of some non-host crops can react to root-knot penetration with local necrosis. In the case of very high nematode densities, roots are badly damaged and the crop does not become well established. This situation can be easily avoided by delaying sowing for a few weeks after soil preparation, to reduce juvenile density through starvation.

Resistance

The use of resistant cultivars is an elegant, economical and environmentally safe method for controlling root-knot nematodes (Netscher & Mauboussin, 1973). Fassuliotis (1979) gives a comprehensive review of most aspects of resistance to *Meloidogyne*.

There are few sources of resistance amongst crops susceptible to *Meloidogyne*. Resistance has been found in pepper and bean cultivars and was incorporated into tomato via an embryo culture of a hybrid between a resistant line of *Lycopersicum peruvianum* and tomato (Smith, 1944). In most cases, the genetic basis for resistance is determined by one major gene (Gilbert & McGuire, 1956; Hare, 1957). However, Hendy *et al.*, (1985) reported the presence of five dominant genes which when present in one genotype protect against *M. incognita, M. javanica* and *M. arenaria*.

Resistance has been found in melons and eggplants. It was originally detected in *Solanum sisymbrifolium*, closely related to the eggplant. Several wild *Cucumis* species with resistance to root-knot also have been reported (Fassuliotis, 1979). However, genetic barriers make it extremely difficult to introduce the resistance of the "wild" species in the cultivated ones. Modern techniques like protoplast culture and somatic hybridization may make it possible to create viable hybrids and attempts are being made to develop interspecific hybrids.

Solanum torvum which has shown a high level of resistance to *M. incognita* and *M. arenaria*, but is a poor host for *M. javanica*, has been successfully used as a rootstock for eggplant (Dunay & Dalmasso, 1985). In some cases such "Wild" species can be used as resistant rootstock of susceptible grafts. In the Congo, the use of a local eggplant (N'drowa) seems to protect grafts of eggplant against root-knot and *Pseudomonas solanacearum* (Declert, pers. comm.).

Lists of plants reported resistant to species of nematodes in general (Armstrong & Jensen, 1978) and crop cultivars with resistance to species of *Meloidogyne* specifically (Sasser & Kirby, 1979) have been compiled. A list of vegetable cultivars resistant to root-knot nematodes is given in Table 9. The list should be used with caution, because it is often based on a limited number of field observations and does not guarantee that a cultivar is resistant to all populations of *Meloidogyne*. Resistant cultivars of crops susceptible to *Meloidogyne* do not necessarily protect the crop against all species of the genus. In addition, races may exist which are able to break resistance. The Mi gene does not confer immunity to *M. incognita* and *M. javanica* (Roberts & Thomson, 1986). Resistance breaking races have been selected out of field populations of *M.incognita, M. javanica* and *M. arenaria* (Riggs & Winstead, 1959; Sauer & Giles, 1959). Root-knot populations which were capable of attacking resistant cultivars have been detected even though they had previously never been exposed to the cultivars (Sikora *et al.*, 1973*b*; Netscher, 1977; Prot, 1984; Fargette, 1987; Berthou *et al.*, 1989). Resistance breaking races were also selected from single egg mass populations of *M. incognita* and *M. javanica* in laboratory experiments (Triantaphyllou & Sasser, 1960; Netscher, 1977). Resistant cultivars therefore should be used judiciously and with caution or should be tested using small microplots with the cultivar or cultivars in question (Roberts *et al.*, 1986). Approximately 30% of all processing tomato now produced in California has the Mi gene for resistance or enough to cover over 70% of the area infested with root-knot (P. A. Roberts, pers. comm.). This must be considered an important development in any growing region where the growers have been totally dependent on fumigants for crop production.

TABLE 9. Vegetable cultivars reported as resistant to *M. arenaria, M. incognita* and *M. javanica*.

Crop	*Meloidogyne* species		
	M. incognita	*M. javanica*	*M. arenaria*
Bean			
Contender	S	MR	
Kibuu	R	R	
Manoa Wonder	R	R	
Red Haricot	R	R	
Rono	R	R	
Saginaw	R	R	
2.2.3.V	R	R	
Lima bean			
Nemagreen	R		
Ventura N	MR		
Westan	HR		
Pea			
Wando	HR	MR	
Edible soybean			
Kahala	R		
Kailua	R		
Muskmelon			
Edisto		RH	
Honey Rock		R	
Perlita		R	
Watermelon			
Dixie Queen		R	
Okra			
Clemson spineless			MR
Eggplant			
Black Beauty	MR or S, HR or S		
Vijaya	MR		
Banaras Giant	MR		
Pusa Purple V	T		
Pepper			
All big	MR		
Black indica	R		
California Wonder		R	
Early Cal. Wonder	S	MR	S
Naharia	R	R	R
Pant Cl	R		
Tomato			
Allround	R		
Anahu	R	R	
Anahu R	R	R	
Atkinson	**R**	**R**	**R**

TABLE 9. *Continued*

Crop	*Meloidogyne* species		
	M. incognita	*M. javanica*	*M. arenaria*
Auburn 76	R		
Beefeater	R		
Beefmaster	R		
Better Boy	R		
Bicol	R		
Big Seven	R		
Big seven	R		
Calmart	R	R	
Carmen	R		
Catala	R		
Cavalier	R		
Chicogrande	R		
Duchess	R		
Eurocross	R		
Extase	R		
Florida	R	R	
Florida-Hawaii Cross	R		
Gawaher (Giza-1)	R	R	
Gilestar	R		
Hawaii-55	R		
Hawaii-7746	R		
Hawaii-7747	R		
Hawaiian Cross	R	R	
Healani	R	R	
H.-7741	R		
Hope 1	R		
Hope 2	R		
Ife-1	R		
Illinois T-19	R		
Jackpot	R		
Kalohi	R	R	
Kewalo	R		
Kewalo-C	R	R	
KNVC	R		
Kolea	R		
Komea-C	R	R	
Kyoryoku Goko	R		
Leader		R	
Linda	R		
Manalucie K	R	R	R
Marmar		R	
Marsol	R	R	R
Martarum	R	R	
Meltino	R		
Monita	R		
Montfavet	T		
Motabo	R	R	R
Nemacross	R		
Nemared	R	R	
Nematex	R	R	R
NVFC	R		
NFVR	R		

TABLE 9. *Continued*

Crop	*Meloidogyne* species		
	M. incognita	*M. javanica*	*M. arenaria*
Patriot	HR	HR	
Pearson VFN	R	R	
Pelican	R	R	
Peto 662 VFN	R		
Piernita	R		
Piersol	R	R	R
Pinta	R		
Ponderoda	MR		
President	R		
Puunui	R		
Red glow	R		
Red Supreme	R		
Rich Reward	R		
Rossol	R	R	R
Royal Flush	R		
Super Fantastic	R		
Valerie	R		
VFN 8	R	R	R
70T 82		R	
Sweet potato			
Arcadian			R
Carver	MR		
Centennial			R
Drivi Drivi	S	MR	S
Dliula	MR	HR	S
Gold Rush			R
Jasper	R		
Jewel	R		
Navuso Local	MR	MR	S
N.C. Porto Rico	S	R	R
Porto Rico	S	R	R
Samoa Pink	MR	HR	S
Whitestar	R		

HR = highly resistant; MR = moderately resistant; R = resistant; T = tolerant; S = susceptible.
Sasser & Kirby, 1979; Sumeghy, 1979; Nandawa *et al.*, 1980; Bridge, 1983; Ogbuji & Okafor, 1984; Peter *et al.*, 1984; Roberts & Thomason, 1986

Dropkin (1969) showed that at 28°C the resistant cultivar Nematex was highly resistant to *M. incognita*, whereas at 32°C it was susceptible. In Senegal as well as in India a breakdown in resistance due to high soil temperatures has been observed (Sikora *et al.*, 1973*b*; Berthou *et al.*, 1989). In areas with extreme temperatures, cultural practices such as appropriate watering and mulching, may reduce soil temperature to counteract and prevent loss of resistance. However, plastic mulches used for fumigation and solarization may elevate soil temperature above 28°C if planting is made directly through the plastic tarp (R. Dunn, pers. comm.). The root-knot – *F. oxysporum* wilt complex can be controlled by growing cultivars resistant to either the fungus or the nematode or both. The root-knot – *Rhizoctonia solani* root-rot complex, which is common in the tropics and responsible for severe losses, can only be suppressed by controlling *Meloidogyne*, because of the lack of resistance to the fungus.

Chemical

Nematicides used in control of root-knot nematodes are either fumigants which are usually liquids and enter the soil water solution from a gas phase, or non-fumigants, granular or liquid compounds which are water soluble. In most cases the fumigants are broad spectrum contact nematicides effective against juveniles and eggs as well as fungal pathogens and weeds. Non-fumigant nematicides have either contact and/or systemic activity. In most cases the mechanism of action is associated with suppression of nematode mobility during the period when adequate concentrations are in the soil solution. The non-fumigant nematicides are not effective against the eggs of nematodes and in most cases do not kill the juveniles at the concentrations now being recommended for use. They give the plant a "head start" by delaying nematode penetration during the highly sensitive seedling or post-transplant stage of plant development.

Fumigant nematicides are generally more effective in controlling root-knot nematodes and in increasing crop yield than are non-fumigant nematicides, because fumigant nematicides have a broader spectrum of activity, controlling soil insects, fungal diseases and weeds in addition to other plant parasitic nematodes. This broad spectrum of activity also decreases the need for additional pesticide inputs and field work, reducing overhead costs associated with crop production. Most of the fumigant nematicides listed in Appendix A have been shown to be highly effective in control programmes designed to reduce losses due to *Meloidogyne* in vegetables (Lamberti, 1979*b*; Johnson, 1985). They are extensively used for nematode control in large scale production systems. Many vegetables grown on a large scale basis in infested areas, can only be produced economically together with fumigant application (Radewald *et al.*, 1987). In some growing areas fumigants are applied under plastic mulch and the vegetables are planted through the mulch. In these areas, soil temperatures may be too high for effective use of resistant cultivars.

The majority of small farmers, especially those living at the subsistence level, cannot use fumigants because of a lack of capital for equipment and nematicides. Although a number of fumigant nematicides have been removed from the market because of detection in groundwater and/or other negative side effects on the environment, some fumigants are still in widespread use and are effective control tools. When used as directed they will give excellent nematode control and increase yield significantly. Because registration requirements and efficacy vary with country and crop, no attempt will be made here to list those still being used for the control of root-knot nematodes in vegetables.

The granular or liquid formulations of contact and/or systemic nematicides are more suitable for use on small farms, provided the growers are made aware of proper handling and application techniques as well as time of application. They are often not as effective as fumigants in increasing yields because they usually do not have broad spectrum activity. It must be realized that climatic conditions in many tropical countries do not favour high yields. A yield of 40 t/ha of canning tomatoes in northern Senegal is considered exceptionally good. Under subtropical conditions, for example in Italy and California, yields of 65 t/ha can be attained. When good growing conditions exist, however, yields in excess of 100 t/ha are possible. High yield, increased costs for nematicides, and competition with tomato concentrate from other countries leaves a rather small margin for the use of nematicides in many tropical countries.

Nematicides can be applied effectively by surface and drip irrigation (Overman 1974; Johnson, 1985; IFAS, 1989). The fumigant, metam-sodium, was effective in controlling root-knot and soil fungi when applied through drip irrigation (Roberts, 1988). Local experimentation is, however, needed to determine optimum dosage and time of application. Alternative approaches such as dip treatment or treatment of transplants in nurseries (Ahuja, 1978; Mateille & Netscher, 1985) and seed coating (Schiffers *et al.*, 1985) have been suggested.

Biological

Progress has been made regarding the incorporation of nematode parasites or antagonists into the soil for control of root-knot nematodes on vegetables (Kerry, 1987). Too little is known, however, about the factors affecting survival and infection once they are introduced into the soil. A strain of

Arthrobotrys irregularis grown on rye grain reduced root-knot galling and increased tomato yields when it was introduced in the soil at 140 g/m^2 (Cayrol & Frankowski, 1979; Cayrol, 1983). The large amounts of inoculum (1.4 t/ha) and the need for alkaline soils favourable to fungal growth probably limit this approach to glasshouse production systems.

Pasteuria penetrans is an obligate parasite of some plant parasitic nematodes including *Meloidogyne* (Birchfield & Antonpoulos, 1976) but cannot be produced, at the present time, in large numbers *in vitro*. *P. penetrans* is a very common parasite of *Meloidogyne* and is often observed attached to juveniles. The spore form can resist both drought and exposure to non-fumigant nematicides (Mankau & Prasad, 1972). Stirling and Wachtel (1980) were able to produce large numbers of spores by inoculating tomato with infected *Meloidogyne* juveniles. Dried tomato roots were then milled into a powder containing *Pasteuria* spores. This method might be adapted to produce inoculum of the parasite for local use on small farms. There is also a possibility of increasing the parasite in root-knot nematode infested fields by growing tolerant or moderately resistant crops.

The colonization of plants with endomycorrhizal fungi apart from providing plants with nutrients has been reported to have a depressive effect on root-knot nematodes. According to Sikora (1978) penetration and development of *M. incognita* in tomato was significantly reduced by *Glomus mosseae* in glasshouse studies. Attempts to find highly active symbiont-crop combinations that are effective in suppressing the nematode in the field are needed.

Conflicting reports exist on the efficacy of the fungal egg parasites for control of root-knot nematodes. The high amounts of organic matter needed for fungal establishment and spread in the soil environment, at the present time, limit practical application in most large scale production systems. The alternative use of cereal grain for fungal inoculum production prevents any application in subsistence agriculture.

A promising group of microorganisms that may be effective in reducing nematode damage are the plant health promoting rhizobacteria (Sikora, 1988; Oostendorp & Sikora, 1989) which could be applied as seed dressings or as a drench treatment for transplants. Application through drip-irrigation systems may prove to be an effective method of post-planting application (Zavaleta-Meija & Van Gundy, 1982).

Summary of control measures

The principles and main components of effective control programmes and integrated pest control in vegetables as well as other crops have been discussed in this chapter and elsewhere in detail (Taylor & Sasser, 1978; Johnson & Fassuliotis, 1984; IFAS, 1989). The main aspects we consider important are listed below.

1) Prevention of infestations by controlling nematode spread must be top priority.

2) Only root-knot nematode free transplants should be used as planting material.

3) In view of the high multiplication rate of root-knot nematodes and difficulty in determining occurrence of low population densities, previously infested land should always be considered infested, even if the presence of *Meloidogyne* can not be demonstrated by soil analysis.

4) Efforts should be made when planning vegetable crop rotations to select and develop pest management approaches that prevent the build-up of high nematode densities.

5) Integrated pest management should combine rotations with non-host crops, resistant, tolerant and susceptible cultivars as well as judicious use of nematicides, based on proper soil sampling estimations of damage threshold levels.

6) An integrated approach will control economically important nematodes, reduce pesticide costs and prevent unnecessary environmental contamination.

7) Proper selection of a combination of resistant, moderately resistant and tolerant vegetable crops can increase the number of vegetables in a short rotation cropping system.

8) Resistant cultivars should be used in rotation with susceptible cultivars and with other control techniques to prevent the development of resistant breaking pathotypes.

9) All non-host crops and resistant cultivars should be challenged by local populations to determine true host status.

10) In regions where irrigated rice (or flooding) constitute one of the components of the farming system, inundation can give good control.

11) Destruction of roots after harvest, soil drying and cultivation as well as "clean" fallow will significantly reduce population densities.

12) Time of planting may be effective in the cooler upland tropics and in the winter season in the subtropics.

13) Organic amendments or the use of non-host cover crops and green manures can reduce nematode densities.

Methods of diagnosis

The scattered or clustered distribution of most nematodes in the field makes reliable estimation of occurrence and/or population density extremely difficult. Due to the presence of egg masses, the spatial distribution of root-knot is very heterogeneous. Techniques have been developed for extraction that are based on the fact that the egg masses remain intact in the soil either free or attached to host roots or root fragments (Dickson & Strubel, 1965; Byrd *et al.*, 1972; Gooris & d'Herde, 1972). After separating the organic matter from the soil using sieving or elutriation techniques, eggs are liberated from egg masses either chemically (Byrd *et al.*, 1972) or mechanically (Gooris & d'Herde, 1972). Demeure and Netscher (1973) observed egg masses present in the coarse sandy soil fraction and suggested incubation of this fraction also.

Even if the methods of extraction are sufficiently reliable, it is still virtually impossible to determine whether or not land is free from root-knot, even when the results of soil analyses are negative. The majority of the methods used will not always detect egg masses in fields with low to moderate root-knot infestation levels. Accuracy can be increased by increasing the volume of the soil sample taken from the field as well as the number of cores taken per unit area and by extracting greater quantities of soil than the usual 100–250 cm^3 recommended. The accuracy of the extraction method used in determining population densities is extremely important in estimating threshold levels. Barker (1985*a*, *b*) discusses sampling and extraction techniques and lists their relative efficiency.

Another problem, related to determination of population densities in sandy soils, is the migration of juveniles over substantial distances to the plant (Prot & Netscher, 1978).

Bioassay techniques, in which susceptible plants growing in the field are uprooted and examined for the presence of galls after a period of three to six weeks, constitute a means to evaluate the infestation levels of soils with greater accuracy than soil analysis (McSorley & Parrado, 1983).

An accurate evaluation of root-knot infestations in a field can be obtained at the end of the vegetative cycle of a susceptible crop. Plants are systematically uprooted and scored for severity of root galling, thereby giving an accurate estimation of the severity and the distribution of *Meloidogyne* in a field. This is the only method available for workers lacking basic nematological extraction equipment. A number of different root-knot indices have been proposed (Barker, 1985*b*). The root-gall index proposed by Zeck (1971) is typical of those often used in the field (Fig. 5). Yield losses and root-gall indices have a linear relationship which vary in degree as to crop and environmental conditions (Barker *et al.*, 1981). A nomograph of root-knot galling indices is shown in Fig. 6.

Rotylenchulus

After *Meloidogyne*, the reniform nematode, *Rotylenchulus reniformis*, is the most important nematode affecting vegetables. The nematode attacks over 100 plant species including many vegetable crops and is a limiting factor in vegetable production, but is often neglected or overlooked where it occurs concomitantly with *Meloidogyne*. The nematode has been detected in more than 36 countries

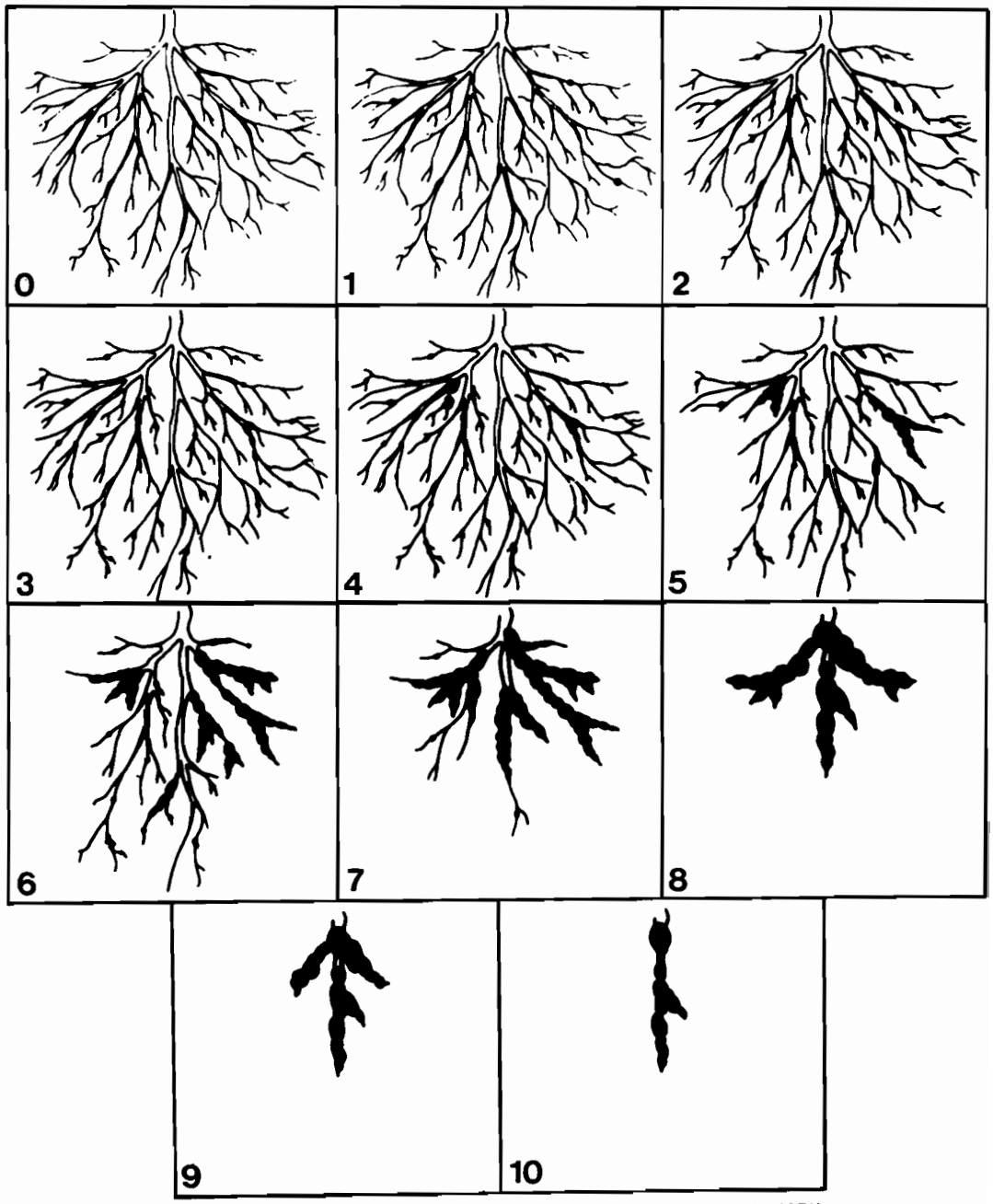

Fig. 5. Rating scheme for evaluation of root-knot infestation (Zeck, 1971).

Explanation of ratings (modified)

0 = Complete and healthy root system, no infestation
1 = Very few small galls can only be detected upon close examination
2 = Small galls as in "1" but more numerous and easy to detect
3 = Numerous small galls, some grown together, function of roots not seriously affected
4 = Numerous small galls, some big galls, majority of roots still functioning
5 = 25% of root system severely galled and not functioning
6 = 50% of root system severely galled and not functioning
7 = 75% of root system severely galled and lost for production
8 = No healthy roots, nourishment of plant interrupted, plant still green
9 = The completely galled root system is rotting, plant is dying
10 = Plant and roots are dead

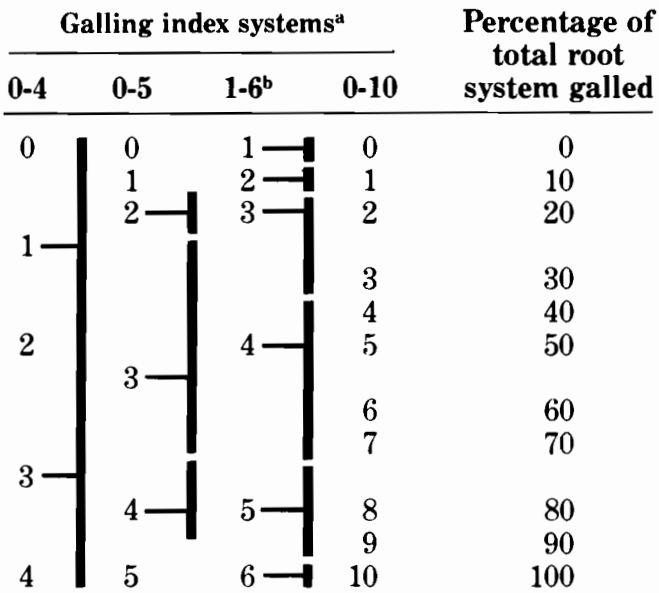

Fig. 6. Nomograph of root-knot galling indices for *Meloidogyne* spp. (Barker, 1978).

(Heald & Thames, 1982). It has been recorded in Hawaii where it was first described (Linford & Oliviera, 1940) and in the southern U.S.A., Mexico, the Caribbean, South America, the Middle East, most of Africa, India, South East Asia and the Pacific.

Symptoms of damage

Above-ground symptoms include stunting and leaf curling (Singh & Khera, 1979). Root necrosis and cortical necrosis has been observed following infection. Cantaloupe growing in heavily infested soil was badly stunted and yields were greatly reduced (Heald, 1975). Leaf chlorosis can be produced (Bridge 1983). Females and their adhering egg masses can be easily observed under the dissecting microscope (Fig. 7). Soil adhering to the gelatinous egg masses often give them a dark appearance aiding in detection.

Biology

Immature females penetrate the root and become sedentary. Galls are not produced. The life cycle is completed on okra in 24 to 29 days (Sivakumar & Seshadri, 1971). The existence of amphimictic and parthenogenetic races of *R. reniformis* has been demonstrated by Hirschmann and Triantaphyllou (1964).

The reniform nematode can survive in soil in the absence of hosts for seven months in moist soil and for six months in dry soil. After four months, 84% of the nematodes were still alive (Sivakumar & Seshadri, 1979). Stoyanov (1971) reported that *R. reniformis* was able to survive 29 months in the absence of host plants.

Intensity of Brinjal Mosaic Virus and Okra Yellow Vein Mosaic were promoted on plants parasitized by *R. reniformis* (Naqvi & Alam, 1975; Sivakumar & Merrzainudeen, 1973). Charcoal rot caused by *Macrophomena phaseolina* on cantaloupe was significantly higher when the roots were infested with the reniform nematode (Carter, 1980).

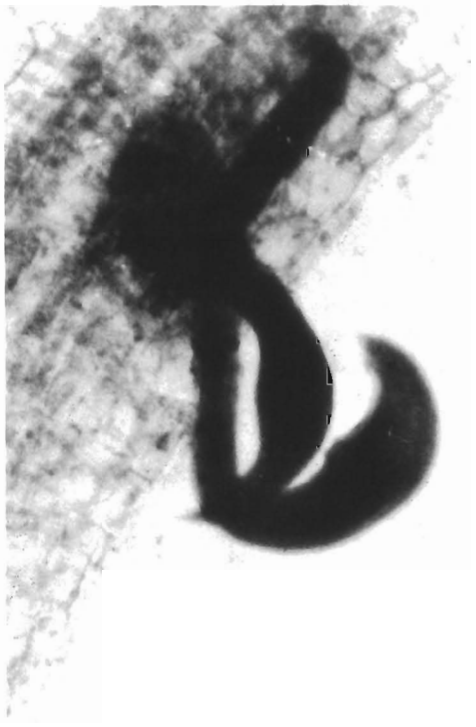

Fig. 7. Females of *Rotylenchulus reniformis* on roots of tomato.

Economic importance

Tomato yield was reduced following inoculation with 100 juveniles/plant (Singh & Khera, 1979). Snake gourd (*Trichosanthus dioica*) plants inoculated with 1000 nematodes were stunted and had smaller leaves than controls and the roots were brown and showed cortical necrosis (Nath *et al.*, 1979). The nematode has been shown to damage a number of vegetable and melon crops. Yield increases on okra, tomato, lettuce and squash of 19, 15, 57 and 69% were obtained with granular nematicides, respectively (Heald, 1978).

Control

Cultural

A two year rotation of cotton with sorghum was as effective as fumigation in reducing the nematode (Thames & Heald, 1974). Rotations which include soybeans resistant to the nematode also reduce densities (Gilman *et al.*, 1978). Nematode densities have also been reduced in rotations with maize, sugarcane and Pangolagrass (Heald & Thames, 1982). A number of other crops are also known to be resistant to the nematode including finger millet, peanut, chillies, sugarcane, and other grasses (Armstrong & Jensen, 1978; Bridge, 1983).

Soil amendments such as animal manure and cotton seed cakes have been used with success to

control the reniform nematode (Badra *et al.*, 1979). In glasshouse experiments, peanut was a poor host of two populations of *R. reniformis* (Germani, 1978). Short periods of flooding of tomato in pot experiments reduced populations of the reniform nematode (Castillo *et al.*, 1976*a*). The nematode was also eradicated from infested soil following treatment with 50°C hot water for 5 minutes (Heald & Wayland, 1975).

Resistance

There are only a few reports concerning resistance in vegetables to *R. reniformis*. In Egypt, the tomato cv VFN 8 was shown to be moderately resistant to the reniform nematode (Oteifa & Osman, 1974). Balsubramanian and Ramakrishnan (1983) found that the tomato cvs Kalyanpur Sel 1 and Sel 2 were immune to the reniform nematode while lines EC 118272 and EC 118276 were resistant. Sitaramaiah and Sikora (1982) were able to demonstrate that the penetration and reproduction of *R. reniformis* on tomato and cucumber was significantly reduced in the presence of the endomycorrhizal fungus *Glomus fasciculatum*.

Chemical

A wide range of fumigant and non-fumigant nematicides are effective in controlling *R. reniformis* (Birchfield & Martin, 1976; Heald & Thames, 1982). Rich and Bird (1973) were able to reduce nematode penetration by a single foliar application of oxamyl. However, McSorley (1980) could not demonstrate effective nematode control following six weekly sprays with oxamyl on snapbean.

Nacobbus

Little is known about the distribution and importance of the false root-knot nematode, *Nacobbus*, in tropical and subtropical agriculture. The two species *N. aberrans* and *N. dorsalis* have been detected in North, Central and South America. The nematode has also been detected in glasshouses in Europe. *N. aberrans* has been reported from cabbage, turnip, sweet pepper, chilli pepper, squash gourd, lettuce, tomato, *Cucumis sativus*, and *Daucus carota*.

Symptoms of damage

The nematode produces galls similar in size to *Meloidogyne hapla*. The galls are characteristically produced in strands or a bead-like fashion along the root (Plate 5G). The penetration of juveniles and immature females into the root can cause root necrosis (Bridge, 1983). Stunting, poor growth and chlorosis are typical above-ground symptoms associated with the endoparasitic nematode. Yield reduction can be significant (Schuster *et al.*, 1965). *N. aberrans* may be an important pathogen in Mexico (Marbán, pers. comm. cited in Johnson & Fassuliotis, 1984) and, according to Román (1978), causes yield loss on pepper and tomato.

The galls of *Nacobbus* spp. are often overlooked or mistaken for those produced by root-knot nematodes, *Meloidogyne* species, because of the similarity in gall form. Galls only occur in the presence of the adult females which retain their eggs, in contrast to root-knot nematode females.

Biology

The females vary greatly in shape and will produce an egg sac that extends to the outside of the root (Clark, 1967; Johnson & Fassuliotis, 1984). According to Prasad and Webster (1967) the nematode completes a life cycle in 36 days at 25°C and in 43 days at 20°C or 30°C. There are indications that races may exist.

Control

Nacobbus can be controlled with both fumigant and non-fumigant nematicides. However, crop rotation with non-host crops is effective and more economical. Gomes Tovar (1973) reported that *Erodium cicutariuim* and *Brassica campestris* were not susceptible and hybrids of *Solanum andigenum*

were resistant to the nematode. Bridge (1983) listed melon, squash, watermelon, peanut, soybean, lucerne, oats, barley, rye, sorghum, wheat, maize, onion, okra, cotton, sunflower, *Phaseolus* spp., sesame, winged bean, and rice as non-host crops that could be used in rotation. Because of the possible existence of races, re-testing each crop with local populations was suggested as a necessary precaution.

Methods of diagnosis

The nematode can be easily detected by examining the root system during the growing season. Attention should be given to the size of the galls and their orientation along the root system. If they are small and form bead-like strands along the root, they should be examined for *Nacobbus* females either by teasing out the females or by staining (Chapter 2).

Globodera

G. rostochiensis

The potato cyst nematode, *G. rostochiensis* will infect and damage tomato and eggplant. The potato cyst nematode has been found infesting tomato in North, Central and South America (Bridge, 1983). The nematode is also present in Pakistan, India, Mediterranean basin, South Africa, and the Philippines. Symptoms include chlorosis, stunting and general poor growth. Detailed studies on yield losses and control, however, have not been reported for either crop.

Heterodera

Heterodera schachtii

This nematode has been found in Mexico (Sosa-Moss, 1986), U.S.A. and Canada (Miller, 1986), Iraq (Stephan, 1986), Libya (Edongali, 1986), Senegal (Luc & Netscher, 1974) and Gambia (Bridge & Manser, 1980). The nematode causes significant losses on cruciferous crops. Yield reductions of 50 percent or more have been measured on Brussels sprouts, cabbage, broccoli and cauliflower when population densities are high (Miller, 1986). The nematode also attacks kale, Chinese cabbage, red beet, rutabagas, spinach and turnip (Anon, 1987).

The sugar beet cyst nematode is often found together with the cabbage cyst nematode, *H. cruciferae*. Proper identification therefore, is necessary in selecting control measures. Approximately 2–4 eggs/g of soil is used as a rough guideline for damage threshold levels in the Imperial Valley in California, U.S.A. (Anon., 1987). The nematode is controlled by long rotations or with fumigant nematicides (Lear *et al.*, 1966; Anon., 1987). Winter season crops and crops grown at higher altitudes are not damaged as severely.

Heterodera cruciferae

The cabbage cyst nematode, *H. cruciferae*, has been detected in California (Siddiqui *et al.*, 1973) and Libya (Edongali & Dabaj, 1982). The nematode causes significant damage to cruciferous crops in California, where it often occurs together in the same fields with *H. schachtii* (Anon., 1987). Although the nematode has many common hosts with the sugar beet cyst nematode, its host range is somewhat smaller (Johnson & Fassuliotis, 1984). Seedlings infested with the nematode are stunted and exhibit interveinal chlorosis or leaf reddening (McCann, 1981). Cauliflower curd quality is reduced at 75 eggs/g soil (Sykes & Winfield, 1966) and cabbage are severely stunted at 20 cysts/100 g of soil (McCann, 1981). Control is usually accomplished by crop rotation with non-host plants or by pre-plant fumigation (Anon., 1987).

Cactodera

Cactodera amaranthi

This cyst nematode has been found attacking spinach in central Mexico (Sosa-Moss, 1986) on *Amaranthus viridis* in Cuba (Stoyanov, 1972) and was detected in Florida (G. Rau, unpub. cited in Luc, 1986). The host range of the nematode is limited to *A. viridis, A. Spinosus*, and *A. retroflexus* (Luc, 1986). Golden and Raski (1977) discussed the biology of the nematode.

Methods of diagnosis

All these endosedentary nematodes produce cysts on the surface of the root system at specific times in their life cycle. The presence of cyst nematodes can be determined by carefully removing growing plants at different intervals during the growing season and examination of the roots with a hand lens. The detection of cysts imbedded in the root tissue is a clear sign of pathogenicity. Cysts can also be extracted from the soil using the techniques described in Chapter 2. The time of cyst appearance on the root surface is determined mainly by temperature. The cysts will also vary in colour from white through beige to dark brown. Cyst production and detection will also vary depending on the number of life cycles produced e.g. the potato cyst nematode only has one generation per year, whereas the cabbage and sugar beet cyst nematodes have many generations in a cropping season.

Ditylenchus

The normal race of the stem nematode, *D. dipsaci*, can cause severe damage to species of *Allium*, especially onion and garlic, in the winter season and in the cooler upland tropical and subtropical regions. The nematode is a problem on lucerne in the subtropical regions of the U.S.A., but does not seem to affect other crops in the region. *D. dipsaci* is known to attack *Beta vulgaris* (M. Ammati, pers. comm.) and *Vicia faba* during the cool rainy winter growing season in the subtropical regions of North Africa (Saxena *et al.*, 1987). There are also reports from Europe that the nematode can attack carrot, celery, tomato and cucumber (Decker, 1969). Vegetables growing in the warm tropics or during the summer season in the subtropics are not attacked. The nematode has been reported attacking species of *Allium* in a number of subtropical and tropical countries: Mexico, Venezuela, Ecuador, Peru, Colombia, Dominican Republic, and various countries in the Mediterranean, Asia and the Pacific (Bridge & Hunt, 1986).

Symptoms of damage

Penetration of onion leaves by this endoparasite causes leaf deformation and leaf swellings or blister-like areas on the surface (Fig. 8). The leaves grow in a disorderly fashion and often hang as if wilted. As the season progresses they become chlorotic (Decker, 1969). Young plants can be killed when high infestations exist. Infected onions become swollen (bloat) and the bulbs may rot during storage (Bridge & Hunt, 1986). The inner scales of the bulb are usually more severely attacked than the outer scales. As the season advances the bulbs become soft and when cut open show browning of the scales in concentric circles. Conversely, *D. dipsaci* on garlic does not induce deformation or swellings, but causes leaf yellowing and death (Decker, 1969).

Biology

The fourth stage juveniles penetrate the stem and leaf tissue through the stomata. Egg laying begins at temperatures of 1–5°C with the optimum at 13–18°C. *D. dipsaci* completes one generation in 19–23 days at 15°C. Nematode activity stops at 36°C. The nematode prefers the cool moist climatic conditions existing in the upland tropics and wet winter seasons in the subtropics. *D. dipsaci* can parasitize plants on both heavy and light soils, although a higher incidence of infestation seems to occur on heavy soils.

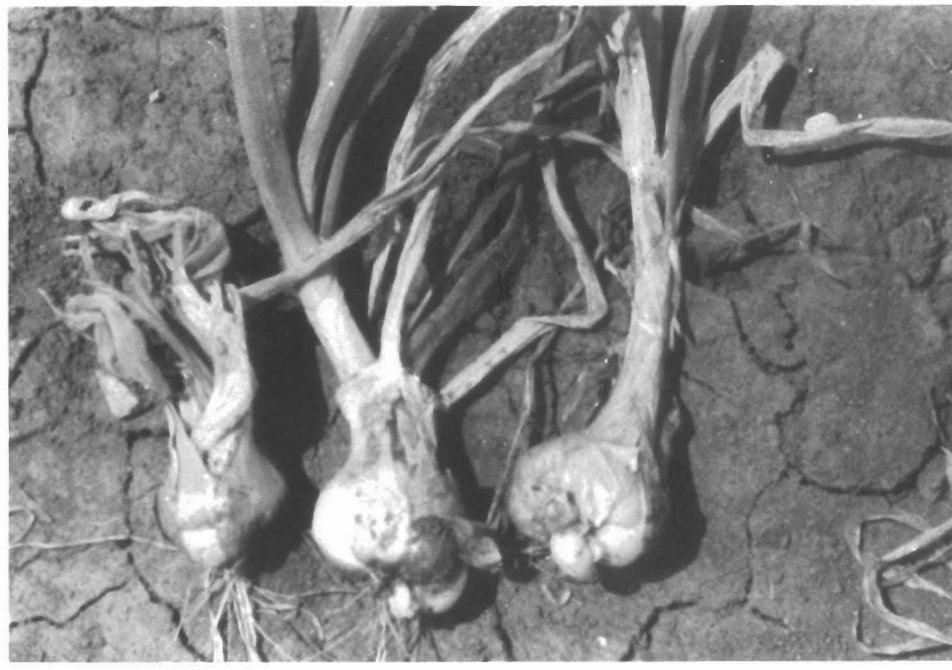

Fig. 8. Deformed onions in a field infested with *Ditylenchus dipsaci* (Photo: D. Taylor & D. Edwards).

Races

Although many races of *D. dipsaci* have been described (Sturhan, 1969) nothing is known about the race spectrum in those countries in the tropics where the nematode has been detected. It should be noted that onion is attacked by a number of known races, which could make determination of threshold levels difficult. The host range of many races has not been adequately determined.

Survival and means of dissemination

The nematode can survive in the soil without a host plant for more than one year and the fourth juvenile stage can survive in anabiosis for many years. The nematode can be disseminated by transportation in infested bulbs, plant residue and adhering soil. Seed-borne infections also are responsible for long distance dissemination in onion, broad bean, beet and lucerne. Other hosts and weeds are responsible for maintaining infestations between onion and garlic. Bulbs harbouring light infestations will survive storage, and increase the level of infestation and losses in the following season when used as planting material.

Economic threshold level

According to Seinhorst (1956) the economic threshold level for onion is reached when 10 or more nematodes are detected in 400 cm^3 of soil.

Control

Rotations with non-host crops for 3 years can be an effective means of control once the host range for a specific population or race is determined. Resistant cultivars of onion and garlic have not been developed for the commercial market (Bergquist & Riedel, 1972).

The nematode can be controlled in onion bulbs by dipping in hot water at 44–45°C for 3 h (Bridge & Hunt, 1986). Temperature and time ratios are important for control and may vary with

crop and cultivar. Formaldehyde was used until recently for control in onion bulbs but has been removed from use for environmental and toxicological reasons.

Fumigant nematicides are effective in reducing nematode infestation levels in the field.The stem nematode also can be controlled in infested onion and garlic seed by treatment with methyl bromide (Hague, 1968; Infante & Sosa-Moss, 1971).

The nematode also attacks many weeds (Augustin & Sikora, 1989) present in field crops and these must be examined for host status, since the high nematode densities can be maintained on these hosts.

Methods of diagnosis

The presence of *D. dipsaci* can be easily determined by submerging small amounts of seed, stem, leaf or bulb tissue in water overnight to allow the active stages to escape (See Chapter 2). Detection in soil is more difficult because of the low population levels normally present.

Pratylenchus and *Radopholus*

Ten species of the lesion nematode, *Pratylenchus* have been found in the rhizosphere or roots of vegetable crops: *P. brachyurus, P. barkati, P. dasi, P. coffeae, P. delattrei, P. loosi, P. singhi, P. thornei* and *P. zeae*. All species of *Pratylenchus* should be considered of potential importance when encountered in root tissue. Lesion nematodes are important parasites of many crops and are known to form disease complexes with many different soil-borne root rotting fungi, thereby increasing root damage. *Pratylenchus brachyurus* and *P. zeae* have been detected in great numbers in the roots of vegetables. Little is known, however, about their impact on vegetable production. The overriding importance of *Meloidogyne* in vegetable production, and the resulting lack of research on other plant parasitic nematode species, has limited our knowledge as to the exact importance of lesion nematodes in vegetable production.

The closely related burrowing nematode, *Radopholus*, has been detected in a number of vegetable crops, including: kale, radish, tomato, eggplant, okra, carrot, onion, African spinach, watermelon, melon, calabash, pumpkin, and squash. Crop loss studies have not been conducted.

Control

Lesion nematodes can be controlled with fumigant and non-fumigant nematicides, although this is probably not practical on an economic basis. Many species of *Pratylenchus* have wide host ranges making the development of rotations difficult. Plants having been reported to be resistant to the various species of *Pratylenchus* have been compiled by Armstrong and Jensen (1978).

Methods of diagnosis

Lesion nematodes produce small dark necrotic lesions on the root surface on many crops, which is the result of interrelationships with soil-borne fungal pathogens. The presence of lesions is a good indication that lesion nematodes are causing damage. The presence of the nematode should then be determined by extraction from the root tissue (see Chapter 2).

Belonolaimus

The sting nematodes, *B. gracilis, B. longicaudatus, B. euthychilus, B. maritimus* and *B. nortoni*, are common plant parasitic nematodes in the subtropical regions of the lower Coastal Plain of the southeastern U.S.A. from Virginia to Florida and along the Gulf Coast into Texas. Note that the genus *Ibipora* found in Brazil is considered to be identical to *Belonolaimus*. Physiological races of *B. longicaudatus* have been detected (Abu-Gharbieh & Perry, 1970).

Symptoms

Damaged plants are stunted, chlorotic and wilt prematurely with severe damage leading to plant death (Fig. 9). Nematode feeding induces stubby roots and necrotic lesions which can expand to girdle the root (Fig. 10). Perry and Rhoades (1982*a*) stated that "infested areas consist of spots that vary in size and shape, but the boundary between diseased and healthy plants usually is fairly well defined" (Fig. 11). Although disease complex associations have been detected on other hosts, they have not been observed on vegetable crops.

Biology

The nematodes are obligate parasites that cause damage to vegetables by feeding ectoparasitically on or near the root tip. The ectoparasite completes one generation within 28 days at an optimum temperature of 28–30°C.

Survival and means of dissemination

There is no definite survival stage in the life cycle of the nematode with all stages of development present in the rhizosphere. The nematode may have been spread to many warmer regions of the world on golf course bermudagrass sod (Perry & Rhoades, 1982*a*), but because of its dependency on extreme sandy soil (Thames, 1959; Brodie & Quattlebaum, 1970) establishment has probably only occurred in a limited number of instances. The nematode seems to be most damaging on irrigated light soils, because of the nematodes requirement of uniform soil moisture, sandy soil and temperatures of 25–30°C for survival and multiplication.

Other hosts

The nematode causes severe damage to most agricultural crops including many wild plants and most vegetable crops (Graham & Holdeman, 1953; Good & Thornton 1956; Robbins & Barker, 1973; Williams, 1974). Forage grasses and turf are also damaged by the nematode, whereas, tobacco and watermelon are considered non-hosts. Because of the presence of races, variation in host range between populations should be expected.

Fig. 9. Celery growth in a *Belonolaimus longicaudatus* infested field in Florida (left) furadan 2 pd/acre (right) check (Photo: H. Rhoades).

Fig. 10. Root damage and poor growth caused by *Belonolaimus longicaudatus* on celery (right) in Florida (Photo: H. Rhoades).

Fig. 11. Stunted celery plants in a field infested with *Belonolaimus longicaudatus* in Florida (Photo: H. Rhoades).

Economic importance

B. longicaudatus is the only species that has been shown to cause serious crop loss to vegetables. The species has been considered responsible for greater yield loss to vegetables in Florida than any other single plant pest of any type (Perry & Rhoades, 1982*a*). The nematode is highly pathogenic and even a single specimen in a soil sample can indicate that severe damage to a vegetable crop can occur. The sting nematode has been shown to damage a wide range of crops including okra, onion, celery, beetroot, cabbage, pepper, cucumber, pumpkin and carrot.

Control

Cultural

The addition of organic amendments that alter soil conditions has been shown to suppress the nematode, because of its extreme sensitivity to changes in soil environmental conditions (Heald & Burton, 1968). Rotations designed to reduce population densities are difficult to select because of the wide host range, lack of resistant cultivars and possible presence of races in the species. A number of non-hosts are listed by Armstrong and Jensen (1978). Perry and Norden (1964) developed successful rotations using peanut, bahiagrass and maize, although only the latter is a non-host throughout the nematode's range. The nematode did not reproduce on *Crotalaria spectabilis* in glasshouse tests (Rhoades, 1964) and, in the field, a summer cover crop of hairy indigo prevented population increase (Rhoades, 1976*a*; Rhoades & Forbes, 1986). Fallowing and summer cover crops also reduced populations and increased yield (Rhoades, 1983). In field experiments, high populations developed on *Tagetes patula*, whereas, low build-up was detected on joint vetch, *Aeschynomene americana* (Rhoades, 1980).

Physical

In Florida some growers control the nematode by flooding the land for periods of about three months (IFAS, 1989). Soil drying can also be used to reduce nematode densities.

Chemical

Nematicides are effective and widely used to control this nematode (Williams, 1974; Perry & Rhoades, 1982*a*). Good control has been obtained with pre-plant fumigant and non-fumigant nematicide treatment of cabbage and onion (Rhoades, 1969, 1971) and with both granular and transplant water application of non-fumigant nematicides on cabbage (Rhoades, 1976*b*). Johnson and Dickson (1973) obtained improved results when the nematicides were applied at planting as compared to pre-plant or post-plant treatments.

Methods of diagnosis

The nematode is an ectoparasite and can be easily extracted from the sandy soils with modified Baermann dishes or sieving and elutriation techniques (See Chapter 2).

Trichodorus and *Paratrichodorus*

Species of stubby-root nematodes, *Trichodorus* and *Paratrichodorus*, have been found throughout the world associated with vegetable crops. *Paratrichodorus minor* is considered an important limiting factor on vegetables grown in light soils in the subtropical regions of the U.S.A. (Perry & Rhoades, 1982*b*). *P. minor* attacks a wide range of vegetable crops and most other cultivated crop plants (Rohde & Jenkins, 1957; Perry & Rhoades, 1982*b*). (*Paratrichodorus mirzai* and *T. viruliferus* are considered important on carrot and pepper, respectively. The stubby-root nematodes prefer sandy or sandy-loam soils, but can occur in high numbers in organic soils (Perry & Rhoades, 1982*b*). This is probably true for all species in the two genera.

The nematodes are ectoparasites feeding mainly on the root tip where damage suppresses

elongation of the root and is responsible for the stubby-root symptoms associated with these nematodes. The amount of damage to the root system varies with vegetable crop attacked, but is characterized by reduced size and fewer shorter rootlets (Johnson & Fassuliotis, 1984). The roots become discoloured and necrotic as the season advances. Netscher (1970) reported that *P. minor* caused a 50% reduction in root weight of tomato.

Plant growth is retarded and the foliage on stunted plants may become chlorotic (Christie & Perry, 1951). Some vegetables wilt when exposed to moisture stress. The nematodes cause severe crop losses to a variety of vegetable crops including: onion, tomato, pepper, eggplant, beet, broccoli, Brussels sprouts, cabbage, cauliflower, Chinese cabbage, radishes, rutabagas, turnips, endive, lettuce and spinach (IFAS, 1989). This group of nematodes are also known virus vectors and in potato can be important both for direct damage and as a virus vector.

Control by crop rotation is difficult because of the wide host range of this nematode. *Crotalaria spectabilis* has been shown to be a non-host of the nematode and when used as a cover crop will reduce nematode densities (Rhoades, 1964). *Asparagus officinalis* var. *altilis* L. has also been shown to be resistant to attack which is induced by the production of a highly toxic glycoside (Rohde & Jenkins, 1958). Fumigant and non-fumigant nematicides are effective in reducing initial damage and in giving the vegetable crop a head-start on the nematode. However, it has been shown that nematode populations build-up quickly (Perry, 1953). Some of the carbamate and phosphate non-fumigant nematicides exhibit longer durations of control than the fumigants (Rhoades, 1967, 1968). Flooding for two weeks reduced populations significantly and the effect was improved by flooding followed by two weeks of drying (Overman, 1964).

Longidorus, Paralongidorus and *Xiphinema*

These nematodes have been shown to be potential problems in local areas. They can cause severe damage especially on sandy soils and are probably often overlooked wherever root-knot nematode predominate.

Longidorus africanus caused damage to lettuce in the subtropical regions of southern California. Patchy growth and wilted seedlings were observed together with leaf margin chlorosis (Radewald *et al.*, 1969). Nematode feeding caused a reduction in elongation of the tap root and root tip swelling, typical of damage by a number of species of *Longidorus* and *Xiphinema* on other crops. *L. vineacola* was reported to cause damage to celery in Israel (Cohn & Auscher, 1971). Although viruliferous *Xiphinema americanum* have been found associated with watermelon, virus transmission does not seem to be a major problem in melon or vegetables (McGuire, 1982).

Other Nematodes of Vegetables

Stunt nematodes, are often found associated with vegetables. Twenty-two species of *Tylenchorhynchus* (three formerly named *Telotylenchus* and two *Quinisulcius*) and four species of *Merlinius* have been found in the rhizosphere of vegetable crops. With the exception of *Tylenchorhynchus brassicae*, none of the other species have been shown to be of significant economic importance on vegetable crops. *T. mashoodi* has been considered to be of potential importance on tomato.

Tylenchorhynchus brassicae has been detected in India, the Sultanate of Oman (Waller & Bridge, 1978) and Egypt (Oteifa & Elsharkawi, 1965). The nematode is a serious problem on most cruciferous crops and, when high populations of this nematode occur, growth is negatively affected (Khan, 1969). The nematodes penetrate through the cortical region and are mainly confined in the outer layers of the cortex with their body lying parallel to the longitudinal axis of the roots and the anterior part of the body curved towards the conducting tissue. Occasionally the nematodes are situated in the stellar region with their entire body embedded in the stele. Of 22 vegetables inoculated with 1000 nematodes, cabbage and cauliflower were the most suitable hosts. Great differences in the response of cultivars to the stunt nematode exist. The most favourable temperature for reproduction

Fig. 12. Stubby-root injury to celery caused by *Dolichodorus heterocephalus* (Photo: H. Rhoades).

was 30°C and the most favourable soil moisture was 25–30%. In the absence of hosts, the nematode could survive up to 240 days in moist soil. When the nematode was associated with *Rhizoctonia solani*, the emergence of vegetable seedlings was strongly reduced (Khan & Saxena, 1969).

The awl nematode, *Dolichodorus heterocephalus*, can cause damage to vegetables, especially on wet, sandy soils. In Florida, the nematode causes severe damage to tomato and celery with losses on heavily infested soil often exceeding 50% (Tarjan *et al.*, 1952; Perry, 1953; Johnson & Fassuliotis, 1984). The nematode causes stubby root symptoms and severe root necrosis (Fig. 12), indicating a close association with root-rotting fungi. The nematode also can attack the base of the hypocotyl where necrotic tissues can be observed (Johnson & Fassuliotis, 1984).

Spiral nematodes, *Helicotylenchus* spp. and *Scutellonema* spp. are commonly found in vegetable crops. Although more than 14 species of *Helicotylenchus* and 3 of *Scutellonema* have been detected in the rhizosphere of the various vegetable crops, none has been shown to be of economic importance in the field.

Species of *Hoplolaimus*, *Aorolaimus* (*syn. Peltamigratus*) and *Zygotylenchus* have been found in soil samples from vegetable crops. Their importance to vegetable production has still not been determined.

Six species of ring nematodes, *Criconemella* (under the names *Criconemoides* or *Macroposthonia*) have been detected in the rhizosphere of a wide range of vegetables. These nematodes are known to increase to high numbers in many subtropical soils and have been implicated as important limiting factors on a number of perennial crops and could be important on vegetables.

Future prospects

Agricultural production is increasing in most subtropical and tropical countries, in contrast to forced reduction in production being experienced in western Europe and north America. Similarly, the

increase in vegetable production in the subtropics and tropics will require increased inputs in the form of fertilizer and pesticides; components being reduced in western Europe and North America, because of a lack of government subsidies and public awareness of the impact of agricultural inputs on the environment.

If environmentally safe nematicides are available in the future, an increase in use can be expected in many subtropical and tropical vegetable growing regions. A new generation of nematicides is needed that are both effective and safe. There still will be an imbalance in the availability of pesticides between commercial growers and poor or subsistence farmers, with the latter in most cases excluded for cost reasons.

Determination of threshold levels will be required to aid in selection of specific control measures for pest management programmes. Vegetables are often attacked simultaneously by a multitude of different plant parasitic nematodes. This requires an expanded view of threshold levels, involving the effects of all the species involved. Therefore, when determining damage intensity in the field, composite threshold levels, which include the interrelationship between all economically important nematode species, must be developed.

More emphasis must, therefore, be placed on determining the importance of plant parasitic nematodes, other than root-knot nematodes, to vegetable production. The losses caused by *Belonolaimus, Trichodorus, Ditylenchus, Heterodera, Pratylenchus, Nacobbus* and those species that may be of potential importance, indicate a need for more intensive study of these groups.

The development of resistant cultivars is playing an important role today and will increase in importance in the future. More stress must be placed on breeding for resistance to nematodes and diseases as well as for plant growth and quality characteristics important in tropical zones. This programme should be a priority in planning national and international research strategies. The use of embryo, tissue and protoplast cultures, as well as somatic hybridization will undoubtedly enable research to incorporate resistant genes present in botanical, but incompatible relatives, into useable cultivars.

Biological control is an alternative that is being studied in detail in many areas of the world. Fungal egg or female parasites, mycorrhizal fungi and plant health promoting rhizobacteria may prove to be effective control alternatives in future control programmes. Advances in biotechnology should make some of these biological control systems available to the farmer in the future. In most cases, however, they will not be as effective as present day nematicides and will require integration in extended rotation programmes.

With a reduction in the use of nematicides, the amount of nematode damage to vegetables will increase in those areas where alternative control components do not exist. Stress must be placed on developing integrated control programmes involving non-host crops and vegetable crops with resistance or tolerance not only to root-knot nematodes but other important species. Integrated pest management, however, must be developed to prevent monoculture of these cultivars and the consequent selection of resistant breaking pathotypes.

The "all or nothing approach" to nematode control is most probably a thing of the past, while "living with the nematodes" at or below threshold levels a thing of the near future.

References

Abawi, G. S. & Barker, K. R. (1984). Effects of cultivars, soil temperature and population levels of *Meloidogyne incognita* on root necrosis and *Fusarium* wilt of tomatoes. *Phytopathology*, 74: 333–338.

Abu-Gharbieh, W. I. & Perry, V. G. (1970). Host differences among Florida populations of *Belonolaimus longicaudatus* Rau. *Journal of Nematology*, 2: 209–216.

Abu-Gharbieh, W. I., Saleh, H. M. & Abu-Blan, H. A. (1987). Effect of "Solarization" using different thicknesses of black plastic tarping on soil-borne pathogens. Workshop, *Advances in agriculture through plastic house technology*. Amman, Jordan: 25.

Ahuja, S. (1978). The effect of root-dip treatments on infestation of brinjal by *Meloidogyne incognita*. *Nematologia Mediterranea*, 6: 133–134.

Anonymous. (1985). Nematodes. In: University of California Statewide Integrated Pest Management Project (Eds). *Integrated pest management for tomatoes*. Division of Agriculture and Natural Resources. Publication 3274: 61–65.

Anonymous. (1987). Nematodes. In: University of California Statewide Integrated Pest Management Project (Eds). *Integrated pest management for cole crops and lettuce*. Division of Agriculture and Natural Resources. Publication 3307: 81–88.

Armstrong, J. M. & Jensen, H. J. (1978). *Indexed Bibliography of Nematode-Resistance in Plants*. Corvallis, Oregon. *Agricultural Experiment Station Bulletin 639*, 248 p.

Augustin, B. & Sikora, R. A. (1989). Studies on the host range of the normal and giant faba bean races of *Ditylenchus dipsaci* in Syria and Germany. *Nematologia mediterranea*, 17: 63–66.

Badra, T., Salem, M. A. & Oteifa, B. A. (1979). Nematicidal activity of some organic fertilizers and soil amendments. *Revue de Nématologie*, 2: 29–36.

Balasubramanian, P. & Ramakrishnan, C. (1983). Resistance to the reniform nematode *Rotylenchulus reniformis* in tomato. *Nematologia Mediterranea*, 11: 203–204.

Barker, K. R. (Chairman). (1978). Determining nematode population responses to control agents. In: Zehr, E. I., Committee Chairman (Ed). *Methods for evaluating plant fungicides, nematicides, and bactericides*. American Phytopathological Society, St. Paul, Minn: 114–125.

Barker, K. R. (1985*a*). Sampling nematode communities. In: Barker, K. R., Carter, C. C. & Sasser, J. N. (Eds). *An Advanced Treatise on Meloidogyne, Volume II, Methodology*. Raleigh, North Carolina, U.S.A., North Carolina State University Graphics: 3–17.

Barker, K. R. (1985*b*). Nematode extraction and bioassays. In: Barker, K. R. Carter, C. C. & Sasser, J. N. (Eds). *An Advanced Treatise on Meloidogyne, Volume II, Methodology*. Raleigh, North Carolina, U.S.A., North Carolina University Graphics: 19–35.

Barker, K. R. & Olthof, T. H. A. (1976). Relationships between nematode population density and crop responses. *Annual Review of Phytopathology*, 14: 327–353.

Barker, K. R., Schmitt, D. P. & Imbriani, J. L. (1985). Nematode population dynamics with emphasis on determining damage potential to crops. In: Sasser, J. N. & Carter, C. C. (Eds). *An advanced Treatise on Meloidogyne Volume II. Methodology*. Raleigh, North Carolina, U.S.A., North Carolina University Graphics: 135–148.

Barker, K. R., Todd, F. A., Shane, W. W. & Nelson, L. A. (1981). Interrelationships of *Meloidogyne* species with flue-cured tobacco. *Journal of Nematology*, 13: 67–79.

Bergquist, R. R. & Riedel, R. M. (1972). Screening onion (*Allium cepa*) in a controlled environment for resistance to *Ditylenchus dipsaci*. *Plant Disease Reporter*, 56: 329–331.

Berthou, F., Ba-Diallo, A. & de Guiran, G. (1989). Caractérisation chez les nématodes *Meloidogyne* Goeldi (Tylenchida) de types virulents viv à vis du gène Mi de la tomate dans deux zones maraichères au Sénégal – *Agronomie*, 9:877–885.

Birchfield, W. & Antonpoulos, A. A. (1976). Scanning electron microscope observations of *Duboscquia penetrans* parasitizing root-knot larvae. *Journal of Nematology*, 8: 272–283.

Birchfield, W. & Martin, W. J. (1976). Effects of some organophosphates and carbamate nematicides on reniform nematode and sweet potato yields. *Journal of Nematology*, 8: 279–280.

Bridge, J. (1983). Nematodes. In: *Pest Control in Tropical Tomatoes*. Centre for Overseas Pest Research, Overseas Development Administration, London: 69–84.

Bridge, J. (1987). Control strategies in subsistence agriculture. In: Brown, R. H. & Kerry, B. R. (Eds). *Principles and Practice of Nematode Control in Crops*. Australia, Academic Press: 389–420.

Bridge, J. & Hunt, D. (1986). Nematodes. In: Tropical Development and Research Institute and Office of Overseas Development Administration (Eds). *Pest control in tropical onions*. London, Tropical Development and Research Institute: 65–77.

Bridge, J. & Manser, P. D. (1980). The beet cyst nematode in tropical Africa. *Plant Disease*, 64: 1036.

Bridge, J. & Page, S. L. J. (1977). *An assessment of the importance and control of plant-parasitic nematodes in*

Malawi. ODM report on the visit to Malawi, 2 January to 21 April 1977. Ascot Berks, UK. Ministry of Overseas Development, 8 p.

Brodie, B. B. & Quattlebaum, B. H. (1970). Vertical distribution and population fluctuations of three nematode species as correlated with soil temperature, moisture and texture. *Phytopathology*, 60: 1286.

Byrd, D. W., Ferris, H. & Nusbaum, C. J. (1972). A method for estimating number of eggs of *Meloidogyne* spp. in soil. *Journal of Nematology*, 4: 266–299.

Carter, W. W. (1980). Interaction of *Rotylenchulus reniformis* and *Macrophomina phaseolina* in charcoal rot of cantaloupe. *Journal of Nematology*, 12: 217.

Castillo, M. B., Alegar, M. S. & Harwood, R. R. (1976*a*). Effect of flooding on pot populations of *Rotylenchulus reniformis* and *Meloidogyne incognita*. *Philippine Phytopathology*, 12: 11–16.

Castillo, M. B., Arceo, M. B. & Litsinger, J. A. (1976*b*). Nematodes in cropping patterns. IV. Populations of plant parasitic nematodes associated with cropping patterns under different rice-growing environments in Manaoag, Pangasinan. *Philippine Phytopathology*, 12: 24–29.

Cayrol, J. C. (1983). Lutte biologique contre les *Meloidogyne* au moyen d'*Arthrobotrys irregularis*. *Revue de Nématologie*, 6: 265–273.

Cayrol, J. C. & Frankowski, J. P. (1979). Une méthode de lutte biologique contre les nématodes à galles des racines appartenant au genre *Meloidogyne*. *Pépinièristes Horticulteurs Maraîchers. Revue Horticole*, 143: 15–23.

Chitwood, M. G. (1949). "Root knot nematodes" Part I. A revision of the genus *Meloidogyne* Goeldi, 1887. *Proceedings of the Helminthological Society of Washington*, 16: 90–104.

Choudhury, B. C. (1981). Root-knot problem on various crop plants in Bangladesh. *Proceedings of the 3rd Research Planning Conference on root-knot nematodes Meloidogyne species*. Region VI, July 20–24, Jakarta: 142–145.

Christie, J. R. & Perry, V. G. (1951). A root disease of plants caused by a nematode of the genus *Trichodorus*. *Science*, 113: 491–493.

Clark, S. A. (1967). The development and life history of the false root-knot nematode, *Nacobbus serendipiticus*. *Nematologica*, 13: 91–101.

Cohn, E. & Auscher, R. (1971). Seasonal occurrence of *Longidorus vineacola* on celery in Israel and its control. *Israel Journal of Agricultural Research*, 21: 23–25.

Culbreath, A. K., Rodrigues-Kabana, R. & Morgan-Jones, G. (1985). The use of hemicellulosic waste matter for reduction of the phytotoxic effect of chitin and control of root-knot nematodes. *Nematropica*, 15: 49–75.

Dao, D. F. (1970). Climatic influence of temperature on distribution pattern of plant parasitic and soil inhabiting nematodes. *Mededelingen van de Landbouwhogeschool, Wageningen*, 70: 187.

Decker, H. (1969). *Phytonematologie*. Berlin, VEB Deutscher Landwirtschaftsverlag, 526 p.

Demeure, Y. (1977). Persistance de l'infestation d'un sol par *Meloidogyne* sp. en saison sèche au Sénégal. *Cahiers O.R.S.T.O.M. Série Biologie*, 11: 167–172.

Demeure, Y. (1978). *Les causes de la survie de certains nématodes phytoparasites (Scutellonema cavenessi et Meloidogyne spp.)* pendant la saison sèche dans le sahel sénégalais. Thèse présentée devant l'Université Claude Bernard (Lyon I), 105 p.

Demeure, Y. & Netscher, C. (1973). Méthode d'estimation des populations de *Meloidogyne* dans le sol. *Cahiers O.R.S.T.O.M., Série Biologie*, 21: 85–90.

Dickson, D. W. & Strubel, F. B. (1965). A sieve-staining technique for extraction of egg masses of *Meloidogyne incognita* from soil. *Phytopathology*, 50: 215–217.

Di Vito, M., Greco, N. & Carella, A. (1986). Effect of *Meloidogyne incognita* on the yield of eggplant. *Journal of Nematology*, 18: 487–490.

Dropkin, V. (1969). The necrotic reaction of tomatoes and other hosts resistant to *Meloidogyne:* Reversal by temperature. *Phytopathology*, 59: 1632–1637.

Duc, T. M. (1980). *Système de cultures irriguées à partir des eaux sous-terraines*. Collection C.I.E.H.- CEFIGRE Bamako, February, 1980.

Dunay, M. C. & Dalmasso, A. (1985). Multiplication de *Meloidogyne javanica, M. incognita*, et *M. arenaria* sur divers *Solanum*. *Revue de Nématologie*, 8: 312–334.

Edongali, E. A. (1986). Cyst forming nematodes in Libya. In: Lamberti, F. & Taylor, C. E. (Eds). *Cyst Nematodes*. New York, Plenum Press, Nato Advanced Study Institute, Series A: Life Sciences, Vol. 121: 389.

Edongali, E. A. & Dabaj, M. (1982). Cauliflower (*Brassica oleracea* cv. *capitata*) cyst nematode in Libya. *Libya Journal of Agriculture*, 11: 205.

Esser, R. P., Perry, V. G. & Taylor, A. L. (1976). A diagnostic compendium of the genus *Meloidogyne* (Nematoda: Heteroderidae). *Proceedings of the Helminthological Society of Washington*, 43: 138–150.

FAO, Food and Agricultural Organization. (1985). *Production Year Book*, Vol. 39, 289.

Fargette, M. (1987). Use of the esterase phenotype in taxonomy of the genus *Meloidogyne*. 2. Esterase phenotypes in West African populations and their characterization. *Revue de Nématologie*, 10: 45–55.

Fassuliotis, G. (1979). Plant breeding for root-knot nematode resistance. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes (Meloidogyne species). Systematics, Biology and Control*. London, Academic Press: 425–453.

Faulkner, L. R. & Bolander, W. J. (1970). Acquisition and distribution of nematodes in irrigation waterways of the Columbian Basin in Eastern Washington. *Journal of Nematology*, 2: 362–367.

Ferris, H. & Van Gundy, S. D. (1979). *Meloidogyne* ecology and host interrelationships. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes (Meloidogyne species). Systematics, Biology and Control*. London, Academic Press: 205–230.

Ferris, H., Ball, D. A., Beem, L. S. & Gudmundson, L. A. (1986). Using nematode count data in crop management decisions. *California Agriculture*, 40: 12–14.

Germani, G. (1978). Tests préliminaires de sensibilité de deux cultures de tomate et d'un cultivar d'arachide à deux souches de *Rotylenchulus reniformis*. *Revue de Nématologie*, 1: 11–12.

Gilbert, J. C. & McGuire, D. C. (1956). Inheritance of resistance to severe root-knot from *Meloidogyne incognita* in commercial type tomatoes. *American Society of Horticulture Science Proceeding*, 68: 437–442.

Gilman, D. G., Jones, J. E., Williams, C. & Birchfield, W. (1978). Cotton-soybean rotation for control of reniform nematodes. *Louisiana Agriculture*, 21: 10–11.

Golden, A. M. & Raski, D. J. (1977). *Heterodera thornei*, n. sp., (Nematoda: Heteroderidae) and a review of related species. *Journal of Nematology*, 9: 93–112.

Gomes Tovar, J. (1973). Contribution to the study of infestation and dispersion of Cobb's false root-knot nematode *Nacobbus serendipiticus* Franklin in Peru. *Nematropica*, 3: 4.

Good, J. M. & Thornton, B. D. (1956). Relative increases of populations of sting nematode, *Belonolaimus gracilis*, on six winter legumes. *Plant Disease Reporter*, 40: 1050–1053.

Gooris, J. & Herde, C. J. de (1972). *A method for the quantitative extraction of eggs and second stage larvae of* Meloidogyne *populations from soil*. Publication of the State Nematology and Entomology Research Station, Merelbeke, Belgium, 36 p.

Graham, R. W. & Holdeman, Q. L. (1953). The sting nematode *Belonolaimus gracilis*, on cotton and other crops in South Carolina. *Phytopathology*, 43: 434–439.

Guiran, G. de (1979). A necessary diapause in root-knot nematodes. Observations on its distribution and inheritance in *Meloidogyne incognita*. *Revue de Nématologie*, 2: 223–231.

Guiran, G. de & Demeure, Y. (1978). Influence du potentiel hydrique des sols sur les masses d'oeufs de *Meloidogyne incognita*. *Revue de Nématologie*, 1: 119–134.

Guiran, G. de & Villemin, M. A. (1980). Spécificité de la diapause embryonnaire des oeufs de *Meloidogyne incognita* (Nematoda). *Revue de Nématologie*, 3: 115–121.

Hague, N. G. M. (1968). Fumigation of shallot seed with methyl bromide to control stem eelworm, *Ditylenchus dipsaci*. *Plant Pathology*, 17: 127–128.

Hare, W. W. (1957). Inheritance of resistance to root-knot nematodes in pepper. *Phytopathology*, 47: 455–459.

Hartman, K. M. & Sasser, J. N. (1985). Identification of *Meloidogyne* species on the basis of differential host test and perineal-pattern morphology. In: Barker, K. R., Carter, C. C. & Sasser, J. N. (Eds).

Advanced Treatise on Meloidogyne. Volume II Methodology. Raleigh, North Carolina, U.S.A., North Carolina University Graphics: 69–78.

Heald, C. M. (1975). Pathogenicity and histopathology of *Rotylenchulus reniformis* infecting cantaloupe. *Journal of Nematology*, 7: 149–152.

Heald, C. M. (1978). Effect of the reniform nematode on vegetable yields. *Plant Disease Reporter*, 62: 902–904.

Heald, C. M. & Burton, G. W. (1968). Effect of organic and inorganic nitrogen on nematode populations on turf. *Plant Disease Reporter*, 52: 46–48.

Heald, C. M. & Thames, W. H. (1982). The reniform nematode, *Rotylenchulus reniformis*. In: Riggs, R. D. & Editorial Committee, Southern Regional Research Committees S–76 and S–154 (Eds). *Nematology in the Southern Region of the United States*. Southern Cooperative Series Bulletin, No. 276: 139–143.

Heald, C. M. & Wayland, J. R. (1975). Factors affecting the control of *Rotylenchulus reniformis* with UHF electromagnetic energy. *Journal of Nematology*, 7: 171–174.

Hendy, H., Pochard, E. & Dalmasso, A. (1985). Transmission héréditaire de deux nouvelles sources de résistance aux nématodes du genre *Meloidogyne* chez le piment *Capsicum annum* L. *Comptes rendus de l'Académie d'Agriculture*: 817–822.

Hirschmann, H. & Triantaphyllou, A. C. (1964). Reproduction in plant and soil nematodes. *Annual Review of Phytopathology*, 2: 57–80.

Ibrahim, I. K. A. & El Saedy, M. A. (1976). Development and pathogenesis of *Meloidogyne javanica* in peanut roots. *Nematologia mediterranea*, 4: 231–234.

IFAS, Institute of Food and Agricultural Sciences. (1989). *Florida Nematode Control Guide*. Entomology and Nematology Department and Cooperative Extension Service, University of Florida, Gainesville, 138 p.

Infante, M. & Sosa-Moss, C. (1971). Chemical control of *Ditylenchus dipsaci* (Kühn) Filipjev in garlic seed. *Nematropica*, 1: 13–14.

Jenkins, W. R. & Coursen, B. W. (1957). The effect of root-knot nematodes *Meloidogyne incognita acrita* and *Meloidogyne hapla* on *Fusarium* wilt of tomato. *Plant Disease Reporter*, 41: 182–186.

Jensen, H. J., Hopper, W. E. R. & Page, G. E. (1964). Control of stubby root nematode in Oregon plantings by soil fumigation. *Plant Disease Reporter*, 48: 225–227.

Jepson, S. B. (1987). *Identification of root-knot nematodes (*Meloidogyne *species*). Wallingford, UK. Commonwealth Agricultural Bureau International, 265 p.

Johnson, A. W. (1985). The role of nematicides in nematode management. In: Sasser, J. N. & Carter, C. C. (Eds). *An advanced Treatise on Meloidogyne Volume I. Biology and Control*. Raleigh, North Carolina, U.S.A., North Carolina University Graphics: 249–267.

Johnson, J. T. & Dickson, D. W. (1973). Evaluation of methods and rates of application of three nematicide-insecticides for control of the sting nematode on corn. *Proceedings Soil Crop Science of Florida*, 32: 171–173.

Johnson, A. W. & Fassuliotis, G. (1984). Nematode parasites of vegetable crops. In: Nickle, W. R. (Ed). *Plant and insect nematodes*. Marcel Dekker Inc., New York and Basel: 323–372.

Kassam, A. H. (1976). *Crops of the West African Semi-Arid Tropics*. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). Hyderabad, India, 154 p.

Katan, J. (1981). Solar heating (solarization) of soil for control of soilborne pests. *Annual Review of Phytopathology*, 19: 211–236.

Kerry, B. R. (1987). Biological control. In: Brown, R. H. & Kerry, B. R. (Eds). *Principles and practice of nematode control in crops*. London, Academic Press Inc.: 233–263.

Khan, A. M. (1969). *Studies on plant parasitic nematodes associated with vegetable crops in Uttar Pradesh*. Final Technical Report of Grant No. FG 1n 225. Allighar Muslim University, India, Project No. A7-CR–65.

Khan, A. M. & Saxena, S. K. (1969). Effect of *Rhizoctonia solani* and *Tylenchorhynchus brassicae* on the emergence of cauliflower seedlings. *All Indian Nematology Symposium*, 1967, The Indian Agricultural Research Institute, New Delhi, 12 p.

Krishnamurthy, G. V. G. & Elias, N. A. (1969). Note on effects of nematicides and heat treatment on the control of root-knot nematodes in tobacco nurseries. *Indian Journal of Agricultural Science*, 39: 263–265.

Lamberti, F. (1979*a*). Economic importance of *Meloidogyne* spp. in subtropical and mediterranean climates. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes* (Meloidogyne *species*) *Systematics, Biology and Control*. London, Academic Press: 341–357.

Lamberti, F. (1979*b*). Chemical and cultural control. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes* (Meloidogyne *species*) *Systematics, Biology and Control*. London, Academic Press: 403–423.

Lear, B., Miyagawa, S. T., Johnson, D. E. & Atlee, C. B., Jr., (1966). The sugarbeet cyst nematode associated with reduced yields of cauliflower and other vegetable crops. *Plant Disease Reporter*, 50: 611–612.

Linford, M. B. & Oliveira, J. M. (1940). *Rotylenchulus reniformis* novum genus; new species, a nematode parasite of roots. *Proceedings of the helminthological Society of Washington*, 7: 35–42.

Luc, M. (1986). Cyst nematodes in equatorial and hot tropical regions. In: Lamberti, F. & Taylor, C. E. (Eds). *Cyst Nematodes*. New York, Plenum Press, Nato Advanced Study Institute, Series A: Life Sciences Vol. 121: 355–372.

Luc, M. & Netscher, C. (1974). Presence of the sugar-beet nematode at Dakar. *FAO Plant Protection Bulletin*, 22: 24.

Mankau, R. & Prasad, N. (1972). Possibilities and problems in the use of sporozoan endoparasite for biological control of plant parasitic nematodes. *Nematropica*, 2: 7–8.

Martin, G. C. (1956). The common root-knot nematode (*Meloidogyne javanica*) and crop rotation. 5. Cotton (*Gossypium hirsuitum* var. 9L34). *Rhodesian Farmer*, 27: 33.

Mateille, Th. & Netscher, C. (1985). Temporary protection of egg-plant from *Meloidogyne incognita* by minute quantities of isazophos and aldicarb applied at seedling stage. *Revue de Nématologie*, 8: 41–44.

Mayol, P. S. & Bergeson, G. B. (1970). The role of secondary invaders in *Meloidogyne incognita* infection. *Journal of Nematology*, 2: 80–83.

McCann, J. (1981). Threshold populations of *Heterodera cruciferae* and *H. schachtii* causing damage to cabbage seedlings. *Plant Disease Reporter*, 65: 264–266.

McGuire, J. M. (1982). Nematode transmission of viruses. In: Riggs, R. D. & Editorial Committees, Southern Regional Research Committees S–76 and S. 154. (Eds). *Nematology in the southern region of the United States*. Southern Cooperative Series Bulletin No. 276: 190–192.

McSorley, R. (1980). Effect of *Rotylenchulus reniformis* on snap bean and methods for control by oxamyl. *Nematropica*, 10: 89–95.

McSorley, R. & Parrado, J. L. (1983). A bioassay sampling plant for *Meloidogyne incognita*. *Plant Disease*, 67: 182–184.

Miller, L. I. (1986). Economic importance of cyst nematodes in North America. In: Lamberti, F. & Taylor, C. E. (Eds). *Cyst Nematodes*. New York, Plenum Press, Nato Advanced Study Institute, Series A: Life Sciences Vol. 121: 373–385.

Minton, N. A., McGill, J. F. & Golden, A. M. (1969). *Meloidogyne javanica* attacks peanuts in Georgia. *Plant Disease Reporter*, 53: 668.

Moura, R. M. de., Echandi, E. & Powell, N. T. (1975). Interaction of *Corynebacterium michiganense* and *Meloidogyne incognita* on tomato. *Phytopathology*, 65: 1332–1335.

Muller, R. & Gooch, P. S. (1982). Organic amendments in nematode control. An examination of the literature. *Nematropica*, 12: 319–326.

Nandwana, R. P., Yadav, B. S., Varma, M. K. & Lal, A. (1980). Susceptibility of certain brinjal varieties to the root-knot nematode *Meloidogyne incognita*. *Indian Journal of Mycology and Plant Pathology*, 10: 181–182.

Naqvi, S. Q. A. & Alam, M. M. (1975). Influence of brinjal mosaic virus in the populations of *Tylenchorhynchus brassicae* and *Rotylenchulus reniformis* around eggplant roots. *Geobios*, 2: 120–121.

Nath, R. P., Haidar, M. G., Akhter, S. W. & Prasad, H. (1979). Studies on the nematodes of vegetables in Bihar. Effect of the reniform nematode *Rotylenchulus reniformis* on *Trichosanthes dioica*. *Indian Journal of Nematology*, 6: 175–177.

Netscher, C. (1970). Les nématodes parasites des cultures maraïchères au Senegal.*Cahiers O.R.S.T.O.M. Série Biologie*, 11: 209–229.

Netscher, C. (1975). Studies on the resistance of groundnut to *Meloidogyne* spp. in Senegal. *Cahiers O.R.S.T.O.M. Série Biologie*, 10: 227–232.

Netscher, C. (1977). Observations and preliminary studies on the occurrence of resistance breaking biotypes of *Meloidogyne* spp. on tomato. *Cahiers O.R.S.T.O.M. Série Biologie*, 11: 173–178.

Netscher, C. (1978). Morphological and physiological variability of species of *Meloidogyne* in West Africa and implications for their control. *Mededelingen Landbouwhogeschool Wageningen*, 46 p.

Netscher, C. (1981*a*). Preliminary studies on the control of *Meloidogyne* species. *Proceedings of the 3rd Research Planning Conference on root-knot nematodes* Meloidogyne *species. Regions IV and V.* Ibadan, Nigeria: 247–253.

Netscher, C. (1981*b*). Arbres résistants au *Meloidogyne* spp.: Utilization comme brise vent au Sénégal. *Agronomic tropicale Nogent*, 36: 175–177.

Netscher, C. & Luc, M. (1974). Nématodes associés aux cultures maraïchères en Mauritanie. *Agronomic tropicale Nogent*, 29: 697–701.

Netscher, C. & Mauboussin, J. C. (1973). Résultats d'un essai concernant l'efficacité comparée d'une variéte résistance et de certains nématicides contre *Meloidogyne javanica. Cahiers O.R.S.T.O.M. Série Biologie*, 21: 97–102.

Netscher, C. & Taylor, D. P. (1979). Physiologic variation within the genus *Meloidogyne* and its implications on integrated control. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes* (Meloidogyne *species*). *Systematics, Biology and Control.* London, Academic Press: 269–294.

Norman, D. W., Newman, M. D. & Ouedraogo, I. (1989). *Farm and village production systems in the semi-arid tropics of West Africa.* International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). Hyderabad, Research Bulletin, No. 4., 94 p.

Ogbuji, R. O & Okafor, M. O. (1984). Comparative resistance of nine pepper (Capsicum annum) cultivars to three root-knot nematode (*Meloidogyne*) species and their related use in traditional cropping systems. *Beiträge zur Tropischen Landwirtschaft und Veterinärmedizin*, 22: 167–170.

Oostendorp, M. & Sikora, R. A. (1989). Seed treatment with antagonistic rhizobacteria for the suppression of *Heterodera schachtii* early root infection of sugar beet. *Revue de Nématologie*, 12: 77–83.

Orr, C. C. & Newton, O. H. (1971). Distribution of nematodes by wind. *Plant Disease Reporter*, 55: 61–63.

Oteifa, B. A. & El-Shakawi, S. E. (1965). Species of some Egyptian parasitic nematodes on onion. *Bulletin of the zoological society of Egypt*, 20: 1632–1637.

Oteifa, B. A. & Osman, A. A. (1974). Host-parasite relations of *Rotylenchulus reniformis* on Lycopersicon esculentum. *Simposia Internacional (XII) de Nematologia. Sociedad Europe de Nematologos*, Septiembre 1974, Granada, Spain: 78–79.

Overman, A. J. (1964). The effect of temperature and flooding on nematode survival in fallow sandy soil. *Soil Crop Science Society of Florida Proceedings*, 24: 141–149.

Overman, A. J. (1974). Nematicides in linear drip irrigation for full-bed mulch of tomato. *Proceedings of the Soil and Crop Science Society of Florida*, 34: 197–200.

Overman, A. J. & Jones, J. P. (1986). Soil solarization, reaction, and fumigation effects on double-cropped tomato under full-bed mulch. *Proceedings Florida State Horticultural Society*, 99: 315–318.

Page, S. L. J. (1979). *An assessment of the importance and control of plant-parasitic nematodes of vegetable crops in Bangladesh.* O.D.M. Report of visit to Bangladesh. Ascot, Berks., UK. Ministry of Overseas Development, 36p.

Perry, V. G. (1953). The awl nematode, *Dolichodorus heterocephalus*, a devastating plant parasite. *Proceedings of the helminthological Society of Washington*, 20: 21–27.

Perry, V. G. & Norden, A. J. (1964). Some effects of a cropping sequence on populations of certain plant nematodes. *Proceedings Soil and Crop Scientific Society of Florida*, 23: 116–121.

Perry, V. G. & Rhoades, H. L. (1982*a*). The genus *Belonolaimus*. In: Riggs, R. D. & Editorial Committees, Southern Regional Research Committees S–76 and S–154. (Eds). *Nematology in the Southern Region of the United States.* Southern Cooperative Series Bulletin No. 276: 144–149.

Perry, V. G. & Rhoades, H. L. (1982*b*). The Trichodorid Nematodes. In: Riggs, R. D. & Editorial Committees, Southern Regional Research Committees S–76 and S–154. (Eds). *Nematology in the Southern Region of the United States*. Southern Cooperative Series Bulletin No. 276: 183–186.

Peter, K. V., Goth, R. W. & Webb, R. E. (1984). Indian hot peppers as new sources of resistance to bacterial wilt, *Phytophthora* root-rot and root-knot nematode. *Horticultural Science*, 19: 277–278.

Pitcher, R. S. (1963). Interrelationships of nematodes and other pathogens of plants. *Helminthological Abstracts*, 34: 1–17.

Powell, N. T. (1971*a*). Interactions between nematodes and fungi in disease complexes. *Annual Review of Phytopathology*, 9: 253–274.

Powell, N. T. (1971*b*). Interaction of plant parasitic nematodes with other disease causing agents. In: Zuckermann, B. M., Mai, W. F. & Rohde, R. A. (Eds). *Plant Parasitic Nematodes Volume II*. New York and London, Academic Press: 119–136.

Prasad, S. K. & Webster, J. M. (1967). Effect of temperature on the rate of development of *Nacobbus serendipiticus* in excised tomato roots. *Nematologica*, 13: 85–90.

Prot, J. C. (1977). Amplitude et cinétique des migrations de nématode *Meloidogyne javanica* sous l'influence d'un plant de tomate. *Cahiers O.R.S.T.O.M. Série Biologie*, 11: 157–166.

Prot, J. C. (1984). A naturally occurring resistance breaking biotype of *Meloidogyne incognita* on tomato. Reproduction and pathogenicity on tomato cultivars Roma and Rossol. *Revue de Nématologie*, 7: 23–28.

Prot, J. C. & Netscher, C. (1978). Improved detection of low population densities of *Meloidogyne*. *Nematologica*, 24: 129–132.

Prot, J. C. & Van Gundy, S. D. (1981). Effect of soil texture and the clay component on migration of *Meloidogyne incognita* second stage juveniles. *Journal of Nematology*, 13: 213–219.

Radewald, J. D., McKenry, M. V., Roberts, P. A. & Westerdahl, B. B. (1987). The importance of soil fumigation for nematode control. *California Agriculture*, 41: 16–17.

Radewald, J. D., Osgood, J. W., Mayberry, K. S., Paulus, A. O. & Shibuya, F. (1969). *Longidorus africanus* a pathogen of head lettuce in the Imperial Valley of southern California. *Plant Disease Reporter*, 53: 381–384.

Rehm, S. & Espig, G. (1976). *Die Kulturpflanzen der Tropen und Subtropen*. Stuttgart, Eugen Ulmer GmbH, 496 p.

Rhoades, H. L. (1964). Effect of *Crotalaria spectabilis* and *Sesbania exaltata* on plant nematode populations and subsequent yield of snap beans and cabbage. *Proceedings Florida State Horticultural Society*, 77: 233–237.

Rhoades, H. L. (1967). Efficacy of some experimental nematicides applied in-the-row on vegetables. *Proceedings Florida State Horticultural Society*, 80: 156–161.

Rhoades, H. L. (1969). Nematicide efficacy in controlling sting and stubby-root nematodes attacking onions in central Florida. *Plant Disease Reporter*, 53: 728–730.

Rhoades, H. L. (1971). A comparison of pre-plant and post-plant nematicides for controlling sting nematodes. *Soil and Crop Science Society of Florida*, 31: 260–262.

Rhoades, H. L. (1976*a*). Effect of *Indigofera hirsuta* on *Belonolaimus longicaudatus, Meloidogyne incognita* and *M. javanica* and subsequent crop yields. *Plant Disease Reporter*, 60: 384–386.

Rhoades, H. L. (1976*b*). Comparison of granular and transplant water application of nonfumigant nematicides for controlling the sting nematode. *Belonolaimus longicaudatus*, on cabbage. *Soil and Crop Science Society of Florida*, 36: 205–206.

Rhoades, H. L. (1980). Relative susceptibility of *Tagetes patula* and *Aeschynomene americana* to plant nematodes in Florida. *Nematropica*, 10: 116–120.

Rhoades, H. L. (1983). Effects of cover crops and fallowing on populations of *Belonolaimus longicaudatus* and *Meloidogyne incognita* and subsequent crop yields. *Nematropica*, 13: 9–16.

Rhoades, H. L. (1986). Effects of fumigant and nonfumigant nematicides on *Belonolaimus longicaudatus* and *Hoplolaimus galeatus* populations and subsequent yield of cabbage. *Plant Disease*, 70: 581–582.

Rhoades, H. L. & Forbes, R. B. (1986). Effects of fallow, cover crops, organic mulch and phenimaphos on nematode populations, soil nutrients and subsequent growth. *Nematropica*, 16: 141–151.

Rich, J. R. & Bird, G. W. (1973). Inhibition of *Rotylenchulus reniformis* penetration of tomato and cotton roots with foliar applications of oxamyl. *Journal of Nematology*, 5: 221–224.

Riggs, R. D. & Winstead, N. N. (1959). Studies on resistance in tomato to root-knot nematodes and on the occurrence of pathogenic biotypes. *Phytopathology*, 49: 716–724.

Robbins, R. T. & Barker, K. R. (1973). Comparisons of host range and reproduction among populations of *Belonolaimus longicaudatus* from North Carolina and Georgia. *Plant Disease Reporter*, 57: 750–754.

Roberts, P. A. (1987). The influence of planting date of carrot on *Meloidogyne incognita* reproduction and injury to roots. *Nematologica*, 33: 335–342.

Roberts, P. A. (1988). Effects of metam-sodium applied by drip irrigation on root-knot nematodes, *Pythium ultimum*, and *Fusarium* sp. in soil and on carrot and tomato roots. *Plant Disease*, 72: 213–217.

Roberts, P. A. & Thomason, J. (1986). Variability in reproduction of isolates of *Meloidogyne incognita* and *M. javanica* on resistant tomato genotypes. *Plant Disease*, 70: 547–551.

Roberts, P. A., Van Gundy, S. D. & McKinney, H. E. (1981). The effects of soil temperature and planting date of wheat on *Meloidogyne incognita* reproduction, soil populations and grain yield. *Journal of Nematology*, 13: 338–345.

Roberts, P. A., May, D. & Metthew, W. C. (1986). Rootknot resistance in processing tomatoes. *California Agriculture*, 40: 24–26.

Roca, F., Conti, M. & Lamberti, F. (1977). *Trichodorus viruliferus* (Nematoda Trichodoridae) vettore del virus "rattle" (TRV) nell Asstigiano. *Nematologia mediterranea*, 5: 185–194.

Rohde, R. A. & Jenkins, W. R. (1957). Host range of a species of *Trichodorus* and its host-parasite relationships on tomatoes. *Phytopathology*, 47: 295–298.

Rohde, R. A. & Jenkins, W. R. (1958). Basis for resistance of *Asparagus officinalis* var. *altilis* L. to the stubby-root nematode *Trichodorus christiei* Allen 1957. *Maryland Agriculture Experiment Station Bulletin, A–97*, 19 p.

Román, J. (1978). *Fitonematologia Tropical*. Estación Experimental Agricola, Universidad de Puerto Rico, 256 p.

Ruthenberg, H. (1983). *Farming systems in the tropics*. England, Third Edition, Oxford Press, 180 p.

Saleh, H., Abu-Gharbieh, W. I. & Al-Banna, L. (1988). Effect of solarization combined with solar-heated water on *Meloidogyne javanica*. *Nematologica*, 34: 290–291.

Sasser, J. N. (1954). *Identifications and host-parasite relationships of certain root-knot nematodes* (Meloidogyne *spp.*). Bulletin of the Maryland Agricultural Experiment Station. A–77, 31 p.

Sasser, J. N. (1966). Behaviour of *Meloidogyne* species from various geographical locations on ten host differentials. *Nematologica*, 12: 98–99.

Sasser, J. N. (1979*a*). Pathogenicity and host ranges in *Meloidogyne* species. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes (*Meloidogyne *species). Systematics, Biology and Control*. London, Academic Press: 256–268.

Sasser, J. N. (1979*b*). Economic importance of *Meloidogyne* in tropical countries. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes (*Meloidogyne *species). Systematics, Biology and Control*. London, Academic Press: 359–374.

Sasser, J. N. & Kirby, M. F. (1979). *Crop cultivars resistant to root-knot nematodes* Meloidogyne *species*. A cooperative publication of the Department of Plant Pathology, North Carolina State University and the United States Agency for International Development. Raleigh, North Carolina, 24 p.

Sauer, M. R. & Giles, J. E. (1959). A field trial with root-knot resistant tomato variety. *C.S.I.R.O. Australian Irrigation Research Station Technical Paper*, 3: 1–10.

Saxena, M. C., El-Moneim, A. A., Mamluk, O. & Hanounik, S. B. (1987). A review of nematology research in ICARDA. In: Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (Eds). *Nematodes Parasitic to Cereals and Legumes in Temperate Semi-Arid Regions*. Proceedings of a Workshop, Larnaca, Cyprus 1987. ICARDA, Aleppo, Syria: 69–84.

Schiffers, B. C., Fraselle, J. & Jaumin, L. (1985). Comparaison d'efficacité contre le *Ditylenchus dipsaci* (Kühn)

Fil. de 4 traitements nématicides incorporés aux enrobages de semences de féverolle (*Vicia faba* L.). *Mededelingen Landbouwhogeschool Wageningen*, 50: 797–807.

Schuster, M. L., Sandstedt, R. & Estes, L. W. (1965). Host-parasite relations of *Nacobbus batatiformis* and the sugar beet and other hosts. *Journal of the American Society of Sugar Beet Technology*, 13: 523–537.

Seinhorst, J. W. (1956). Biologische Rassen von het stengelaaltje *Ditylenchus dipsaci* (Kühn) Filipjev en hun waardplanten. *Tijdschrift over Planteziekten*, 62: 179–188.

Seinhorst, J. W. (1965). The relation between nematode density and damage to plants. *Nematologica*, 11: 137–154.

Siddiqui, I. A., Sher, S. A. & French, A. M. (1973). *Distribution of plant parasitic nematodes in California*. Sacramento, U.S.A., California Department of Food and Agriculture, 324 p.

Sidhu, G. & Webster, J. M. (1977). Predisposition of tomato to the wilt fungus (*Fusarium oxysporum lycopersici*) by the root-knot nematode (*Meloidogyne incognita*). *Nematologica*, 23: 436–442.

Sikora, R. A. (1978). Einfluss der endotrophen Mykorrhiza (*Glomus mosseae*) auf das Wirt-Parasit-Verhältnis von *Meloidogyne incognita* in Tomaten. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*, 85: 197–202.

Sikora, R. A. (1988). Interrelationship between plant health promoting rhizobacteria, plant parasitic nematodes and soil microorganisms. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit. Gent, Belgium*, 53: 867–878.

Sikora, R. A. (1989). *Importance of plant parasitic and entomopathogenic nematodes to vegetable production in the Philippines*. GTZ Report, Eschborn, 37 p.

Sikora, R. A. & Carter, W. W. (1987). Nematode Interactions with Fungal and Bacterial Pathogens – Fact or Fantasy. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Maryland, Society of Nematologists: 307–312.

Sikora, R. A., Reckhaus, P. & Adamou, I. (1988). Presence, distribution and importance of plant parasitic nematodes in irrigated agricultural crops in Niger. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit. Gent, Belgium*, 53: 821–834.

Sikora, R. A., Singh, R. S. & Sitaramaiah, K. (1973*a*). Control of root-knot through organic and inorganic soil amendments. 3. Effect of rice husk and sugarcane bagasse. *Haryana Journal of Horticultural Science*, 2: 123–127.

Sikora, R. A., Sitaramaiah, K. & Singh, R. S. (1973*b*). Reaction of root-knot nematode resistant tomato cultivars to *Meloidogyne javanica* in India. *Plant Disease Reporter*, 57: 141–143.

Singh, R. V. & Khera, S. (1979). Pathogenicity of *Rotylenchulus reniformis* on brinjal (*Solanum melongena* L.). *Indian Journal of Nematology*, 9: 117–124.

Singh, R. S. & Sitaramaiah, K. (1966). Incidence of root-knot of okra and tomatoes in oil-cake amended soil. *Plant Disease Reporter*, 50: 668–672.

Singh, R. S. & Sitaramaiah, K. (1967). Effect of decomposing green leaves, sawdust and urea on the incidence of root-knot to okra and tomato. *Indian Phytopathology*, 20: 349–355.

Sitaramaiah, K. & Sikora, R. A. (1982). Effect of the mycorrhizal fungus *Glomus fasciculatus* on the host parasite relationship of *Rotylenchulus reniformis*. *Nematologica*, 28: 412–419.

Sivakumar, C. V. & Meerzainuddeen, M. (1973). The effect of yellow vein mosaic disease of okra on the reniform nematode, *Rotylenchulus reniformis*. *South Indian Horticulture*, 21: 68–69.

Sivakumar, C. V. & Seshadri, A. R. (1971). Life history of the reniform nematode, *Rotylenchulus reniformis*, Linford and Oliveira, 1940. *Indian Journal of Nematology*, 1: 7–20.

Sivakumar, C. V. & Seshadri, A. R. (1979). Longevity of the reniform nematode, *Rotylenchulus reniformis* in host free soil. *Indian Journal of Nematology*, 6: 138–144.

Smith, P. G. (1944). Embryo culture of a tomato species hybrid. *Proceedings of the American Society for Horticultural Science*, 44: 413–416.

Sosa-Moss, C. (1986). Cyst nematodes in Mexico, Central and South America. In: Lamberti, F. & Taylor, C. E. (Eds), *Cyst Nematodes*. New York, Plenum Press, Nato Advanced Study Institute, Series A: Life Sciences Vol. 121: 397–398.

Southards, C. J. & Priest, M. F. (1973). Variation in pathogenicity of seventeen isolates of *Meloidogyne incognita*. *Journal of Nematology*, 5: 63–67.

Stephan, Z. A. (1986). Host status of cyst nematode in Iraq. In: Lamberti, F. & Taylor C. E. (Ed). *Cyst Nematodes*. New York, Plenum Press, Nato Advanced Study Institute, Series A: Life Sciences Vol. 121: 391.

Stirling, G. R. & Wachtel, M. F. (1980). Mass production of *Bacillus penetrans* for biological control of root-knot nematodes. *Nematologica*, 26: 308–312.

Stoyanov, D. (1971). Control de los nematodos parasitos de plantanos por medio de rotaciones y su duracion en tierra sin hospedos. *Revista de Agricultura Cuba*, 4: 75–81.

Stoyanov, D. (1972). *Heterodera amaranthi* n. sp. (Tylenchida: Heteroderidae); un nemátodo formador de quistes en Cuba. *Poeyana*, 97: 1.

Sturhan, D. (1969). Das Rassenproblem bei *Ditylenchus dipsaci*. *Mitteilung der Biologischen Bundesanstalt für Land- und Forstwirtschaft*, 136: 87–98.

Sumeghy, J. B. (1979). New hybrid tomatoes resist diseases. *Agricultural Gazette of New South Wales*, 90: 22–23.

Sykes, G. B. & Winfield, A. L. (1966). Studies on Brassica cyst nematode *Heterodera cruciferae, Nematologica*, 12: 530–538.

Tarjan, A. C., Lownsbery, B. F. & Hawley, W. O. (1952). Pathogenicity of some plant-parasitic nematodes from Florida soils. I. The effect of *Dolichodorus heterocephalus* Cobb on celery. *Phytopathology*, 42: 131–132.

Taylor, A. L. & Sasser, J. N. (1978). *Biology, identification and control of root-knot nematodes* (Meloidogyne *spp.*). Cooperative Publication Department of Plant Pathology, North Carolina State University and U.S. Agency International Development, Washington D. C., North Carolina State University Graphics, 111 p.

Taylor, A. L., Sasser, J. N. & Nelson, L. A. (1982). *Relationship of climate and soil characteristics to geographical distribution of* Meloidogyne *species in agricultural soils*. Cooperative Publication Department of Plant Pathology, North Carolina State University and U.S. Agency International Development, Washington D. C., North Carolina State University Graphics, 65 p.

Taylor, C. E. (1979). *Meloidogyne* interrelationships with microorganisms. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes (*Meloidogyne *species) Systematics, Biology and Control*. London, Academic Press: 375–398.

Taylor, D. P. (1976). Plant nematology problems in tropical Africa. *Helminthological Abstracts Series B, Plant Nematology*, 45: 269–284.

Taylor, D. P., Netscher, C. & Germani, G. (1978). *Adansonia digitata* (Baobab), a newly discovered host for *Meloidogyne* sp. and *Rotylenchulus reniformis*. Agricultural implications. *Plant Disease Reporter*, 62: 276–277.

Thames, W. H. Jr. (1959). *Plant parasitic nematode populations of some Florida soils under cultivated and natural conditions. Dissertation Abstracts*, 20: 1109–1110.

Thames, W. H. & Heald, C. M. (1974). Chemical and cultural control of *Rotylenchulus reniformis* on cotton. *Plant Disease Reporter*, 58: 337–341.

Thames, W. H. & Stoner, W. N. (1953). A preliminary trial of lowland culture rice in rotation with vegetable crops as a means of reducing root-knot nematode infestations in the Everglades. *Plant Disease Reporter*, 37: 187–192.

Tobar, A. & Palacios, F. (1974). Nematode dispersal by irrigation water. *Symposia Internacional (XII) de Nematologia. Sociedad Europe de Nematologos*, Septiembre 1974, Granada, Spain: 103–105.

Triantaphyllou, A. C. & Sasser, J. N. (1960). Variation in perineal patterns and host specificity of *Meloidogyne incognita*. *Phytopathology*, 50: 724–735.

Valdez, R. B. (1978). Nematodes attacking tomato and their control. *1st International Symposium on Tropical Tomato, AVRDC Publ. 78/59, Taiwan*, 136–152.

Van der Linde, W. J. (1956). The *Meloidogyne* problem in South Africa. *Nematologica*, 1: 177–183.

Van Gundy, S. D., Kirkpatrick, J. D. & Golden J. (1977). The nature and role of metabolic leakage from root-knot nematode galls and infection by *Rhizoctonia solani*. *Journal of Nematology*, 9: 113–121.

Wallace, H. R. (1966). Factors influencing the infectivity of plant parasitic nematodes. *Proceedings of the Royal Society, B*, 164: 592–614.

Wallace, H. R. (1983). Interactions between nematodes and other factors on plants. *Journal of Nematology*, 15: 221–227.

Waller, J. M. & Bridge, J. (1978). Plant disease and nematodes in the sultanate of Oman. *PANS, 24*: 136–140.

Webster, J. M. (1985). Interaction of *Meloidogyne* with fungi on crop plants. In: Sasser, J. N. & Carter, C. C. (Eds). *An advanced Treatise on Meloidogyne Volume I. Biology and Control*. Raleigh, North Carolina, U.S.A., North Carolina University Graphics: 183–192.

Williams, K. J. O. (1974). *Belonolaimus longicaudatus*. C. I. H. *Description of Plant-Parasitic Nematodes*. Set 3, No. 40, 4 p.

Zavaleta-Meija, E. & Van Gundy, S. D. (1982). Effects of rhizobacteria on *Meloidogyne* infection. *Journal of Nematology*, 15: 475–476.

Zeck, W. M. (1971). A rating scheme for field evaluation of root-knot nematode infestations. *Pflanzenschutz-Nachrichten. Bayer AG*, 24: 141–144.

Zeven, A. C. & Wet, J. M. J. de (1982). *Dictionary of cultivated plants and regions of diversity*. Wageningen, Pudoc-Centre for Agricultural Publications and Documentation, 275 p.

Chapter 8

Nematode Parasites of Peanut

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The cultivated groundnut or peanut (*Arachis hypogaea* L.) is an annual, self-pollinating, herbaceous legume, native to South America (Hammons, 1982). It is geotropic, producing its pods (fruits) underground. Flowering begins four to six weeks after planting and extends over a period of several weeks. Within about one week after fertilization, a pointed needle-like structure, the carpophore, commonly called the "peg" develops, elongates and grows into the soil 2–7 cm deep. Upon entering the soil, the fertilized ovaries located behind the tip of the peg enlarge rapidly and pod growth begins. The length of time necessary for pod development to maturity may vary with cultivar and environmental conditions. Williams and Drexler (1981) determined that the cultivar Florunner required 63–70 days from the time the ovary began enlarging to maturity.

Peanut was listed as one of the twenty crop plants that stand between man and starvation (Wittwer, 1981). Peanut seeds are rich in calories and contain 25% protein. They may be boiled, broiled, roasted, fried, ground into peanut butter or crushed for oil. Peanut-containing foods such as peanut butter, salted peanuts, candies, and snack-type crackers and cookies are popular because of their unique roasted peanut flavour (McWatters & Cherry, 1982). On a worldwide scale, however, peanuts are grown primarily for cooking and salad oil. Oil extraction also produces a protein-rich byproduct which may be used for human consumption if processed from edible-grade peanuts, otherwise, it is used for animal feed.

The peanut today is cultivated on all six continents in about 80 countries. Eight countries, China, India, United States, Senegal, Sudan, Brazil, Argentina, and South Africa, produce about 77% of the world supply (United States Department of Agriculture, 1989). In 1988–89, approximately 21.98 million/t were produced on 18.95 million hectares. Production is distributed generally in the tropical, sub-tropical, and warm temperature zones. In addition, many of the major production regions are characterized by having loose friable sandy soils.

Nematodes of Peanut

Nematodes damage peanuts in all production regions of the world. Based on a worldwide survey of nematologists, annual losses caused by all nematodes to peanut were estimated at 12% and monetary losses were estimated at 1.03 billion U.S. dollars (Sasser & Freckman, 1987). The nematodes that are known to cause damage to peanut are *Meloidogyne* spp., *Pratylenchus brachyurus, Belonolaimus longicaudatus, Criconemella ornata, Aphelenchoides arachidis, Aphasmatylenchus straturatus, Scutel-*

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lonema cavenessi, Tylenchorhynchus brevilineatus, and *Ditylenchus destructor*, although many other species have been found in association with peanut (Sharma, 1985).

Meloidogyne

The three *Meloidoyne* species parasitizing peanut are *M. arenaria* (peanut root-knot nematode), *M. javanica* (Javanese root-knot nematode) and *M. hapla* (northern root-knot nematode). These three species are known to occur in North, Central and South America, Africa, India, Europe including the Mediterranean region, Japan, Australia and Fiji Islands (Sasser, 1977). Their distribution and economic importance are purported to be related to biological and environmental factors favourable to the nematodes. *Meloidogyne arenaria* and *M. javanica* are common in warm and hot regions of the world whereas *M. hapla* occurs only in cool regions.

According to a recent report, *M. arenaria* is the predominant *Meloidogyne* species parasitizing peanut in Alabama, Georgia, Texas and Arkansas, and *M. hapla* is the most damaging species in North Carolina, Virginia, and Oklahoma (Anon., 1987). Both *M. arenaria* and *M. hapla* were reported to cause damage in Georgia, North Carolina and Oklahoma. *Meloidogyne javanica* is present in some of the peanut growing regions of the United States, but it was reported parasitizing peanuts only in Georgia in one location (Minton *et al.*, 1969*b*).

In other regions of the world, *Meloidogyne arenaria* has been reported on peanut in Zimbabwe (Martin, 1958), Israel (Orion & Cohn, 1975), Egypt (Ibrahim & El-Saedy, 1976*a*), India (Sharma *et al.*, 1978; Dhruj & Vaishnav, 1981; Sakhuja & Sethi, 1985*c*), Taiwan (Cheng & Tu, 1980; Cheng *et al.*, 1981) and China (Zhang, 1985). In Senegal, Netscher (1975) reported that an isolate of *Meloidogyne* species resembling *M. arenaria* reproduced slightly on peanut, but that juveniles collected from peanut failed to reproduce on susceptible tomato. Even though *Meloidogyne* spp., including *M. arenaria* and *M. javanica*, occur in Senegal, they do not damage peanut.

Meloidogyne hapla was reported parasitizing peanut in Israel (Minz, 1956), South Africa (van der Linde, 1956), Australia (Colbran, 1958; Saint-Smith *et al.*, 1972), Zimbabwe (Martin, 1961), Japan (Mitsui *et al.*, 1976), Korea (Choi, 1981) and China (Yin & Feng, 1981; Yang, 1984; Zhang, 1985).

The first report of *M. javanica* parasitizing peanut was by Martin (1958) in Zimbabwe. A few years later Minton *et al.* (1969*b*) found this species parasitizing peanut in one location in Georgia, USA. In addition, *M. javanica* was reported on peanut in Egypt (Ibrahim & El-Saedy, 1976*b*), Brazil (Lordello & Gerin, 1981) and India (Sakhuja & Sethi, 1985*b*).

Symptoms of damage

Juveniles of *Meloidogyne* spp. enter and damage peanut roots, pegs and pods. Juveniles upon entering the root tips cause only slight mechanical injury, except when large numbers enter in a limited area.

Minton (1963) studied the infectivity and histopathology of *M. arenaria* on peanut. Roots inoculated with *M. arenaria* second stage juveniles were invaded by the second day. Large, multinucleate, densely stained giant cells developed by the eighth day. Hyperplasia occurred in tissue adjacent to the nematode and hyperplasia and hypertrophy resulted in disorganization of vascular tissue. Galls resulted as the parenchymatous cells associated with developing nematodes at the periphery of the stele multiplied and grew out into the cortex. Adjacent cortical cells were crushed by the expanding nematodes and parenchyma cells and necrosis was associated with the damage. Elongation of severely galled roots was slowed.

The anatomical changes induced by *M. javanica* in peanut root tissues include cell hyperplasia and hypertrophy that results in the formation of giant cells in the cortical and stelar tissues (Ibrahim & El-Saedy, 1976*b*). A major consequence of nematode development and giant cell formation in the stele was the malformation of the xylem elements and the inhibition of secondary growth of the xylem and phloem tissues.

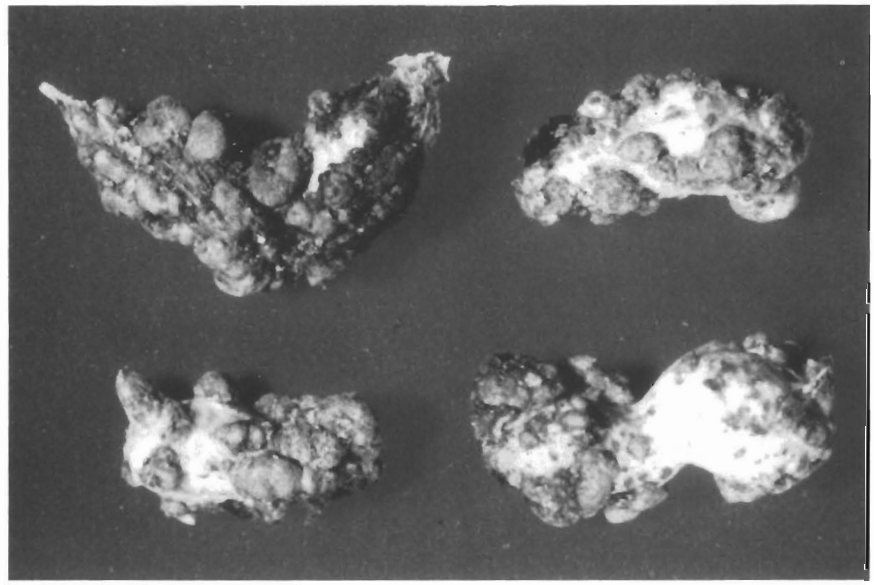

Fig. 1. *Meloidogyne arenaria* galls on peanut pods (Photo: D. W. Dickson).

Galls on peanut roots, pods and pegs caused by *M. arenaria* (Fig. 1, Plate 6A) and *M. javanica* are similar and are larger than those caused by *M. hapla* (Fig. 2, Plate 6B) (Sasser, 1954; Minton *et al.*, 1969*b*; Taylor & Sasser, 1978). Galls produced by *M. arenaria* and *M. javanica* may attain a diameter several times that of the adjacent root; thus the roots become much enlarged with fewer than normal small feeder roots. Sakhuji and Sethi (1985*b*) observed that roots infected with *M. javanica* proliferated with two to five lateral roots arising at the gall sites. *Rhizobium* nodules on peanut roots may be mistakenly diagnosed as root-knot galls. However, the appearance of root-knot nematode galls and *Rhizobium* nodules is distinctively different: galls result from an internal swelling of the root tissue and are of a woody consistency, whereas nodules are of a spongy consistency and are mostly appended laterally and can be rubbed off easily (Fig. 3). Damaged pods may become disfigured and fail to produce seeds (Fig. 1). *M. hapla* infected roots develop small galls and heavily infected roots develop extensive root proliferation above the galls resulting in a dense mat or bushy root system (Sasser, 1954).

Machmer (1951) described the field symptoms of *M. arenaria* on peanut as follows: "Galling occurs on all underground parts of peanut plants including the pods which appear warty. Pod stems are often heavily galled and are easily severed. Early infection of the peg (ovary) is detrimental to the seed embryo. Heavily galled plants frequently have a great many necrotic pegs but less than a dozen mature pods." Machmer further stated that the peanut vegetation usually does not exhibit conspicuous symptoms until near harvest. "At this time plants are becoming discoloured (Plate 6C) and are stunted so that they fail to cover the soil between rows (Fig. 4). The slowly dying and browning plants present a mottled effect among the greener plants and weeds. When the roots of such plants show conspicuous root-knot nematode galls the neighbouring plants in apparent vigour are usually well infected also." In China, Zhang (1985) reported that *M. arenaria* infected plants may become yellow and stunted as early as 40 days after planting. Above ground symptoms of *M. hapla* (Taylor & Sasser, 1978) and *M. javanica* (Minton *et al.*, 1969*b*) are similar to those of *M. arenaria*. Plants affected make poor top growth and yield poorly.

Fig. 2. Peanut roots galled by *Meloidogyne hapla*. Root proliferation near galls results in a matted root system (Photo: L. I. Miller).

Biological races

Taylor and Sasser (1978) suggested that the word "race" should be used only for populations of *Meloidogyne* that have been shown by numerous experiments to have host preferences significantly different from those established as "normal" for the species concerned, and also have wide geographical distribution. Sasser and Nusbaum (1955) observed that a population of *M. arenaria* in North Carolina did not infect peanut and suggested that this population differed from populations in Georgia and other states. Based on extensive differential host tests using populations of *M. arenaria, M. javanica* and *M. hapla* from widely separated regions of the world, Sasser (1972), Taylor and Sasser (1978) and Eisenback *et al.* (1981) separated *M. arenaria* into two races; race 1 reproduces on peanut but race 2 does not. Host races of *M. arenaria* are distributed throughout the world and are morphologically indistinguishable (Sasser, 1979*a*; Osman *et al.*, 1985). Reactions of the different populations of *M. javanica* and *M. hapla* to the differential hosts were relatively uniform, hence different biological races were not detected, although, some variability within populations of *M. javanica* was noted. Most *M. javanica* populations did not reproduce on peanut. *M. javanica* has been reported infecting peanut in Zimbabwe and Malawi (Martin, 1958), Georgia, USA (Minton *et al.*, 1969*b*) and Brazil (Lordello & Gerin, 1981).

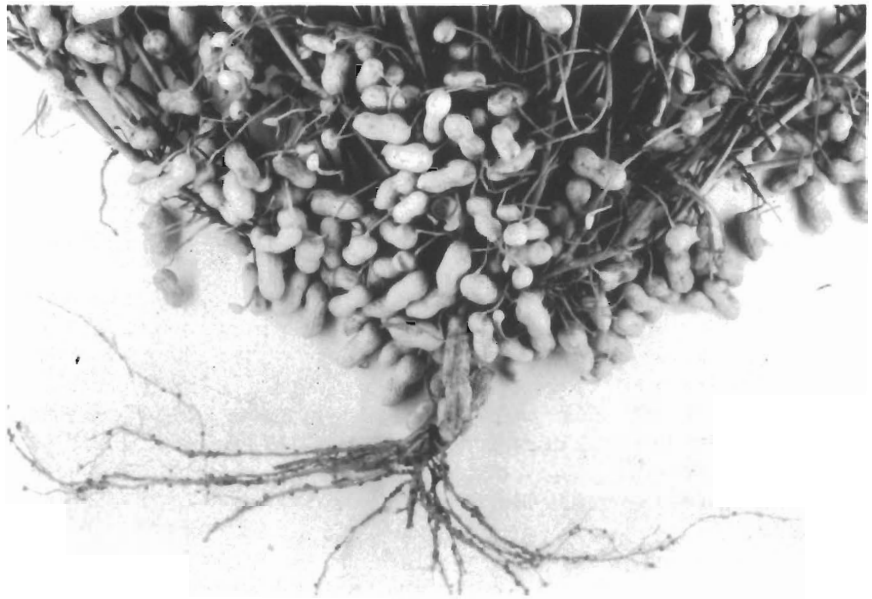

Fig. 3. Peanut plant with no nematode damage but with numerous nitrogen-fixing nodules attached to roots.

Fig. 4. A peanut field in Georgia with severe *Meloidogyne arenaria* damage in the foreground.

Survival and means of dissemination

Orr and Newton (1971) found *Meloidogyne* juveniles among 28 genera recovered from dust traps placed 2 m above the ground in Western Texas. Dispersal by surface run-off water and by irrigation also occurs (Faulkner & Bolander, 1966; Meagher, 1967; Sauer, 1968), but, for the most part, *Meloidogyne* species are disseminated widely by human activities. They may be spread in freshly dug peanut, including pods and roots, but generally they do not survive in well dried pods. Refuse from packing and processing plants that has not been thoroughly dried may harbour viable eggs and infective juveniles. Soil from infested fields transported on tillage equipment and the feet of farm animals and humans may also be a source of eggs and juveniles to infest fields.

Environmental factors affecting parasitism

Temperature is considered the most important environmental factor affecting *Meloidogyne* species survival and parasitism, and the lower and upper temperatures for survival are approximately 0° to 5°C and 35°C to 40°C, respectively (Taylor & Sasser, 1978). In general, the optimum temperature for survival of eggs and juveniles is 10°C–15°C (Bergeson, 1959; Thomason *et al.*, 1964). The optimum temperature for hatching of *M. hapla* and *M. javanica* is 25°C and 30°C, respectively (Bird & Wallace, 1965). *M. javanica* had a significantly higher hatch at 30° C than *M. hapla*. Milne and Du Plessis (1964) found that the life cycle time for *M. javanica* at 14.3°C was 56 days and 21 days at 26.1°C.

There is general agreement that *Meloidogyne* species damage is greater in sandy soils than in soils with a large percentage of clay. In Arizona, heaviest infestations of *M. incognita* occurred on coarse-textured soils (O'Bannon & Reynolds, 1961). Also in China the incidence and severity of *M. arenaria* on peanut was found to be related to soil texture (Zhang, 1985).

Soil moisture is necessary to sustain all activities of *Meloidogyne* spp. In moist soils, of 40–60% of field capacity, juveniles are active and move through the soil in water films. In dry soils they become inactive and die through desiccation (Van Gundy, 1985). In wet soils, hatching may be inhibited and juvenile movement slowed by lack of oxygen. Baxter and Blake (1969) found that all activities of *M. javanica* increased as oxygen concentrations increased from 0.2 to 21% and concluded that a favourable environment would be provided when moist soils drain rapidly and allow oxygen concentrations to increase above 10%. Zhang (1985) reported that *M. arenaria* is less serious in low fields that have a high water table than in well drained fields. Also, *M. arenaria* is less serious on peanut that follow a flooded crop than in fields that are not flooded. In controlled temperature studies, Vrain (1978) found that infectivity of *M. incognita* and *M. hapla* were lower after having been exposed to temperatures ranging from 20°C to –8°C in saturated soil than when exposed to these temperatures in soil at 51 cm moisture tension.

Meloidogyne species survive, hatch and reproduce over a wide pH range. If the soil pH is in the range favourable for plant growth the nematodes are active (Wallace, 1971).

The addition of organic amendments to the soil reduced the severity of *M. arenaria* on peanut (Zhang, 1985).

Disease complexes

Garcia and Mitchell (1975*a*) observed synergistic interactions in the incidence of pod rot of peanut when *Pythium myriotylum* was combined with *Fusarium solani* or *M. arenaria*, or a combination of both pathogens. Garcia and Mitchell (1975*b*) also reported that a combination of *P. myriotylum* and *M. arenaria* resulted in a significantly greater percentage of damping-off of peanut seedlings than the sum of the effects of the pathogens separately. Peanut plants inoculated with 2 g and 4 g of *F. solani* mycelia mat per pot plus 1000 to 2000 *M. arenaria* wilted sooner after inoculating than when *F. solani* was used alone (Patel *et al.*, 1985). Results of a two-year study in 25 cm clay pots indicated that the presence of *M. arenaria* had no effect on the incidence of *Aspergillus flavus* (Lk.) Fr. in peanut seeds (Minton & Jackson, 1967). However, one year the incidence of *A. flavus* was greater in shells of plants inoculated with both organisms than with only *A. flavus*. In a microplot study,

the incidence of *A. flavus* was greater in seeds of plants inoculated with *A. flavus* and *M. hapla* than in seeds of plants inoculated with only *A. flavus* (Minton *et al.*, 1969*a*). Aflatoxin was not detected in seeds of any treatment and was present in only one shell sample each of *A. flavus* or *A. flavus* plus *M. hapla* inoculated plants.

In greenhouse studies, Diomandé and Beute (1981*a*) demonstrated that cylindrocladium black rot (CBR) of peanut caused by *Cylindrocladium crotalariae* was increased in the presence of *M. hapla* on CBR-susceptible Florigiant and CBR-resistant NC 3033 cultivars. In field experiments, there was a significant positive correlation between final populations of *M. hapla* and *C. crotalariae* and CBR indicating that *M. hapla* affected CBR development (Diomandé & Beute, 1981*b*). Diomandé *et al.* (1981) also found that two populations of *M. arenaria* enhanced development of CBR on the CBR-resistant peanut, NC 3033 cultivar.

Economic importance and population damage threshold levels

Information on the economic importance of *Meloidogyne* species on peanut is unavailable in many areas of the world. Yield loss estimates for the individual species is difficult because damage is seldom confined to a single nematode species (Sasser *et al.*, 1970; 1975*a*).

In Georgia, Motsinger *et al.* (1976) found that 9.7% of the fields surveyed in seventeen counties were infested with *M. arenaria* or *M. hapla*. In eleven counties in Alabama, Ingram and Rodríguez-Kábana (1980) found 41.4% of the fields surveyed infested with *Meloidogyne* species. Twenty-six percent of the 127 fields surveyed or 15.5% of the 343 soil samples examined from five counties surveyed in Texas were infested with *Meloidogyne* species (Wheeler & Starr, 1987). At least 10% of the survey samples were estimated to have root-knot nematode population densities of 44–83 *M. arenaria*/500 cm^3 soil, exceeding that necessary for a 10% yield loss.

Losses in infested fields may exceed 50%, however, infestations are usually unevenly distributed and losses may average less than 50%. Recently, estimated production losses due to *M. arenaria* in major peanut-producing states of the USA ranged from 0.5% in Oklahoma to 5.4% in Alabama (Anon., 1987). Losses for *M. hapla* ranged from 0.3% in Georgia to 4.7% in North Carolina. Sasser (1979*b*) reported that the estimated peanut losses due to *Meloidogyne* species in West Africa and Southeast Asia was 15%.

In the Punjab State of India, *Meloidogyne* spp. juveniles were present in eleven peanut soil samples out of 28 examined from Ludhiana, seven out of twenty from Sangrur and eight out of twelve from Patiala districts (Sakhuja & Sethi, 1985*c*). *Meloidogyne* species were also found in Jalandhar and Kapurthala districts. Galling on peanut due to *Meloidogyne* spp. was noted in 22 locations of the 70 locations sampled. Ibrahim and El-Saedy (1976*a*) found that 65% of the 146 soil and root samples collected from declining peanut in Egypt contained *Meloidogyne* spp. *Meloidogyne javanica* was the dominant species with *M. arenaria* present in a few of the root samples. Singh (1972) reported that nine out of twelve soil samples collected around peanut plants in Guyana contained *Meloidogyne* spp.

Meloidogyne arenaria was reported to be a major disease of peanut in China (Zhang, 1985). *M. arenaria* occurs primarily in the southern area of the peanut production region and *M. hapla* in the northern area (Yang Baojun, pers. comm.). Investigations revealed that 61% of peanuts grown on 6200 ha in Leizhou Peninsula were infected with *M. arenaria* (Zhang, 1985).

In India, Sakhuja and Sethi (1985*b*) found that peanut plants grown in pots were stunted when inoculated with one *M. javanica* egg per cm^3 soil. A reduction of 27.3% in shoot length and 54.6% of dry shoot weight was obtained when plants were inoculated with eight eggs per cm^3 soil. The commonly used extraction procedures do not recover *Meloidogyne* eggs from the soil (Garcia, 1976; Rodríguez-Kábana *et al.*, 1986). Therefore, population evaluations for research and advisory purposes are usually based on numbers of juveniles in the soil. Population levels of *M. arenaria* juveniles in the soil in southeastern United States at planting time are usually relatively low and damaging populations may be near undetectable levels (Fig. 5). Hence, population levels for grower

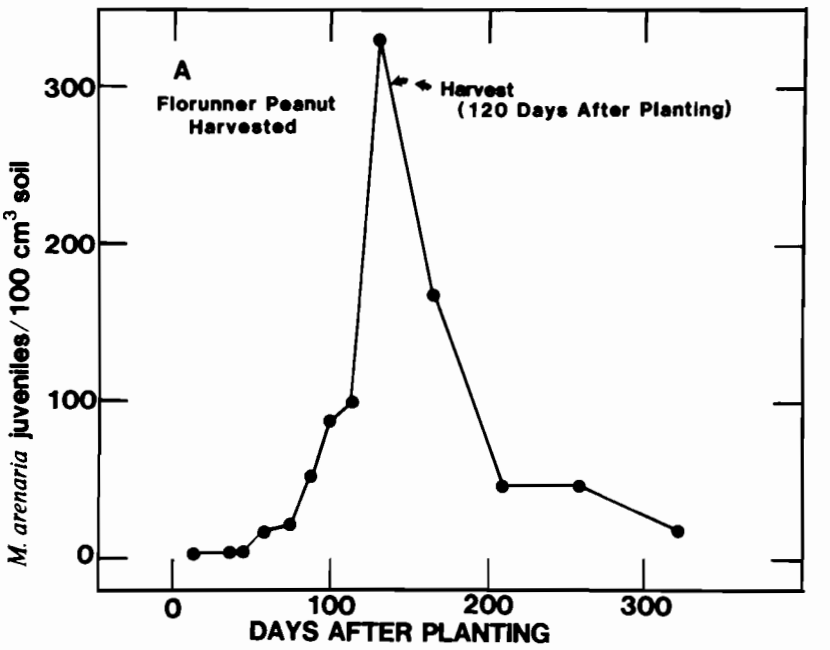

Fig. 5. Changes in the juvenile population of *Meloidogyne arenaria* during the peanut growing season and after harvest. (From Rodriguez-Kábana *et al.*, 1986.)

advisory purposes are usually determined as soon after harvest as practical rather than eight months later at planting.

In nematicide experiments, yields are usually negatively correlated with numbers of *Meloidogyne* juveniles in the soil. Regression analysis on data from 16 peanut experiments in Alabama indicated that yields were negatively related to numbers of *M. arenaria* juveniles in the soil determined near harvest (Rodríguez-Kábana *et al.*, 1982*b*).

On the basis of a linear regression model, Rickard *et al.* (1977) determined that peanut yield loss in microplots was 8.6% for each ten-fold increase in initial population of *M. hapla* juveniles in the soil.

Wheeler and Starr (1987) reported a significant negative relationship between initial populations of *M. arenaria* in microplot tests and peanut yields. A linear model estimated a 10% yield loss with initial populations of 44 to 83 eggs and juveniles per 500 cm^3 soil. Dhruj and Vaishnav (1981) found that 1000 *M. arenaria* juveniles per kg of soil caused a reduction of peanut plant shoot growth, shoot weight and root length of 23.9%, 33.1% and 31.9%, respectively.

Control measures

Control of *Meloidogyne* species may be necessary in some fields for profitable peanut production but not in others. Therefore, each field should be evaluated based on the history of nematode damage to peanut, the other crops growing in rotation with peanut, and the present nematode population level. Based on a survey, Motsinger *et al.* (1976) estimated that only 26.6% of the peanut fields in Georgia would respond to nematicides. However, this should not be interpreted to imply that other control measures such as rotations and cultural practices should not be considered in the remainder of the peanut production area. Preventing the development of a nematode problem may be more economical than managing the nematode once the problem develops.

Fig. 6. A peanut field in North Carolina infested with *Meloidogyne hapla*. Left, after cotton; right, after soybean. (Photo: J. N. Sasser).

Cultural practices

Rotations that include plants resistant to *M. arenaria, M. hapla* and *M. javanica* can be effective in reducing the damage to peanut caused by these nematodes (Fig. 6). When the cash value for peanut is low, this may be the only control method that can be used profitably.

Sasser (1954) published a susceptibility rating for a number of plants to *M. incognita, M. incognita* var. *acrita, M. javanica* and *M. arenaria*. In this publication he showed that peanut is susceptible to *M. arenaria* race 1 and *M. hapla*, but resistant to *M. incognita, M. javanica* and *M. incognita* var. *acrita*. However, subsequent research by Martin (1958) showed that some populations of *M. javanica* parasitize peanuts. Sasser listed a number of plants resistant to *M. arenaria* and *M. hapla* that were used effectively in rotation with peanut when one or more of these species is present. Since the pioneer research of Sasser (1954), many additional plants were found resistant to one or more *Meloidogyne* species.

A recently published check list (Sasser & Kirby, 1979) of crop plants listing over 450 cultivars in thirteen botanical families reported to carry resistance to at least one *Meloidogyne* species may serve as a useful guide for selecting cultivars to grow in rotation with peanut. In addition, Cheng *et al.* (1981), reported seven crop plants of thirty tested resistant (non-host) to *M. arenaria* in Taiwan. Care must be exercised in selecting cultivars to rotate with peanut because all cultivars of a crop do not respond the same. Maize (*Zea mays* L.) is an example of a crop that was for a long time considered an excellent rotational crop with peanut. But in recent years, some cultivars have been shown to support relatively high populations of *M. arenaria* and *M. javanica* (Baldwin & Barker, 1970; Norse, 1972). Conversely, most cultivars are resistant to *M. hapla* (Sasser, 1954; Baldwin & Barker, 1970).

Rodríguez-Kábana and Touchton (1984) in Alabama obtained a reduction of *M. arenaria* juveniles in sorghum (*Sorghum vulgare* Pers.) or maize to levels 10–20 times below those in peanut. Cotton effectively reduced *M. arenaria* population levels and yields of peanut planted after one year of cotton were significantly greater than yields in plots grown to peanut the previous year (Rodríguez-Kábana *et al.*, 1987). Rodríguez-Kábana and Morgan-Jones (1987) also found that sesame (*Sesamum indicum* L.), castor bean (*Ricinus communis* L.), joint vetch (*Aeschynomene indica* L.), partridge

peas (*Cassia fasiculata* Michx.), hairy indigo (*Indigofera hirsuta* L.) and bahiagrass (*Paspalum notatum* Flügge) are promising crops for managing *M. arenaria* in peanut.

Rotational crops recommended for *Meloidogyne* management on peanut in the United States varies with the nematode species present, cultivar of rotational crop, etc. Among the rotational crops that have been suggested by the various State Cooperative Extension Service specialists are cotton, maize, small grains and pasture grasses (Bailey, 1988; Dunn, 1988; Hagan, 1988). Maize is also a recommended rotational crop for managing *M. hapla* on peanut in Queensland Australia (Broadley, 1981; Vance, 1981).

Usually long rotations of three or more years out of peanut and other host crops are better than one- or two-year rotations. Rotations should not be expected to abruptly reduce root-knot nematode populations since 1) some nematodes of a population will survive the winter without a host, 2) the most "resistant" crop plant may support at least a low nematode population, and 3) most cultivated fields have at least a few weeds that are good hosts for nematode reproduction. Therefore, rotations should maintain population densities at low levels and reduce high population densities (Dunn, 1988).

Where practical, crop rotations in conjunction with flooding of the soil may effectively reduce damage due to *Meloidogyne* species (Thames & Stoner, 1953; Zhang, 1985).

Rotating a winter small grain crop with peanut can help prevent growth of weeds that are hosts of peanut nematodes, however, since some small grain cultivars may also support low population levels if grown during warm weather, planting should be delayed until cool weather when nematode development and reproduction is reduced (Dunn, 1988).

Destruction of roots of host crops that precede peanut in a rotation to interrupt reproduction will reduce the potential for damage to peanut; turning the soil several weeks before applying nematicides and planting peanut encourages the decay of live plant roots that protect nematodes from their enemies or from nematicides that are applied to the soil (Dunn, 1988). Drying of the soil after it has been turned may reduce the nematode population (Zhang, 1985). Clean fallowing for long periods of time may also be effective.

In China (Zhang, 1985), growers who fertilize well, especially with organic fertilizers, have less *M. arenaria* damage to peanut than growers who use less fertilizer. *M. arenaria* is less serious in China (Zhang, 1985) in low lying areas that have high water tables than in well drained soils. This nematode is also less serious in China in irrigated than in non-irrigated fields.

Resistance and tolerance

Peanut cultivars resistant to *M. arenaria* race 1, *M. hapla*, and populations of *M. javanica* that attack peanut have not been developed. Edwards (1956) reported the cultivars Natal Common and Kumawu Erect to be highly resistant to a root-knot nematode. The species was not reported, therefore it probably was not *M. arenaria* or *M. hapla*. Miller and Duke (1961) reported that a peanut of "a foreign introduction with a purple skin" resistant to *M. arenaria*, but Miller (1972*b*) later reported no resistance to the nematode in 2000 peanut introductions in field plots in Virginia. In greenhouse tests, Minton and Hammons (1975) and Holbrook *et al.* (1983) did not find a high level of resistance to *M. arenaria* among a total of 805 peanut entries. Recently Baltensperger *et al.* (1986) reported resistance to *M. arenaria* in another *Arachis* species, *A. glabrata* Benth., that may provide resistance to transfer to *A. hypogaea* should technology become available for making wide interspecific crosses.

Castillo *et al.* (1973*a*) reported resistance to *M. hapla* in four introductions of unidentified wild *Arachis* spp. and only moderate susceptibility in eight *A. hypogaea* entries. Also, Subrahmanyam *et al.* (1983) reported a wild *Arachis* sp. resistant to *M. hapla*. Sakhuja and Sethi (1985*a*) reported resistance to *M. javanica* in four cultivars.

Chemical control

Chemicals are one of the major means of controlling nematodes including *M. arenaria, M. hapla, Belonolaimus longicaudatus, Pratylenchus brachyurus* and other nematodes in peanut in the United

Fig. 7. A peanut field in Georgia infested with *M. arenaria*. Left, untreated; right, treated with phenamiphos at the rate of 2.8 kg a.i./h.a.

States (Fig. 7). The two general types of materials that have been effective are fumigants and non-fumigants that have systemic and/or contact properties.

Formulations of fumigants containing DD, I,3-D, EDB and DBCP were the first nematicides to be used to control nematodes of peanut (Miller, 1951; Good *et al.* 1958; Miller & Duke, 1961). DBCP was the principal nematicide for use in peanut in the United States during the 1960's and remained so until 1978 when it was suspended by the U. S. Environmental Protection Agency. There was increased use of EDB after the suspension of DBCP until 1983 when EDB was also suspended.

Manufacturers of DD withdrew this material from the market. The less hazardous 1,3-D, that contains only 1,3-dichloropropene as the active ingredient, is still available and is more effective than DD (Porter *et al.*, 1982). In recent years research has been conducted to determine more efficacious methods of applying 1,3-D. Rodríguez-Kábana *et al.* (1985) found that combination treatments of 1,3-D and aldicarb equalled or surpassed the performance of EDB treatments in increasing yields and controlling *M. arenaria* in peanut. There was some degree of phytoxicity in planting time application treatments of 1,3-D. Rodríguez-Kábana and Robertson (1987) later found that the efficacy of 1,3-D applied in the row preplant was dependent on the rates used and depth of application. Minton and Csinos (1986) obtained significant peanut yield increases when 1,3-D was applied in the mouldboard plow sole at rates as low as 41.7 kg ai/ha.

Several non-fumigant compounds having both nematicidal and insecticidal properties were introduced in the late 1950's (Dickson & Smart, 1971; Minton & Morgan, 1974; Sasser *et al.* 1975*b*). Materials such as ethoprop and fensulfothion are contact nematicides with no significant systemic properties. Other materials, such as aldicarb, carbofuran, oxamyl and phenamiphos kill by direct contact or are absorbed by plants and the parent compound or some metabolite in the plant are nematicidal. A number of additional compounds, some of which are used primarily as insecticides, have been found to have nematicidal properties but are usually less effective for nematode control on peanut than those listed above (Dickson & Smart, 1971; Minton & Morgan, 1974; Sasser *et al.*, 1975*b*).

The nonfumigant nematicides have been evaluated for the control of most major peanut nematodes under various cultural conditions. Much of the research with these materials has been done in the United States (Minton & Morgan, 1974; Dickson & Waites, 1978, 1982; Rodríguez-Kábana

Fig. 8. Liquid and granular applicators for applying non-fumigant nematicides mounted on tractor drawn rototiller for incorporating (Photo: A. W. Johnson).

et al., 1981, 1982*a*; Minton *et al.*, 1984; Rodríguez-Kábana & King, 1985); however, some research with these compounds has also been done in India (Singh & Sakhuja, 1984), Australia (Colbran, 1968; Broadley, 1981) and China (Zhang, 1985).

Generally, the non-fumigant nematicides are preferred over the fumigants because of their simplicity of application. Depending on the formulation used, they can be sprayed or applied in an 18–23 cm wide band over the row with a granular applicator mounted on a rototiller or on the planter equipment (Fig. 8). Incorporating these materials five to seven cm deep or less is preferred over deeper incorporation (Rodríguez-Kábana & King, 1979).

Methods of diagnosis

Sampling

Diagnosing *Meloidogyne* damage on peanut can best be done by periodic field observations and root and pod examination in conjunction with soil assays. Characteristic foliage symptoms and galling of underground plant parts may be detected. The type of galls on the roots and pods may be a useful indicator of the *Meloidogyne* species present (Sasser, 1954). Soil samples should be collected at or near harvest to determine the maximum population density. Root and pod samples for nematode extraction should also be collected late in the growing season.

Bioassays to establish the level of infestation (Ingram & Rodríguez-Kábana, 1980) may be useful if samples are collected during the winter or early spring when population levels are low.

Extraction

Meloidogyne juveniles and eggs may be extracted from soil and roots using standard laboratory procedures (Chapter 2). Adult females may be excised from root or pod tissues to be examined to assist with species identification.

Determining relationship of populations to crop loss

A measure of nematode involvement in peanut yield loss may be determined by correlating numbers of *Meloidogyne* juveniles per unit of soil or root-knot nematode indices with yield in nematicide treated and untreated soil. Negative relationships were found between yield and the initial soil population density of *M. hapla* (Rickard *et al.*, 1977) and *M. arenaria* (Dhruj & Vaishnav, 1981; Wheeler and Starr, 1987) as well as the final population denisty of *M. arenaria* in the soil (Rodríguez-Kábana *et al.*, 1982*b*). Root-knot nematode indices at harvest were correlated with yield for *M. arenaria* and *M. hapla* (Minton & Morgan, 1974). Models that will predict yield losses for a wide range of environmental conditions are not available.

Pratylenchus brachyurus

Pratylenchus brachyurus is the major lesion nematode parasitizing peanut. It is distributed chiefly in the warmer zones of the world (Loof, 1964). Steiner (1949) first reported *P. brachyurus* on peanut in Alabama, USA in 1942. *P. brachyurus* is now known to parasitize peanut in most of the peanut producing states in the USA. It has also been reported on peanut in several other countries of the world including Egypt (Oteifa, 1962), Australia (Colbran, 1968) and Zimbabwe (Anon., 1973). Also, *P. coffeae* was reported parasitizing peanut in India (Chabra & Mahajan, 1976).

Symptoms of damage

Lesion nematodes are migratory endoparasites that attack peanut roots, pegs and pods and feed within the parenchymatous tissues. Steiner (1945) and Boyle (1950) described conspicuous lesions on the pods of peanut infected with *P. brachyurus*. Good *et al.* (1958) later reported *P. brachyurus* in roots and pegs, as well as shells of mature pods, but indicated that nematodes were more numerous in the shells, where they colonize in dark-coloured necrotic lesions (Fig. 9, Plate 6D. Colbran (1968) indicated that *P. brachyurus* produces lesions on the underground portion of the stem, as well as on the roots, pegs and pods. Several hundred nematodes may colonize a single lesion and may

Fig. 9. Lesions on peanut caused by *Pratylenchus brachyurus* (Photo: T. E. Boswell).

include all developmental stages. Infected peanut roots develop lesions and with high population densities, these lesions coalesce and cause extensive discolouration and damage that result in slight stunting with unthrifty, yellow-green foliage and reduced root system and pod weight (Miller & Duke, 1961; Boswell, 1968).

In experiments conducted in sterilized soil inoculated with sterile *P. brachyurus*, Boswell (1968) found that unstained cells of peanut shells adjacent to the nematode or through which the nematode had passed had a slight tan to brownish granular appearance. Boswell (1968) characterized lesions on unstained shell tissue free of fungal mycelia by small black pin point to pin head size spots on the shell surface and usually near the center of the lesion with the remainder of the lesion having a somewhat lighter appearance as though the colour faded out into the surrounding tissue. Close examination of these lesions revealed that the colour was due primarily to necrotic parenchyma tissue. The margins of these lesions were not distinctly outlined as were lesions caused when *Rhizoctonia solani* was present. Lesions infected by both organisms were described as appearing rough and more like a scurf with brownish to black discolouration of the surface in the necrotic areas. These lesions have a definite margin even though the shape of the lesion may be irregular. An occasional lesion infected with both *P. brachyurus* and *R. solani* had a slightly raised dark centre and microscopic examinations revealed the presence of sclerotia. The symptoms of *P. brachyurus* damage on peanut shells grown in the field differ slightly from that described by Boswell (1968). Good *et al.* (1958) found that lesions on mature shells were "purplish-brown" and could be distinguished from lesions caused by soil microbial decomposition by their darker colour and distinct boundaries which did not fade gradually into the healthy surrounding tissue, as with microbial decomposition. Miller and Duke (1961) stated that severely infected pods grown in the field had small, brown lesions giving them a speckled appearance. They also stated that fungi and bacteria attack dead tissue of the peg and fruit and, under certain conditions, cause peg rot and seed decay. Reaction differences noted by the various researchers may be related to differences of infecting microorganisms, type of peanut or cultivar. Good *et al.* (1958) noted that lesions were less conspicuous on Virginia-type peanut than on Spanish and Runner types. Minton *et al.* (1970) found that lesions were not as conspicuous on pods of Virginia Bunch 67 and Georgia 186–26 (Virginia type) as on Florunner, Early Runner (Runner type), Argentine and Starr (Spanish type). All cultivars were equally infected by *P. brachyurus* as determined by the number of nematodes recovered from shells and pegs. *P. brachyurus* feeding within the pegs weakens them resulting in pod loss at harvest (Good *et al.*, 1958; Boswell, 1968; Jackson & Sturgeon, 1973). Good *et al.* (1958) reported that the microorganisms that colonize damaged pods may penetrate the shell and damage the seed, thus the yield, as well as quality and value of the crop may be reduced.

Survival and means of dissemination

P. brachyurus infects roots, pegs, and pods of peanut and, because it is able to withstand extremes in temperature and moisture, it may survive in the Southeastern USA in these dead tissues during the winter (Graham, 1951; Good *et al.*, 1958; Feldmesser & Rebois, 1965). In South Africa, Keon (1967) working with potato and maize, found that at the end of winter 66.1% of *P. brachyurus* were found in the soil organic matter although the organic matter constituted only 0.29% of the soil. Boswell (1968) recovered *P. brachyurus* from peanut shells that were stored at 24°C for three, six and 28 months. *P. brachyurus* is a polyphagous nematode and may survive and overwinter in live roots of many winter crops and weeds as well as in dead tissues.

P. brachyurus may be disseminated in many of the same ways as *Meloidogyne* species. Since this is a migratory parasite and attacks most underground plant structures, it can be transported in infected roots and other underground plant parts in the soil. Generally, the major method of spread is by human activity involving movement of plant material, soil and tillage equipment. Peanut shells used as mulch or ground and used as diluents in certain preparations may carry the live nematodes (Good *et al.*, 1958; Colbran, 1968). Also, water movement across the field as the result of either rainfall or irrigation may transport the nematode.

Environmental factors affecting parasitism

The distribution and parasitism of *P. brachyurus* is temperature related and it is restricted to the warmer zones of the world (Loof, 1964). Boswell (1968) found in controlled temperature studies that reproduction in root and shell tissue of peanut was greatest at 26°C. Soil types may also affect the parasitism of peanut by *P. brachyurus* (Endo, 1959; Boswell, 1968).

Soil moisture affected reproduction of *P. brachyurus* on peanut (Good & Stansell, 1965). Approximately ten times more nematodes were recovered from shell tissue of irrigated than from non-irrigated peanut.

Disease complexes

Good *et al.* (1958) suggested the possibility of a disease complex involving *P. brachyurus* and soil microorganisms that would produce a peg rot. They frequently found *P. brachyurus* and *Sclerotium rolfsii* occurring together as pathogens. Boswell (1968) found lesions of peanut pods to contain both *P. brachyurus* and mycelium of fungi, most notably *Rhizoctonia solani, Fusarium* spp. and *Penicillium* spp.

There is some indication that presence of *P. brachyurus* is related to an increase of *Aspergillus flavus* in peanut shells but not in seeds (Jackson & Minton, 1968). Jackson and Sturgeon (1973) reported that the lesion nematode feeds on the peanut root, pod, and peg, allowing fungi and bacteria to enter damaged cells, causing a peg and pot rot. They stated further that the peg is weakened or rots away and allows the mature pod to shed or to be lost during harvest.

Economic importance and population damage threshold levels

P. brachyurus damage often is overlooked. Consequently, damage estimates for this nematode may be low since it has been reported in a large percentage of the peanut production areas in the USA and in other countries.

Minton *et al.* (1963) reported *Pratylenchus* spp. in 37% of the peanut fields sampled in Alabama, USA. In a later survey Ingram and Rodríguez-Kábana (1980) found them in 83.9% of the Alabama fields they surveyed. Alexander (1963) found *P. brachyurus* spp. in two out of fourteen fields surveyed in South Carolina, and Motsinger *et al.* (1976) reported them in 16.9% of the 331 fields surveyed in Georgia. Wheeler and Starr (1987) found *P. brachyurus* in 15.7% of the samples collected from peanut fields in a five county survey in Texas. Severe damage to peanut by *Pratylenchus* spp. has also been reported in Florida (Dickson & Smart, 1971) and Arkansas (Jackson & Sturgeon, 1973). In Egypt, Oteifa (1962) found *P. brachyurus* in 81.2% of the peanut fields, but in a later survey, Ibrahim and El-Ṣaedy (1976*a*) found them in only 9.6% of their samples. *P. brachyurus* occurs in peanut fields in a variety of soils in South Burnett, Australia (Colbran, 1968); it is also widespread throughout Atherton Tablelands in North Queensland, Australia and was absent only in soils that had recently been brought into cultivation (Broadley, 1981). Singh (1972) found *Pratylenchus* spp. in 50% of the samples collected from peanut fields in Guyana.

Production losses due to *Pratylenchus* spp. were estimated for several states in the USA (Anon., 1987). The percentage losses for the various states was as follows: Alabama, 0.1%; North Carolina, 0.5% for 1984 and 0.25% for 1985; Texas, 2.0% and Virginia, trace.

Population damage thresholds for *P. brachyurus* have not been well defined. Numbers of *P. brachyurus* per g of shell have been correlated with yield (Good *et al.*, 1958; Boswell, 1968; Minton & Morgan, 1974). Boswell (1968) obtained significant yield increases in fumigant nematicide treated plots in which there were 242 or less *P. brachyurus* per g of shell compared to the untreated plots that had 2771 per g of shell. Minton and Morgan (1974) obtained a significant yield increase in fumigated plots in which there were 127 *P. brachyurus* per g of shell compared to 2280 per g of shell in untreated plots.

Control measures

Peanut yield losses due to *P. brachyurus* is relatively small in relation to the amount of infested area. Hence, control of this nematode in peanut has not been practiced extensively except in certain areas that have severe infestations and crop losses.

Cultural practices

Generally, crop rotations for control of *P. brachyurus* in peanut are not effective because of the wide host range of crops and weeds and because there are few alternative cash crops for use in rotations with peanut (Endo, 1959; Koen, 1967; Porter *et al.*, 1984).

Good *et al.* (1954) found that population levels of *P. brachyurus* were greater in maize than in peanut in a maize-peanut rotation. *P. brachyurus* were also present in the soil in rotations that included lupine (*Lupinus hirsutus* L.), oats (*Avena sativa* L.) and native grass cover but greater numbers were present in lupine than in oats and native grass (Good *et al.*, 1954). Brodie and Murphy (1975) in U.S.A. found that fallowing for six weeks (May-June) or nine months (May-March) reduced populations of *P. brachyurus* in the soil to zero or near zero.

Good *et al.* (1958) observed that timely harvesting removed more *P. brachyurus* infested pods from the field than late harvesting, hence fewer nematodes were left in the soil to infect subsequent crops. Boswell (1968) also found that timely harvesting increased yield and value of peanuts compared to late harvesting. Good and Stansell (1965) reported that the larger yields from *P. brachyurus* infested soil were from irrigated peanut grown in fumigated soil and harvested earlier than normal for non-irrigated peanut. Although, irrigated peanut yielded more, *P. brachyurus* were ten times more numerous in shell tissue in irrigated than in non-irrigated plots.

Resistance

No commercial peanut cultivar possesses useful levels of resistance to *P. brachyurus*. Minton *et al.* (1970) reported six cultivars of peanut to be equally infected with *P. brachyurus*, but lesion symptoms were not as conspicuous on two of them. Smith *et al.* (1978) reported resistance in two plant introductions, PI290606 and PI295233. Starr (1984) later confirmed their findings and reported an additional resistant plant introduction, PI365553.

Chemical

Severe infestations of *P. brachyurus* can reduce yields by as much as several hundred kilograms per hectare. Where severe infestations occur, chemical treatments may be justified. Nematicides that control *Meloidogyne* species also control *P. brachyurus* (Good & Stansell, 1965; Boswell, 1968; Jackson & Sturgeon, 1973; Minton & Morgan, 1974).

Methods of diagnosis

Sampling

Assays of both soil and subterranean plant parts should be made to assess population levels of *P. brachyurus*. Soil samples should be collected with a large sampling tube (5.0 cm ID) in order to also obtain roots. Alternatively, one may collect soil samples with a smaller sampling tube and collect peanut pods from several plants at harvest and assay shells. Shells usually yield more *P. brachyurus* per unit weight of tissue than roots. Soil samples should be collected shortly before or after harvest when soil populations are greatest. Bioassays to establish the level of infestation (Boswell, 1968) may be useful if samples are collected during the winter or early spring when population levels are low.

Extraction

P. brachyurus adults and juveniles may be extracted from roots by incubating roots in a mist chamber and from soil using standard laboratory procedures (Chapter 2).

Belonolaimus longicaudatus

The sting nematode, *Belonolaimus longicaudatus*, occurs in sandy soils along the Atlantic Coastal Plain from Connecticut and New Jersey to Florida and Westward to Texas, Oklahoma, Arkansas, and Kansas in the United States. Although *B. longicaudatus* has been associated with peanut in most of the peanut-producing states (Owens, 1951; Holderman, 1955; Rau, 1958; Wheeler & Starr, 1987), loss estimates were reported for only Virginia, North Carolina and Oklahoma (Anon., 1987). Cooper *et al.* (1959) reported that *B. longicaudatus* was known to be distributed in sixteen counties in North Carolina with eight of these being major peanut producing counties. In Virginia, *B. longicaudatus* is a serious problem in less than 5% of the peanut fields (P. M. Phipps, pers. comm.). *B. longicaudatus* has not been reported on peanut outside the United States.

Symptoms

B. longicaudatus feeds ectoparasitically at root tips and along the sides of succulent roots as well as on young pegs and pods. Small necrotic lesions may be observed on the roots, pegs and pods (Owens, 1951). Esser (1976) reported that, shortly after being fed up on, root tips swell slightly and some asymmetric recurving occurs. Heavy infestations may cause gnarled and stubby lateral roots

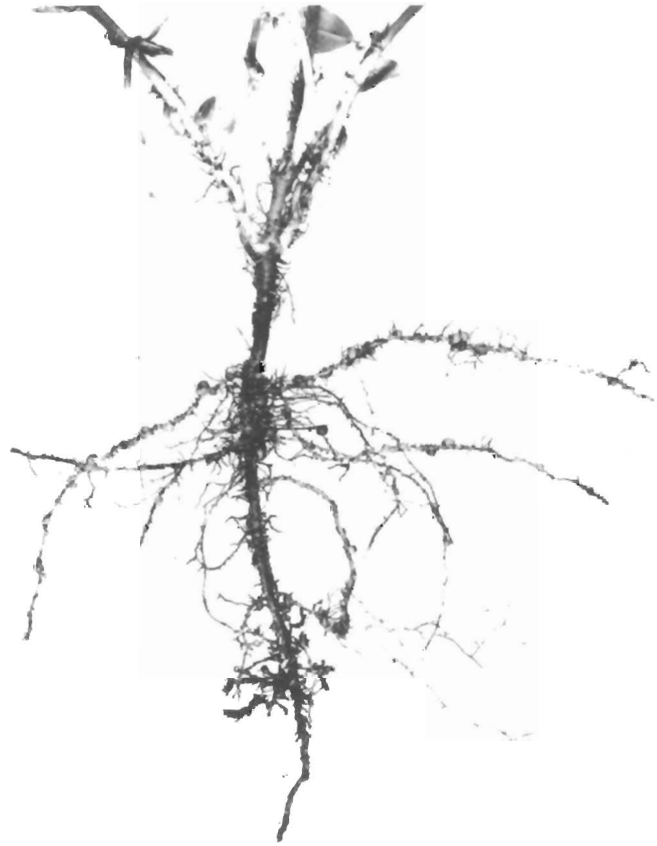

Fig. 10. Peanut plant with root system greatly reduced by *Belonolaimus longicaudatus* (Photo: J. N. Sasser).

and frequently only the taproot is left (Owens, 1951) (Fig. 10). Above ground symptoms include stunting and chlorosis. Peanut growth may be uneven in heavily infested fields and erratic stands may occur. Yield and quality of peanut may be severely reduced.

Biotypes

Rau (1958) described *B. longicaudatus* from Florida and suggested that it was probably the common sting nematode of the southeastern United States. Since Rau's publication, *B. longicaudatus* has been the species referred to most often on peanut. More recent investigations suggest that there are several pathotypes of physiological races or, perhaps, species. This nematode has been reported to be pathogenic on peanut in North Carolina and Virginia (Owens, 1951; Cooper *et al.*, 1959), but not in Georgia (Good, 1968). A population of *B. longicaudatus* from Gainesville, Florida did not cause damage or reproduce well on peanut, whereas a population from Sanford, Florida did (Perry & Norden, 1963).

Robbins and Hirschmann (1974) compared three populations of *B. longicaudatus* from each of Georgia and North Carolina and concluded that the Georgia and North Carolina nematodes were of different species and that neither were *B. longicaudatus* as described by Rau (1958). Their conclusions were based on differences in host range, morphology, and apparent infertility of inter-population offspring (Robbins, 1972; Robbins & Barker, 1973). However, the systematics have not yet been revised.

Survival and means of dissemination

The limited distribution of *B. longicaudatus* suggests that certain biological and environmental restraints affect its dispersal. Research results suggest that soil texture, soil temperature and soil moisture are critical to his reproduction (Perry, 1965; Robbins & Barker, 1974). *B. longicaudatus* can be readily established in new areas that have the required environmental conditions. It may move from one location to another by any means that will transport infested soil such as farm equipment, animal feet, water and transplants to which soil is attached.

Environmental factors affecting parasitism

The limited distribution of *B. longicaudatus* suggests that its ecological requirements may be very specific. Thames (1959) postulated that fine-textured soil inhibits its movement and reproduction. In Virginia, Miller (1972*a*) found *B. longicaudatus* only in the "A"-horizon of soils with a sand content of 84–94%.

Soil temperature and moisture also affect the reproduction and survival of *B. longicaudatus*. Reproduction was greatest at 25–30 °C (Robbins & Barker, 1974) which agreed with results obtained by Perry (1965). Perry observed that reproduction was greater for *B. longicaudatus* at 29.4°C than at 26.7°C and was greatly reduced at 35°C. Boyd and Perry (1969) concluded that this nematode either died or migrated downward when soil temperature at 2.5 cm below the bare soil surface reached 39.5°C or higher. Robbins and Barker (1974) found the optimum soil moisture for reproduction to be 7%.

Economic importance and population damage threshold levels

Economic losses for peanut in the USA due to *B. longicaudatus* are not great despite the extreme damage this nematode inflicts. Losses due to this nematode have been reported for only North Carolina (0.30%), Oklahoma (0.25%) and Virginia (0.50%) (Anon., 1987). Yields were increased as much as 400% in North Carolina (Cooper *et al.*, 1959) in nematicide treated plots compared to untreated soil in which the average population density of *B. longicaudatus* was approximately 50 per 473 cm^3 of soil from 9 June to 30 October. Sasser *et al.* (1960) also in North Carolina, obtained a yield increase of 109% with a nematicide in soil in which population levels ranged from 135 to 205 per 473 cm^3 soil in the untreated control during the growing season.

Fig. 11. A peanut field in North Carolina infested with *Belonolaimus longicaudatus*. Centre row was untreated; rows to right and left of centre were treated with different nematicides (Photo: A. W. Johnson).

Control measures

No commercial peanut cultivar is resistant to *B. longicaudatus*. The nematode has a wide host range and only a few crop plants such as small grain, tobacco (*Nicotiana tabacum* L.) and watermelon (*Citrullus vulgaris* Schrad.) have reduced population densities when grown in rotation with peanut (Holdeman & Graham, 1953; Bailey, 1988). The use of nematicides is the major means of control (Fig. 11). Both fumigant and non-fumigant nematicides have given excellent control and increased peanut yields (Cooper *et al.*, 1959; Sasser *et al.*, 1960; 1975*b*).

Methods of diagnosis

Sampling

Plant damage symptoms for *B. longicaudatus* may occur in the seedling stage of the peanut, especially if population levels are high. Examination of roots of seedlings for damage as well as assessment of population densities in the soil are recommended. Soil samples should be collected using procedures recommended for recovery of most ectoparasitic nematodes (Chapter 2).

Extraction

The extraction of *B. longicaudatus* from the soil may be done using one of a number of standard extraction procedures (Chapter 2).

Determining the relationship of populations to crop loss

The effects of *B. longicaudatus* on peanut is reflected in plant growth, yield and quality (Cooper *et al.*, 1959; Sasser *et al.*, 1975*a*). Significant negative correlations of number of nematodes in the soil with yield and growth may be obtained during most of the growing season.

Criconemella ornata

The ring nematode, *Criconemella ornata*, was first reported associated with peanut in Georgia (Boyle, 1950; Machmer, 1953). It is now known to occur in a large percentage of the peanut production regions of the United States (Minton *et. al.*, 1963; Alexander, 1963; Motsinger *et al.*, 1976; Ingram & Rodríguez-Kábana, 1980; Wheeler & Starr, 1987). *Criconemella* species have been reported in Burkina Faso (Germani & Dhéry, 1973), Egypt (Ibrahim & El-Saedy, 1976*a*) and Gambia (Merny *et al.*, 1974).

Symptoms

Machmer (1953) described a chlorotic condition of peanuts growing in Georgia in soil heavily infested with a species of *Criconemella* which he called "Peanut Yellows". Although he did not identify the species, it was probably *C. ornata*. Barker *et al.* (1982), reported that freshly extracted, greenhouse-grown inoculum caused the typical "Yellows disease" on peanut grown in microplots. As few as 178 freshly introduced *C. ornata*/500 cm^3 soil stunted peanuts. Roots, pods and pegs of peanut plants growing in microplots in soil heavily infested with *C. ornata* were severely discoloured with brown necrotic lesions (Fig. 12) (Minton & Bell, 1969). Small necrotic lesions were often superficial, but necrosis in large lesions usually extended deep into the tissues. Many lateral roots primordia and young roots were killed, resulting in reduced numbers of lateral roots. Pod yields from nematode-infected plants were reduced by about one-half.

Survival and means of dissemination

Information relative to factors affecting survival of *C. ornata* is limited. Little has been done to determine soil type preference, but survey results suggest it favours the lighter soils (Barker, 1974). Population levels decline rapidly in the presence of poor hosts. Since *C. ornata* is an ectoparasite,

Fig. 12. Lesions on peanut pods caused by *Criconemella ornata*. (From Minton and Bell., 1969.)

dispersal occurs primarily in soil transported on farm equipment, feet of animals, in water and in soil clinging to transplants.

Environmental factors affecting parasitism

The environmental factors affecting the parasitism of peanut by *C. ornata* has received little attention. Barker (1974) reported that the previous crop as well as geographic area in the state of North Carolina affected the occurrence and activity of *Criconemella* spp. The Coastal Plain, with warm, sandy soils, had a greater abundance of *Criconemella* spp. than the Piedmont and Mountain areas with soils that are cooler and contain more loam and clay. The frequencey of occurrence of *Criconemella* spp. on peanut (54%) was greater than for any other crop.

Disease complexes

Greenhouse studies in North Carolina revealed an interaction (enhancement of *Cylindrocladium* black rot, CBR) between *Cylindrocladium crotalariae* on CBR-susceptible Florunner but not on CBR-resistant NC 3033 peanut cultivars (Diomandé & Beute, 1981*a*). The severity of CBR on Florunner was increased when the density of *C. ornata* was 10^4 per 15-cm-diameter clay pot and *C. crotalariae* was 0.25 and 2.5 microsclerotia per cm^3 soil. Significant positive correlations between *C. ornata* and *C. crotalariae* and CBR indicated that this nematode can affect CBR development in the field (Diomandé & Beute, 1981*b*).

Economic importance and population damage threshold limits

Damage to peanut due to *C. ornata* in the field is subtle and low levels of damage may go undetected. Also, *C. ornata* is seldom present alone, but usually occurs in polyspecific communities. Therefore, losses due to *C. ornata* have not been well defined. Pod yield in a microplot experiment (Minton & Bell, 1969) was reduced by about one-half in heavily inoculated soil. In a field experiment in which the soil was infested with five genera of nematodes in addition to *C. ornata*, population densities of *C. ornata* were negatively correlated with peanut growth index and pod yield (Sasser *et al.*, 1975*a*).

Based on a linear regression model, Rickard *et al.* (1977) determined that peanut yield loss in microplots was 18.7% for each ten-fold increase in initial populations of *C. ornata* in the soil. Barker *et al.* (1982) found that as few as 178 *C. ornata*/500 cm^3 of soil in a microplot experiment caused a significant yield loss. In a second microplot experiment (Barker *et al.*, 1982), the *C. ornata* that reproduced the previous year on tobacco (a poor host) did not affect peanut yield. These researchers concluded that many of the nematodes present in the soil in the spring following tobacco may have been dead since tobacco is a poor host. Therefore, the previous host may affect the infectivity of the nematodes present in the soil resulting in an important problem for nematode advisory programmes.

Control

Since losses due to *C. ornata* have not been well defined, recommendations for control of this nematode when present as the primary pathogen are seldom made. Also, there is no known resistant commercial peanut cultivar. Certain crops such as cotton, soybean, corn and sorghum grown in rotation with peanut may reduce population levels (Good, 1968; Johnson *et al.*, 1974; Kinloch & Lutrick, 1975). Nematicides, both fumigant and nonfumigant, are effective against this nematode (Minton & Morgan, 1974).

Methods of diagnosis

Sampling

Evaluating soil population densities is the major means of diagnosing possible *C. ornata* damage to peanut. Soil samples should be collected using procedures recommended for recovery of ectoparasitic nematodes (Chapter 2).

Extraction

C. ornata may be extracted from the soil using one of several methods but the modified centrifuge-flotation method is, perhaps, the best for this nematode.

Determining the relationship of populations to crop loss

Even though *C. ornata* is a weakly, pathogenic nematode, negative correlations of population densities with yield and plant growth often suggest plant damage (Minton & Morgan, 1974; Sasser *et al.*, 1975*a*). Soil assays made early in the season (55–73 days after planting) may be more meaningful than assays made near harvest (Sasser *et al.*, 1975*a*).

Aphelenchoides arachidis

Aphelenchoides arachidis, the testa nematode, was described from northern Nigeria on peanut (Bos, 1977*a*; 1977*b*). It has been found at a significant level of infestation in only a limited area around Samaru. It was also found at a low level of infestation in peanut at Kadawa and in one peanut sample from Gwoza. It is not known to be a pest of peanut outside of Nigeria.

Symptoms

A. arachidis is a facultative endoparasite of peanut that parasitizes the tissues of the pods, testas, roots and hypocotyls, but not the cotyledons, embryos, or other parts of the plant (Bos, 1977*a*; Bridge *et al.*, 1977) (Fig. 13). Seed coats were discoloured when more than 2000 *A. arachidis*/testa were present (Bridge *et al.*, 1977) (Plate 6E). Heavily infested seeds, examined immediately after removal from fresh, mature pods, are a light brown, have translucent testas, and dark vascular strands within the testas. After infested seeds are dried, testas are often wrinkled and are darker brown than non-infested seeds (Plate 6E). Nematodes are found mainly in the sub-epidermal parenchymatous layer, and around the tracheids of the testa. Testas infested with *A. arachidis* are thicker and more uneven than normal testas. Nematodes are found in sub-epidermal parenchyma cells where walls are broken and cells enlarged. The epidermal layer of the seed coat is reduced in infested testas and the basal tissues, including the aleurone layer, is disorganized. Infested seeds of cultivar Spanish 205 weighed less than healthy seeds, but nematode damage had little effect on seed germination.

Biology and life cycle

A. arachidis is a facultative endoparasite of the seed, testa, pod shells, roots and hypocotyl of peanut (Bridge *et al.*, 1977). It has also been observed feeding ectoparasitically on roots and on two fungi, *Macrophomina phaseolina* and *Botrytis cinerea* associated with seeds on agar plates. *A. arachidis* were found in the parenchymatous tissues of the testa, root cortex and hypocotyl, but not in the central stele or vascular bundles (Bridge *et al.*, 1977). Pods had been invaded 10 days after the fruiting pegs had penetrated the soil, but numbers of nematodes in pods did not increase rapidly until after 30 days with largest numbers present at about day 60. All stages of the nematode, including eggs, were found throughout the testas, but at the end of the growing season, heavily infested testas of mature seeds contained mainly juvenile stages with few adults. Testas showing no external symptoms contained mostly adults and eggs, often arranged along the vascular elements of the seed coats.

Biotypes

Bos (1977*b*) suggested that there are two biotypes of *A. arachidis*, one occuring on cereals and one on both cereal and peanut.

Survival and means of dissemination

A. arachidis survived desiccation in stored peanut pods for 12 months (Bridge *et al.*, 1977). All juvenile stages were extracted from dried testas and shells with no particular stage predominating,

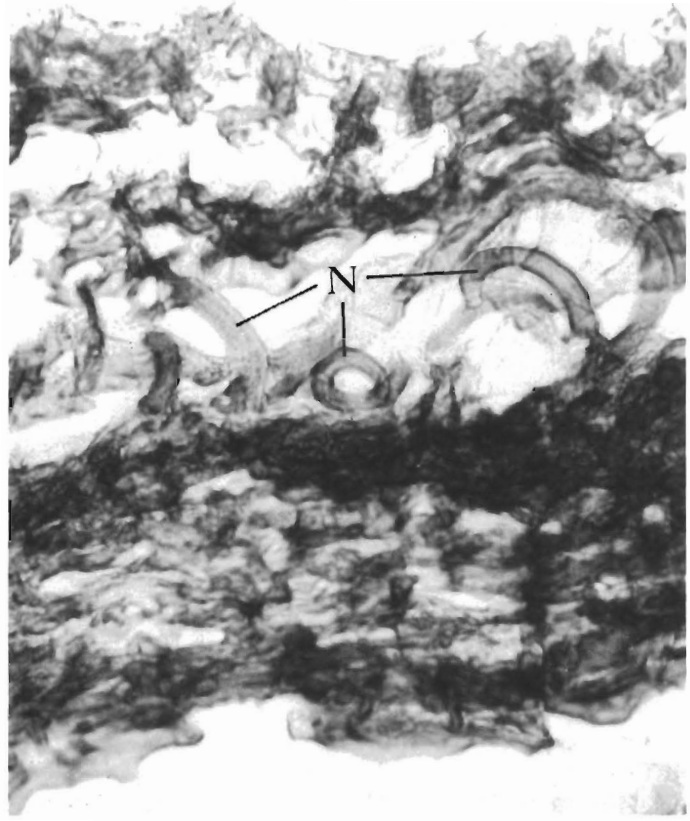

Fig. 13. Transverse section of peanut testa infected with *Aphelenchoides arachidis* (N = nematodes) (From Bridge *et al.*, 1977).

but adults were found alive only occasionally in either testas or shells of stored pods. No active nematodes were extracted from infested pods sun-dried in the field before storage. Volunteer plants in an infested field contained many adult nematodes suggesting that they continue to develop to maturity under natural conditions in pods left in the ground during the dry season in Nigeria. Unless appropriate precautions are taken, *A. arachidis* may become a serious pest world-wide since it can be disseminated in infested seeds (Bridge *et al.*, 1977).

Disease complexes

Aphelenchoides arachidis infestation of peanut seeds in field experiments predisposed seeds to invasion by fungi (McDonald *et al.*, 1979), Nematode infested seeds had higher levels of fungal infection (*Rhizoctonia solani, Sclerotium rolfsii, Macrophomina phaseolina* and *Fusarium* spp.) than the visually nematode-free seeds. Both rates of seedling emergence and total emergence were slightly lower for nematode-seeds than for clean seeds.

Economic importance and population damage threshold levels

A. arachidis devalues the confectionery peanut because it causes shriveled and discoloured seeds (Bridge *et al.*, 1977). Severe infestation of peanuts with *A. arachidis* not only has an adverse effect on the appearance and size of seed, but it may also predispose seeds to invasion by fungi which may lead to reduced seed emergence (McDonald *et al.*, 1979). It has not been shown to decrease yields.

Because of its limited distribution (Nigeria), *A. arachidis* has not caused major economic loss, but if it should become established in other peanut-producing regions of the world, it could possibly become a major economic pest.

Control

Only limited information is available on the control of *A. arachidis* on peanut. No field applied treatments have been reported, but a number of preventative measures are effective against further spread of the nematode. Immersing seeds in four times their volume of water heated to 60°C and allowing to cool for 5 minutes gave complete control of the nematodes without affecting germination (Bridge, 1975; McDonald & Misari, 1976; Bridge *et al.*, 1977). Sun drying the pods after harvest in very dry conditions as occurs in northern Nigeria, reduces the number of nematodes in the pods (Bridge *et al.*, 1977). In more humid areas, sun drying of pods may not be effective. Shelling peanut before planting will also eliminate the tissues in which most of the nematodes occur and in which they survive best (Bridge *et al.*, 1977).

Aphasmatylenchus straturatus

A. straturatus found around the roots of peanut in southwest Burkina Faso, West Africa near Niangoloko village was described in 1970 (Germani, 1970). It has not been reported to occur outside of Burkina Faso.

Symptoms

A. straturatus causes interveinal chlorosis, stunting, a poorly developed root system, reduction of *Rhizobium* nodules on the roots and peanut yield reduction (Germani & Dhéry, 1973; Germani & Luc, 1982*a*; 1982*b*).

Biology and life cycle

A. straturatus is a migratory endo/ectoparasitic nematode on peanut. Field observations indicate that it spends the dry season at a depth of 40 to 60 cm in the soil adjacent to roots of the karite (*Butyrospermum parkii* L.) tree or in the roots of this tree.

Peanuts are interplanted with the karite tree in many fields in Burkina Faso. Therefore, at the beginning of the rainy season, the nematodes move from the tree roots and enter peanut roots. The nematodes are most abundant in the peanut roots about 40 days after seeding the early maturing cultivars and 70 days after seeding the late maturing cultivars. Approximately 100–110 days after seeding, the nematode leaves the peanut roots and returns to roots of the karite tree. *A. straturatus* does not enter into anhydrobiosis.

Economic importance and population damage threshold levels

Yield reductions due to *A. straturatus* were estimated to range from 30 to 70%. In 1971, *A. straturatus* was estimated to infest approximately 4% of the peanut production area of Burkina Faso and in 1974 the estimate had risen to 25%. Since this nematode also parasitizes other economically important leguminous plants grown in Burkina Faso (Germani & Dhéry, 1973), its rapid spread poses a threat to peanut and other legumes.

Disease symptoms may occur in the field when as few as 600 nematodes per dm^3 of soil are present, but approximately 2000 nematodes per dm^3 are required in the greenhouse.

Control

Research to control *A. straturatus* on peanut has been limited, however DBCP applied at planting has given satisfactory control (Dhéry *et al.*, 1975).

Methods of diagnosis

Soil samples for nematode assays must be collected in the root zone of peanut or in the root zone of the karite tree during the dry season. If the samples are collected in the root zone of peanut they should be removed from the 0 to 20 cm depth, but if collected in the root zone of karite tree during the dry season, they should be removed from the 40 to 60 cm depth.

Scutellonema cavenessi

S. cavenessi was described from northern Nigeria (Sher, 1964) but has since been found associated with most cultivated plants in Senegal and Mali. In Senegal, *S. cavenessi* was associated with poor growth of peanut (Germani, 1979*b*; 1981*b*).

Symptoms

Foliage of peanut plants grown in soil infested with *S. cavenessi* were chlorotic (Germani, 1979*b*). *Scutellonema cavenessi* is associated with the reduction of number of lateral roots and *Rhizobium* nodules. Chlorosis was reduced in plots treated with DBCP which also reduced population densities of *S. cavenessi*. Chlorosis was associated with a reduced level of nitrogen fixation and less total nitrogen yield in pods and foliage (Germani, 1979*b*). Application of the fumigants, DBCP and EDB, to infested soil reduced the nematode population densities, increased vine and pod yield, the number and weight of *Rhizobium* nodules, the nitrogen and phosphorus content of foliage and seeds, and the level of endomycorrhyzae infestation (Germani, 1979*b*; 1981*b*; Germani *et al.*, 1981; 1982; 1985; Germani & Reversat, 1982; 1983).

Biology and survival

In Senegal, *S. cavenessi* showed seasonality in activity (Demeure, 1978*a*; Demeure *et al.*, 1980). This nematode is active during the rainy season, but as the dry season progresses and the humidity of the soil drops to approximately 0.2%, nematodes 0–25 cm deep in the soil enter into a state of anhydrobiosis, in which they remain until the next rainy season.

Economic importance and population damage thresholds

S. cavenessi is distributed throughout the peanut production area of Senegal, but the extent of the crop loss has not been fully evaluated. Nevertheless, in experimental plots, nematicides have increased yields of pods from 20% to 220% and vines 40% to 270% (Germani *et al.*, 1985).

Control

There are no known cultivars resistant to *S. cavenessi*. Also, all crops grow in rotation with peanut in the Sahelian zone of Senegal are susceptible to this nematode. Bare fallow between crops of peanut provided excellent control (Duncan, 1986) but because of the high cost, this practice is not practical in the Sahelian zone. Ethylene dibromide and DBCP are the only nematicides tested that have given practical control. These materials used at 20 kg per hectare of active ingredient have given excellent control and yield increases (Germani & Gautreau, 1976; Germani, 1979*a*; 1979*b*; 1981a; Duncan & Baujard, 1986; Baujard *et al.*, 1987). Growth and yield differences due to nematicides are shown in Plate 6F. There is also a residual effect of the nematicide on other crops grown in treated fields the following year. Ethylene dibromide and DBCP injected at an optimal depth of 15 cm at planting and up to 30 days after planting do not cause phytotoxicity. The fumigant nematicides are applied in or near the row with an animal drawn injector metered with a ground driven peristalic pump that applies a uniform rate as the apparatus is drawn across the field.

Methods of diagnosis

Soil samples for nematode assays should be collected in the peanut root zone to a depth of 25 cm using standard sampling and extraction techniques (Chapter 2). However, if samples are taken

during the dry season when the nematode are in the anhydrobiotic state, samples should be moistened before extraction by elutriation or Baermann techniques, or the centrifugation-flotation method should be used (Demeure, 1978*b*; Duncan, 1986; Duncan & Baujard, 1986).

Tylenchorhynchus brevilineatus

Tylenchorhynchus brevilineatus was first observed damaging peanut in 1976 in the Kalahasti area of Andhra Paradesh State, India (Reddy *et al.*, 1984). The disease caused by this nematode is known as "Kalahasti Malady". Since 1976, the disease has been widespread in the Kalahasti area and has also been observed in Nellore District in Andhra Pradesh (Reddy *et al.*, 1984). This nematode has not been reported as a pest of peanut in other parts of the world.

Symptoms of damage

The disease symptoms in farmers' fields (Reddy *et al.*, 1984) are characterized by small pods and a brownish-black discolouration of pod surface. Small, brownish-yellow lesions appear on the pegs and pod stalks and on young, developing pods. Margins of lesions are slightly elevated because of host cell proliferation around lesions. The length of pod stalks are greatly reduced, and in advanced stages of the disease, the pod surface becomes completely discoloured, but seeds from diseased pods are healthy. Discolouration is also observed on roots but is less severe than on pods.

Pathogenicity tests in the greenhouse corroborated field observations (Reddy *et al.*, 1984). Peanut plants inoculated with 500 *T. brevilineatus* per 12-cm-diameter pot were severely stunted and had reduced root systems. Lesions were present on the roots but were not extensive. Pods were severely discoloured and small, but seeds from the discoloured pods were healthy. Brownish-yellow lesions were observed on individually inoculated pods after 15 days. The number of lesions increased and extensive discolouration was observed by 30 days after inoculation.

Control

Aldicarb (10G) and carbofuran (3G) applied to peanut 20 days postplant controlled *T. brevilineatus* at 2.0, 4.0, 6.0 and 8.0 kg ai/ha. These treatments reduced soil population densities of *T. brevilineatus* and the percentage of diseased pods (Reddy *et al.*, 1984). These treatments increased plant height, pod yields and pod and kernel weights. Both materials were more effective at the higher than at the lower rates.

Ditylenchus destructor

D. destructor, the potato rot nematode, was first reported damaging peanut in the Transvaal Province of South Africa in 1987 (Jones & De Waele, 1988). A subsequent survey revealed the presence of this nematode in seven major peanut producing regions (De Waele *et al.*, 1988). Seventy-three percent of 877 seed samples that graded "damaged" were infested. An average of 160 nematodes per seed was recovered. This nematode has not been reported on peanuts in other parts of the world.

Symptoms of damage

D. destructor has been isolated from roots, pegs, shells and peanut seeds (De Waele *et al.*, 1988). Infected pods of cv Sellie were black resembling black hull caused by *Chalara elegans*. Approximately 40 to 60 percent of the pods and seeds were destroyed in heavily infested fields. *D. destructor* was present in both hulls and seeds.

In greenhouse pathogenicity tests (De Waele *et al.*, 1988), nematodes were present in the peg, exocarp, and endocarp, testa, embryo and on the cotyledons. The first symptom to develop was brown necrotic tissue at the pod base at the juncture of the peg and pod. The surface of infected tissue was dark brown and had a corky appearance. The most distinct symptom of advanced disease

was dark brown to black discolouration of veins which entended longitudinally in the exocarp just beneath the pod surface. Infected pods lacked the luster of healthy pods and appeared dead. Infected seeds were usually shrunken and the micropyles were dark brown to black. The testas were flacid, had dark vascular strands and were easily removed. The inner layer of the testa had a distinct yellow discolouration. Infected embryos were usually olive green to brown instead of having the normal colourless to yellow appearance. The extent of losses caused by this nematode and research results relative to its control have not been reported.

Other Nematodes

Sharma (1985) compiled a world list of nematode pathogens associated with peanut. The list is extensive and includes many genera and species that have not been proven to cause economic damage to peanut. Additional research may demonstrate that some of these species are, in fact, pathogenic and pose a serious threat to peanut production, while others may feed on peanut but cause no economic damage.

The possibility of the interaction of two nematodes, not considered serious pests of peanut, with a virus has been suggested. In Senegal, Merny and Mauboussin (1973) eliminated the clump disease of peanut caused by a virus by treating the soil with DD. They suggested that one or more nematodes was acting as a vector and pointed out that *Longidorus siddiqii* was present in soil samples. More recently, Singh and Sakhuja (1984) in India reduced the disease in field experiments by 97% and 84.1% with DBCP (45 l/ha) and aldicarb 3.0 kg a.i./ha, respectively. Soil samples collected from the rhizosphere of diseased plants always contained *Paralongidorus citri*. Occasionally, species of *Helicotylenchus, Tylenchorhynchus*, and *Hoplolaimus* were also present.

Conclusions and Future Prospects

Peanut yield losses due to parasitic nematodes occur in every major peanut production region of the world. If we can accept the estimated loss of 12% (Sasser & Freckman, 1987), it is apparent that losses are substantial and efforts to reduce these losses are needed.

Meloidogyne species are the major nematodes damaging peanut in most regions of the world, but in some regions, as in West Africa, other species may be more serious. In Senegal, for instance, *Meloidogyne* species do not damage peanut and peanut is often rotated with vegetables to suppress *M. arenaria* populations. A number of nematodes such as *A. arachidis, A. straturatus, S. cavenessi, T. brevilineatus* and *D. destructor* have been reported to cause serious damage to peanut in isolated areas of Africa and Asia but not in other areas of the world. *Belonolaimus longicaudatus* is a pathogen of peanut in only certain areas of the United States. Questions may be raised as to why these nematodes have been reported damaging peanuts only in these areas and what is the probability of their becoming pests in other regions of the world.

Nematode management in the past, particularly in industrialized countries has been based to a great extent on chemical control. In these countries, loss of the fumigants, DBCP, EDB and DD, for use on peanuts, the concern for environmental contaminants, and the increased cost of applying chemicals has increased the urgency to seek safer and more economical chemicals and to develop other means of control.

Ideally, nematode resistant cultivars would be the best and most economical means of control. Unfortunately, germplasm resistant to most nematode species that attack peanut has not been identified or has not been incorporated into commercial cultivars. Therefore, there is a need to accelerate research efforts in this area.

Expanded utilization of cultural practices such as crop rotations, cover crops, trap crops, fallow, flooding and organic amendments that reduce nematode damage may be necessary in the future to maintain economical peanut production. Efforts to prevent the spread of nematodes through sani-

tation and quarantine in extreme situations, may contribute to future containment of nematode problems.

Nematologists and advisors to growers in the future will be challenged to devise the most effective control measures that will yield quality peanuts and an economical return to the grower and protect the safety of the consumer and environment.

References

Alexander, P. M. (1963). Stylet-bearing nematodes associated with various plants in South Carolina, 1962–1963. *Plant Disease Reporter*, 47:978–982.

Anon. (1973). Plant nematology. In: *Secretary for Agriculture Report for the Period 1 October 1971 to 30 September 1972*. Salisbury, Rhodesia, 76 p.

Anon. (1987). Bibliography of estimated crop losses in the United States due to plant-parastic nematodes. *Annals of applied Nematology*, a supplement to the *Journal of Nematology*, 1:6–12.

Bailey, J. E. (1988). Peanut disease control. In: *North Carolina Agricultural Extension Service, North Carolina State University, Peanuts, 1988, AG–331*: 51–64.

Baldwin, J. G. & Barker, K. R. (1970). Host suitability of selected hybrids, varieties and inbreds of corn to populations of *Meloidogyne* spp. *Journal of Nematology*, 2:345–350.

Baltensperger, D. D., Prine, G. M. & Dunn, R. A. (1986). Root-knot nematode resistance in *Arachis glabrata*. *Peanut Science*, 13:78–80.

Barker, K. R. (1974). Influence of geographic area and previous crop on occurrence and density of plant-parasitic nematodes in North Carolina. *Plant Disease Reporter*, 11:991–995.

Barker, K. R., Schmitt, D. P. & Campos, V. P. (1982). Response of peanut, corn, tobacco, and soybean to *Criconemella ornata*. *Journal of Nematology*, 14:576–581.

Baujard, P., Duncan, L. W., Pariselle, A. & Sarr, E. (1987). Étude des effets de quatre nématicides fumigants sur les nématodes et l'arachide au Sénégal. *Revue de Nématologie*, 10:355–360.

Baxter, R. I. & Blake, C. D. (1969). Oxygen and the hatch of eggs and migration of larvae of *Meloidogyne javanica*. *Annals of applied Biology* 63:191–203.

Bergeson, G. B. (1959). The influence of temperature on the survival of some species of the genus *Meloidogyne* in the absence of a host. *Nematologica*, 4:344–354.

Bird, H. F. & Wallace, H. R. (1965). The influence of temperature on *Meloidogyne hapla* and *M. javanica*. *Nematologica*, 11:581–589.

Bos, W. S. (1977*a*). *Aphelenchoides arachidis* n. sp. (Nematoda: Aphelenchoidea) on endoparasite of the testa of groundnuts in Nigeria. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*, 84:95–99.

Bos, W. S. (1977*b*). A preliminary report on the distribution and host-range of the nematode *Aphelenchoides arachidis* Bos in the North of Nigeria. *Samaru agricultural Newsletter, 19:21–23.*

Boswell, T. E. (1968). *Pathogenicity* of Pratylenchus brachyurus *to Spanish peanut*. Ph.D. Dissertation. Texas A and M University College Station, 156 p.

Boyd, F. T. & Perry, V. G. (1969). The effect of sting nematodes on establishment, yield and growth of forage grasses on Florida sandy soils. *Proceedings of the Florida Soil Crop and Science Society*. 29:288–300.

Boyle, L. W. (1950). Several species of parasitic nematodes on peanuts in Georgia. *Plant Disease Reporter*, 34:61–62.

Bridge, J. (1975). Hotwater treatment to control plant parasitic nematodes of tropical crops. *Mededelingen van de Faculteit Landbouwwetendchappen Rijksuniversiteit Gent*, 40:249–259.

Bridge, J., Bos, W. S., Page, L. J. & McDonald, D. (1977). The biology and possible importance of *Aphelenchoides arachidis*, a seed-borne endoparasitic nematode of groundnuts from northern Nigeria. *Nematologica*, 23:253–259.

Broadley, R. A. (1981). Distribution and control of root-knot and lesion nematodes on peanuts in North Queensland. *Australian Journal of experimental Agriculture and Animal Husbandry. 21:223–226.*

Brodie, B. B. & Murphy, W. S. (1975). Population dynamics of plant nematodes as affected by combination of fallow and cropping sequences. *Journal of Nematology*, 7:91–92.

Castillo, M. B., Morrison, L. S., Russell, C. C. & Banks, D. J. (1973*a*). Resistance to *Meloidogyne hapla* in peanut. *Journal of Nematology*, 5:281–285.

Chabra, H. K. & Mahajan, R. (1976). *Pratylenchus coffeae*, the root-lesion nematode in groundnut and its control by granular nematicides. *Nematologia mediterranea*, 4:241–242.

Cheng, Y. H., Lo, W. C. & Tu, C. C. (1981). Studies on host range of *Meloidogyne arenaria* and its chemical control. *Research Bulletin of Tainan Dais*, 15:55–64.

Cheng, Y. H. & Tu, C. C. (1980). Identification of *Meloidogyne arenaria* of peanut on Taiwan. *Journal of agricultural Research of China*, 29:47–53.

Choi, Y. E. (1981). The root-knot nematodes, *Meloidogyne* spp., in Korea. In: *Proceedings of the 3rd Research Planning Conference on Root-knot Nematodes, Meloidogyne spp., Region VI, July 20–24, 1981*, Jakarta, Indonesia.

Colbran, R. C. (1958). Studies of plant and soil nematodes. 2. Queensland host records of root-knot nematodes (*Meloidogyne* spp.). *Queensland Journal of agricultural Science*, 15:101–136.

Colbran, R. C. (1968). Nematodes – important pests of peanuts. *Division of Plant Industry, Department of Primary Industries. Queensland, Australia, Advisory Leaflet No. 955*, 5 p.

Cooper, W. E., Wells, J. C., Sasser, J. N. & Bowery, T. G. (1959). The efficacy of preplant and postplant applications of 1,2-dibromo–3-chloropropane on control of the sting nematode, *Belonolaimus longicaudatus*. *Plant Disease Reporter*, 43:903–908.

De Waele, D., Jones, B. L., Bolton, C. & van den Berg, E. 1988. *Ditylenchus destructor* in hulls and seeds of peanut. *Journal of Nematology*, 21:10–15.

Demeure, Y. (1978*a*). Influence des températures élevées sur les états actifs et anhydrobiotiques du nématode *Scuetellonema cavenessi*. *Revue de Nématologie*, 1:13–19.

Demeure, Y. (1978*b*). Résistance à la sécheresse en zone sahélienne du nématode phytoparasite *Scutellonema cavenessi* Sher, 1963. *Cahiers de l'ORSTOM, Série Biologie*, 10:283–292.

Demeure, Y., Netscher, C. & Quénéhervé, P. (1980). Biology of the plant parasitic nematode *Scutellonema cavenessi* Sher, 1964: reproduction, development and life cycle. *Revue de Nématologie*, 3:213–225.

Dhéry, M., Germani, G. & Giard, A. (1975). Résultats de traitements nématicides contre la chlorose et le rabougrissement de l'arachide en Haute Volta. *Cahiers de L'ORSTOM, série Biologie*, 10:161–167.

Dhurj, I. & Vaishnav, M. U. (1981). Pathogenicity of root-knot nematode on groundnut. *Indian Journal of Nematology*, 11:217–218.

Dickson, D. W. & Smart, G. C., Jr. (1971). Control of *Meloidogyne arenaria* and *Pratylenchus penetrans* on peanut with foliar applications of a systemic nematicide. *Journal of Nematology*, 3:307–308.

Dickson, D. W. & Waites, R. E. (1978). Efficacy of at-plant and additional at-pegging applications of nematicides for control of *Meloidogyne arenaria* on peanut. *Proceedings of the American Peanut Research and Education Association*, 10:51 [Abstr.].

Dickson, D. W. & Waites, R. E. (1982). Evaluation of nematicides for managing the peanut root-knot nematode on peanut, 1980. *Fungicide and Nematicide Tests, American Phytopathological Society*, 37:195–196.

Diomandé, M. & Beute, M. K. (1981*a*). Effects of *Meloidogyne hapla* and *Macroposthonia ornata* on *Cylindrocladium* black rot on peanut. *Phytopathlogy*, 71:491–496.

Diomandé, M. & Beute, M. K. (1981*b*). Relations of *Meloidogyne hapla* and *Macroposthonia ornata* populations to *Cylindrocladium* black rot in peanuts. *Plant Disease*, 65:339–342.

Diomandé, M., Black, M. C., Beute, D. K. & Barker, K. R. (1981). Enhancement of *Cylindrocladium crotalaria* root rot by *Meloidogyne arenaria* (race 2) on a peanut cultivar resistant to both pathogens. *Journal of Nematology*, 13:321–327.

Duncan, L. W. (1986). Effect of bare fallow on plant parasitic nematodes in the Sahelian zone of Senegal. *Revue de Nématologie*, 9:75–81.

Duncan, L. W. & Baujard, P. (1986). Influence of nematicide placement depth and time of application on treatment efficacy on the Sahelian zone of Senegal. *Revue de Nématologie*, 9:135–139.

Dunn, R. A. (1988). Peanut nematode management. Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida. *Nematode Plant Protection Pointer*, 3, 4 p.

Edwards, E. E. (1956). Studies on resistance to root-knot nematode *Meloidogyne* Goeldi, 1887. *Proceedings of the helminthological Society of Washington*, 23:112–118.

Eisenback, J. D., Hirschmann, H., Sasser, J. N. & Triantaphyllou, A. C. (1981). *A guide to the four most common species of root-knot nematodes (Meloidogyne species) with pictorial keys*. The Department of Plant Pathology and Genetics, North Carolina State University and USAID, Raleigh, NC, 47 p.

Endo, B. Y. (1959). Responses of root-lesion nematodes, *Pratylenchus brachyurus* and *P. zeae* to various plants and soil types. *Phytopathology*, 49:417–421.

Esser, R. P. (1976). Sting nematodes, devastating parasites of Florida crops. Division of Plant Industry, Florida Department of Agriculture and Consumer Service. *Nematology Circular*, 18:2 p.

Faulkner, L. R. & Bolander, W. J. (1966). Occurrence of large nematode populations in irrigation canals of South Central Washington. *Nematologica*, 12:591–600.

Feldmesser, J. & Rebois, R. V. (1965). Temperature and moisture effects on *Pratylenchus brachyurus*. *Nematologica*, 11:37–38.

Garcia, R. M. (1976). *Vertical distribution and survival stages of* Meloidogyne arenaria *in Florida with peanut as a host crop*. M. S. Thesis, University of Florida, Gainesville, 38 pp.

Garcia, R. & Mitchell, D. J.(1975*a*). Synergistic interactions of *Phythium myriotylum* with *Fusarium solani* and *Meloidogyne arenaria* in pod rot of peanut. *Phytopathlogy*, 65:832–833.

Garcia, R. & Mitchell, J. J. (1975*b*). Interactions of *Pythium myriotylum* with *Fusarium solani, Rhizoctonia solani*, and *Meloidogyne arenaria* in pre-emergence damping-off of peanut. *Plant Disease Reporter*, 59:665–669.

Germani, G. (1970). *Aphasmatylenchus straturatus* n. sp. (Nematode: Hoplolaimidae) from West Africa. *Proceedings of the helminthological Society of Washington*, 37:48–51.

Germani, G. (1979*a*). Nematicide as a tool to study the impact of nematodes on plant productivity. In: Mongi, H. O. & Huxley, P. A. (Eds) *Soil Research in Agroforestry: Proceedings of an Expert Consultation*. Nairobi, Kenya, 26–31 March:297–313.

Germani, G. (1979*b*). Action directe et rémanente d'un traitement nématicide du sol sur 2 cultivars d'arachide au Sénégal. *Oléagineux*, 34:399–404.

Germani, G. (1981*a*). Étude au champ de l'évolution des populations du nématode *Scutellonema cavenessi* et de la cinétique de la fixation de N2 sur 3 cultivars d'Arachide. *Oléagineux*, 36:247–249.

Germani, G. (1981*b*). Pathogenicity of the nematode *Scutellonema cavenessi* on peanut and soybean. *Revue de Nématologie*, 4:203–208.

Germani, G., Baujard, P. & Luc, M. (1985). *La lutte contre les nématodes dans le bassin arachidier sénégalais*. Dakar, ORSTOM, 1985, 8 p.

Germani, G., Cuany, A. & Merny, G. (1982). L'analyse factorielle des correspondances appliquée a l'influence de deux nématodes sur la croissance de l'arachide et la fixation symbiotique de l'azote. *Revue de Nématologie*, 5:161–168.

Germani, G. & Dhéry, M. (1973). Observations et expérimentations concernant le role des nématodes dans deux affections de l'arachide en Haute Volta: la "chlorose" et le "clump". *Oléagineux*, 28:235–242.

Germani, G. & Gautreau, J. (1976). Résultats agronomiques obtenus par des traitements nématicides sur arachide au Sénégal. *Cahiers de l'ORSTOM, série Biologie*, 11:193–202.

Germani, G. & Luc, M. (1982*a*). Études sur la "chlorose voltaïque" des légumineuses due au nématode *Aphasmatylenchus straturatus* Germani. I. *Revue de Nématologie*, 5:139–146.

Germani, G. & Luc, M. (1982*b*). Etudes sur la "chlorose voltaïque" des légumineuses due au nématode *Aphasmatylenchus straturatus* Germani. *Revue de Nématologie*, 5:195–199.

Germani, G., Ollivier, B. & Diem, H. G. (1981). Interaction of *Scutellonema cavenessi* and *Glomus mosseae* on growth and N2 fixation. *Revue de Nématologie*, 4:277–280.

Germani, G. & Reversat, G. (1982). Effet sur les rendements de l'arachide au Sénégal de deux produits nématicides, DBCP et EDB, et d'un amendement organique. *Oléagineux*, 37 ' 521–524.

Germani, G. & Reversat, G. (1983). Effect du dibromochloropropane sur quelques espèces de nématodes reviviscents, parasites de l'arachide au Sénégal. *Revue de Nématologie*, 6:73–78.

Good, J. M. (1968). Relation of plant parasitic nematodes to soil management practices. In: Smart, G. C. & Perry, V. G. (Eds) *Tropical Nematology*. Gainesville, University of Florida Press:113–118.

Good, J. M., Boyle, L. W. & Hammons, R. D. (1958). Studies of *Pratylenchus brachyurus* on peanuts. *Phytopathology*, 48:530–535.

Good, J. M., Robertson, W. K. & Thompson, L. C., Jr. (1954). Effect of crop rotation on populations of meadow nematode, *Pratylenchus leiocephalus*, in Norfolk loamy, fine sand. *Plant Disease Reporter*, 38:178–180.

Good, J. M. & Stansell, J. R. (1965). Effect of irrigation, soil fumigation, and date of harvest on *Pratylenchus brachyurus* (Godfrey). *Nematologica*, 11:38–39.

Graham, T. W. (1951). Nematode root rot of tobacco and other plants. *South Carolina Agricultural Experiment Station Technical Bulletin 390*, 25 p.

Hagan, A. (1988). Disease and nematode control. In: Alabama Cooperative Extension Service, Auburn University. *1988 Peanut Pest Mangement, Weed, Insect, Disease and Nematode Control Recommendations. Circular ANR–360*,:5–6.

Hammons, R. O. (1982). Origin and early history of the peanut. In: Patte, H. E. & Young, C. T. (Eds). *Peanut Science and Technology American Peanut Research and Education Society*. Yoakum, Texas: 1–20.

Holbrook, C. C., Knauft, D. A. & Dickson, D. W. (1983). A technique for screening peanut for resistance to *Meloidogyne arenaria. Plant Disease*, 67:957–958.

Holderman, Q. L. (1955). The present known distribution of the sting nematode, *Belonolaimus gracilis*, in the Coastal Plain of the Southeastern United States. *Plant Disease Reporter*, 39:5–8.

Holderman, Q. L. & Graham, T. W. (1953). The effect of different plant species on the population trends of the sting nematode. *Plant Disease Reporter*, 37:497–500.

Ibrahim, I. K. A. & El-Saedy, M. A. (1976*a*). Plant parasitic nematodes associated with peanuts in Egypt. *Egyptian Journal of Phytopathology*, 8:31–35.

Ibrahim, I. K. A. & El-Saedy, M. A. (1976*b*). Development and pathogenesis of *Meloidogyne javanica* in peanut roots. *Nematologica mediterranea*, 4:231–234.

Ingram, E. G. & Rodriguez-Kabana, R. (1980). Nematodes parasitic on peanuts in Alabama and evaluation of methods for detection and study of population dynamics. *Nematropica*, 10:21–30.

Jackson, C. R. & Minton, N. A. (1968). Pod invasion by fungi in the presence of lesion nematodes in Georgia. *Oléagineux*, 23:531–534.

Jackson, E. E. & Sturgeon, R. V., Jr. (1973). Effects of nematicides upon root lesion nematode populations. *Journal of the American Peanut Research and Education Association*, 5:178–181.

Johnson, A. W., Dowler, C. C. & Hauser, E. W. (1974). Seasonal population dynamics of selected plant parasitic nematodes on four monocultured crops. *Journal of Nematology*, 6:187–190.

Jones, B. L. & De Waele, D. (1988). First report of *Ditylenchus destructor* in pods and seeds of peanut. *Plant Disease*, 72:453.

Kinloch, R. A. & Lutrick, M. C. (1975). The relative abundance of nematodes in an established field crop rotation. *Proceedings of the Soil and Crop Science Society of Florida*, 34:192–194.

Koen, H. (1967). Notes on the host range, ecology and population dynamics of *Pratylenchus brachyurus*. *Nematologica*, 13:118–124.

Lordello, A. I. L. & Gerin, M. (1981). Nematóide javanes parasitando raízes e nódules de amendoim. *Revista de Agricultura Piracicaba*, 56:278.

Loof, P. A. A. (1964). Free-living and plant-parasitic nematodes from Venezuela. *Nematologica*, 10:201–300.

McDonald, D., Bos, W. S. & Gumel, M. H. (1979). Effects of infections of peanut (groundnut) seed by the testa nematode *Aphelenchoides arachidis*, on seed infection by fungi and on seeding emergence. *Plant Disease Reporter*, 63:464–467.

McDonald, D. & Misari, S. M. (1976). Disease and pests of groundnuts and their importance in crop exchange. Interafrican Symposium "The role of plant protection in crop improvement in Africa. Ibadan, Nigeria, 7–12 October, 1974". *African Journal of Plant Protection* 1:75–82.

McWatters, K. H. & Cherry, J. P. (1982). Potential food uses of peanut seed proteins. In: Pattee, H. E. & Young,

C. T. (Eds). *Peanut Science and Technology. American Peanut Research and Education Society, Inc.*, Yoakum, Texas:689–736.

Machmer, J. H. (1951). Root-knot of peanut. I. Distribution. *Plant Disease Reporter*, 35:364–366.

Machmer, J. H. (1953). *Criconemoides* sp., a ring nematode associated with peanut "yellows". *Plant Disease Reporter*, 37:156.

Martin, G. C. (1958). Root-knot nematodes (*Meloidogyne* spp.) in the Federation of Rhodesia and Nyasaland. *Nematologica*, 3:332–349.

Martin, G. C. (1961). Plant species attacked by root-knot nematodes (*Meloidogyne* spp.) in the Federation of Rhodesia and Nyasaland. *Nematologica*, 6:130–134.

Meagher, J. W. (1967). Observations on the transport of nematodes in subsoil drainage and irrigation water. *Australian Journal of experimental Agriculture and Animal Husbandry*, 7:577.

Merny, G., Fortuner, R., & Luc, M. (1974). Plant parasitic nematodes in Gambia. *L' Agronomie tropicale, Nogent*, 29:702–707.

Merny, G. & Mauboussin, J. C. (1973). Action possible des nématodes dans le rabougrissement ou "clump" de l'arachide. *Nematologica* 19:406–408.

Miller, L. I. (1951). A report on the effect of ethylene dibromide soil treatment on root-knot control, nodulation, and yield of peanuts. *Virginia Journal of Science 2, New Series (2)*:109–112.

Miller, L. I. (1972*a*). The influence of soil texture on the survival of *Belonolaimus longicaudatus*. *Phytopathology*, 62:670–671 (abst).

Miller, L. I. (1972*b*). Resistance of plant introductions of *Arachis hypogaea* to *Meloidogyne hapla, Meloidogyne arenaria*, and *Belonolaimus longicaudatus*. *Virginia Journal of Science*, 23:101 [Abstr.].

Miller, L. I. & Duke, G. B. (1961). Peanut nematode disease control. *Virginia Agricultural Experiment Station Bulletin 520*, 26 p.

Milne, D. L. & Du Plessis, D. P.(1964). Development of *Meloidogyne javanica* (Treub) Chitwood on tobacco under fluctuating soil temperatures. *South African Journal of Agricultural Science*, 7:673–680.

Minton, N. A. (1963). Effects of two populations of *Meloidogyne arenaria* on peanut roots. *Phytopathology*, 53:79–81.

Minton, N. A. & Bell, D. K. (1969). *Criconenoides ornatus* parasitic on peanuts. *Journal of Nematology*, 1:349–351.

Minton, N. A., Bell, D. K. & Doupnik, B., Jr. (1969*a*). Peanut pod invasion by *Aspergillus flavus* in the presence of *Meloidogyne hapla*. *Journal of Nematology*, 1:318–320.

Minton, N. A., Cairns, E. J., Minton, E. B. & Hopper, B. E. (1963). Occurrence of plant-parasitic nematodes in Alabama. *Plant Disease Reporter*, 47:743–745.

Minton, N. A. & Csinos, A. S. (1986). Peanut response to 1, 3-D in *Meloidogyne arenaria* and *Sclerotium rolfsii* infested soil. *Proceedings of the American Peanut Research and Education Society.*, 18:62 [Abstr.].

Minton, N. A., Csinos, A. S. & Bell, D. K. (1984). Effects of six nematicides and two fungicides, applied in various combinations on peanuts. *United States Department of Agriculture, Agricultural Research Service, ARS–3*, 14 p.

Minton, N. A. & Hammons, R. O. (1975). Evaluation of peanut for resistance to the peanut root-knot nematode, *Meloidogyne arenaria*. *Plant Disease Reporter*, 59:944–945.

Minton, N. A., Hammons, R. O. & Parham, S. A. (1970). Infection of shell and peg tissues of six peanut cultivars by *Pratylenchus brachyurus*. *Phytopathology*, 60:472–474.

Minton, N. A. & Jackson, C. R. (1967). Invasion of peanut pods by *Aspergillus flavus* and other fungi in the presence of root-knot nematodes. *Oléagineux*, 22:543–546.

Minton, N. A., McGill, J. F. & Golden, A. M. (1969*b*). *Meloidogyne javanica* attacks peanuts in Georgia. *Plant Disease Reporter*, 53:668.

Minton, N. A. & Morgan, L. W. (1974). Evaluation of systemic and nonsystemic pesticides for insect and nematode control in peanuts. *Plant Science*, 1:91–98.

Minz, G. (1956). The root-knot nematode, *Meloidogyne* spp., in Israel. *Plant Disease Reporter*, 40:798–801.

Mitsui, Y., Yoshida, T., Okamoto, K. & Ishii, R. (1976). Relationship between nematode-trapping fungi and *Meloidogyne hapla* in peanut field. *Japanese Journal of Nematology*, 6:47–55.

Motsinger, R. E., Crawford, J.L. & Thompson, S. S. (1976). Nematode survey of peanuts and cotton in Southwest Georgia. *Peanut Science*, 3:72–74.

Netscher, C. (1975). Studies on the resistance of groundnut to *Meloidogyne* spp. in Senegal. *Cahiers de l'ORSTOM, série Biologie*, 10:227–232.

Norse, D. (1972). Nematode populations in a maize-groundnut-tobacco rotation and the resistance of maize varieties to *Meloidogyne javanica*. *Tropical Agriculture, Trinidad*, 49:355–360.

O'Bannon, J. H. & Reynolds, H. W. (1961). Root-knot nematode damage and cotton yields in relation to certain soil properties. *Soil Science*, 92:384–386.

Orion, D. & Cohn, E. (1975). Crop rotation for control of certain nematodes. *Phytoparasitica*, 3:69 [Abstr.].

Orr, C. C. & Newton, O. H. (1971). Distribution of nematodes by wind. *Plant Disease Reporter*, 55:61–63.

Osman, H. A., Dickson, D. W., & Smart, G. C., Jr. (1985). Morphological comparisons of host races 1 and 2 of *Meloidogyne arenaria* from Florida. *Journal of Nematology*, 17:279–285.

Oteifa, B. A. (1962). Species of root-lesion nematodes commonly associated with economic crops in the Delta of the U.A.R. *Plant Disease Reporter*, 46:572–575.

Owens, J. V. (1951). The pathological effects of *Belonolaimus gracilis* on peanuts in Virginia. *Phytopathology*, 41:29 [Abstr.].

Patel, H. R., Vaishnav, M. U. & Dhruj, I. U. (1985). Interaction of *Meloidogyne arenaria* and *Fusarium solani* on *groundnut*. *Indian Journal of Nematology*, 15: 98–99.

Perry, V. G. (1965). Host-parasite relationships of certain nematodes and crop plants in Florida. *University of Florida Agricultural Experiment Stations Annual Report, Gainesville*: 115–116.

Perry, V. G. & Norden, A. J. (1963). Some effect of a cropping sequence on populations of certain plant nematodes. *Proceedings of the Soil and Crop Science Society of Florida*, 23:116–121.

Porter, D. M., Smith, D. H. & Rodríguez-Kábana, R. (1982). Peanut plant diseases. In: Patte, H. E. & Young, C. T. (Eds). *Peanut Science and Technology*. American Peanut Research and Education Society, Inc., Yoakum, Texas:326–410.

Porter, D. M., Smith, D. H. & Rodríguez-Kábana, R. (1984). Introduction. In: Porter, D. M., Smith, D. H. & Rodríguez-Kábana, R. (Eds). *Compendium of Peanut Diseases*. St. Paul, Minnesota, USA, American Phytopathological Society,:1–4.

Rau, G. J. (1958). A new species of sting nematode. *Proceedings of the helminthological Society of Washington*, 25:95–98.

Reddy, D. D. R., Subrahmanyam, P., Sankara Reddy, G. H., Raja Reddy, C. & Siva Ras, D. V. (1984). A nematode disease of peanut caused by *Tylenchorhynchus brevilineatus*. *Plant Disease*, 68:526–529.

Rickard, D. A., Barker, K. R. & Wells, J. C. (1977). Effects of *Macroposthonia ornata* and *Meloidogyne hapla* on yield and value of peanut. *Journal of Nematology*, 9:281. [Abstr.].

Robbins, R. T. (1972). *Morphology and ecology of the sting nematode*, Belonolaimus longicaudatus. Ph.D. Thesis, North Carolina State University, Raleigh:65 p.

Robbins, R. T. & Barker, K. R. (1973). Comparisons of host range and reproduction among populations of *Belonolaimus longicaudatus* from North Carolina and Georgia. *Plant Disease Reporter*, 57:750–754.

Robbins, R. T. & Barker, K. R. (1974). The effects of soil type, particle size, temperature, and moisture on reproduction of *Belonolaimus longicaudatus*. *Journal of Nematology*, 6:1–6.

Robbins, R. T. & Hirschmann, H. (1974). Variation among populations of *Belonolaimus longicautatus*. *Journal of Nematology*, 6:87–94.

Rodríguez-Kábana, R., Ivey, H. & Backman, P. A. (1987). Peanut-cotton rotations for the management of *Meloidogyne arenaria*. *Journal of Nematology*, 19:484–486.

Rodríguez-Kábana, R. & King, P. S. (1979). Relation between the method of incorporation of systemic nematicides into soil and their effectiveness against root-knot nematodes on peanuts. *Nematropica*, 9:167–172.

Rodríguez-Kábana, R. & King, P. S. (1985). Evaluation of selected nematicides for control of *Meloidogyne arenaria* in peanut: A multi-year study. *Nematropica*, 15:155–164.

Rodríguez-Kábana, R., King, P. S. & Pope, M. H. (1981). Comparison of in-furrow applications and banded treatments for control of *Meloidogyne arenaria* in peanuts. *Nematropica*, 11: 53–67.

Rodríguez-Kábana, R. & Morgan-Jones, G. (1987). Novel rotations and organic materials show promise for

management of nematodes. *Alabama Agricultural Experiment Station, Highlights of Agricultural Research*, 34:13.

Rodríguez-Kábana, R. & Robertson, D. G. (1987). Control of *Meloidogyne arenaria* in peanut with 1, 3-D: Relative efficacy and application depth. *Nematropica*, 17:17–29.

Rodríguez-Kábana, R., Shelby, R. A., King, P. S. & Pope, M. H. (1982*a*). Application time and effectiveness of four systemic nematicides against *Meloidogyne arenaria* on Florunner peanut. *Nematropica*, 12:85–96.

Rodríguez-Kábana, R. & Touchton, J. T. (1984). Corn and sorghum as rotational crops for management of *Meloidogyne arenaria* in peanut. *Nematropica*, 14:26–36.

Rodríguez-Kábana, R., Weaver, C. F. & King, P. S. (1985). Combinations of 1, 3-D and Aldicarb for management of *Meloidogyne arenaria* in peanuts. *Nematropica*, 15:93–106.

Rodríguez-Kábana, R., Weaver, C. F., Robertson, D. G. & Snoddy, E. L. (1986). Population dynamics of *Meloidogyne arenaria* juveniles in a field with Florunner peanut. *Nematropica*, 16:185–196.

Rodríguez-Kábana, R., Williams, J. C. & Shelby, R. A. (1982*b*). Assessment of peanut yield losses caused by *Meloidogyne arenaria*. *Nematropica*, 12:279–288.

Saint-Smith, J. H., McCarthy, G. J. P., Rawson, J. E., Langford, S. & Colbran, R. C. (1972). Peanut growing. *Queensland agricultural Journal*, 98:639–644.

Sakhuja, P. K. & Sethi, C. L.(1985*a*). Screening of groundnut germplasm for resistance to root-knot nematode, *Meloidogyne javanica*. *Indian Journal of Nematology*, 15:129–130.

Sakhuja, P. K. & Sethi, C. L. (1985*b*). Growth of groundnut as influenced by different inocula of *Meloidogyne javanica*. *Indian Journal of Nematology*, 15:135–137.

Sakhuja, P. K. & Sethi, C. L. (1985*c*). Frequency of occurrence of various plant parasitic nematodes and root-rot fungi on groundnut in Punjab. *Indian Journal of Nematology*, 15:191–194.

Sasser, J. N. (1954). Identification and host-parasite relationships of certain root-knot nematodes (*Meloidogyne* spp.). *University of Maryland, Agricultural Experiment Station, Technical Bulletin A–77*, 31 p.

Sasser, J. N. (1972). Physiological variations in the genus *Meloidogyne* as determined by differential hosts. *OEPP/EPPO Bulletin* 6:41–48.

Sasser, J. N. (1977). Worldwide dissimination and importance of the root-knot nematodes, *Meloidogyne* spp. *Journal of Nematology*, 9:26–29.

Sasser, J. N. (1979*a*). Pathogenicity, host ranges, and variability in *Meloidogyne* spp. In: Lamberti, F. & Taylor, C. E. (Eds.). *Root-knot nematodes (*Meloidogyne *species): Systematics, Biology, and Control.* London, New York, San Francisco, Academic Press:257–268.

Sasser, J. N. (1979*b*). Economic importance of *Meloidogyne* in tropical countries. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes (*Meloidogyne *species): Systematics, Biology and Control.* London, New York, San Francisco Academic Press: 359–374.

Sasser, J. N., Barker, K. R. & Nelson, L. A. (1970). Relative effects of eight nematode species on growth, yield and value of peanut follwing chemical soil treatment. *Proceedings of the Second International Congress of Parasitology, 6–12 September 1970, Washington, DC, Journal of Parasitology 56, Number 4, Section II, part 1 of 3 parts*:300–301.

Sasser, J. N., Barker, K. R. & Nelson, L. A. (1975*a*). Correlations of field populations of nematodes with crop growth responses for determining relative involvement of species. *Journal of Nematology*, 7:193–198.

Sasser, J. N., Barker, K. R. & Nelson, L. A. (1975*b*). Chemical soil treatment for nematode control on peanut and soybean. *Plant Disease Reporter*, 59:154–155.

Sasser, J. N., Cooper, W. E. & Bowery, T. G. (1960). Recent developments in the control of sting nematode, *Belonolaimus longicaudatus*, on peanuts with 1,2-dibromo–3-chloropropane and EN 18133. *Plant Disease Reporter*, 44:733–737.

Sasser, J. N. & Freckman, D. (1987). A world perpspective on nematology: The role of the society. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Hyattsville, MD, USA, Society of Nematologists:7–14.

Sasser, J. N. & Kirby, M. F. (1979). Crop cultivars resistant to root-knot nematodes, *Meloidogyne* spp., with information on seed sources. *Cooperative Publication, Department of Plant Pathology, North Carolina State University and U. S. Agency of International Development*. Raleigh, NC. 24 p.

Sasser, J. N. & Nusbaum, C. J. (1955). Seasonal fluctuations and host specificity of root-knot nematode populations in two-year tobacco rotation plots. *Phytopathology*, 45:540–545.

Sauer, M. R. (1968). Nematodes in an irrigated vineyard. *Nematologica*, 14:457–458.

Sharma, S. B. (1985). A world list of nematode pathogens associated with chickpea, groundnut, pearl millet, pigeonpea and sorghum. *Pulse Pathology Progress Report 42. International Crops Research Institute for the Semi-Arid Tropics*:5–8.

Sharma, N. K., Sharma, S. K. & Midha, S. K. (1978). Root-knot disease of groundnut in Punjah. *Indian Farming*, 28:19–21.

Sher. S. A. (1964). Revision of the Hoplolaiminae (Nematoda). III. *Scutellonema*, Andrássy, 1958. *Nematologica* 9:421–443.

Singh, N. D. (1972). Plant-parasitic nematodes associated with some economic crops in Guyana. *Plant Disease Reporter*, 56:1059–1062.

Singh, I. & Sakhuja, P. K. (1984). Clump disease of groundnut and its control with nematicides. *Indian Journal of Nematology*, 14:54–55.

Smith, O. D., Boswell, T. E. & Thames, W. H. (1978). Lesion nematode resistance in peanuts. *Crop Science*, 18:1008–1011.

Starr, J. L. (1984). Expression of resistance in peanuts, *Arachis hypogaea*, to *Pratylenchus brachyurus*: Impact on screening for resistance. *Journal of Nematology*, 16:404–406.

Steiner, G. (1945). Meadow nematodes as the cause of root destruction. *Phytopathology*, 35:935–937.

Steiner, G. (1949). Plant nematodes the grower should know. *Proceedings of the Soil Science Society of Florida, 1942, 4-B*:72–117.

Subrahmanyam, P., Ghanekar, A. M., Nolt, B. L., Reedy, D. V. R., & McDonald, D. (1983). Resistance to groundnut diseases in wild *Arachis* species. *Proceedings of an International Workshop on Cytogenetics of* Arachis., *31 Oct. – 2 Nov. 1983*, ICRISAT Centre, Patancheru, India.

Taylor, A. L & Sasser, J. N. (1978). Biology, identification and control of root-knot nematodes (*Meloidogyne* species). *A cooperative publication of the Department of Plant Pathology, North Carolina Sate University and USAID*, North Carolina State University Graphics, 111 p.

Thames, W. H., Jr. (1959). Plant parasitic nematode populations of some Florida soils under cultivated and natural conditions. *Dissertation Abstract*, 20:1109–1110.

Thames, W. H., Jr. & Stoner, W. N. (1953). A preliminary trial of lowland culture rice in rotation with vegetable crops as a means of reducing root-knot nematode infestations in the Everglades. *Plant Disease Reporter*, 37:187–192.

Thomason, I. J., Van Gundy, S. D. & Kirkpatrick, J. D. (1964). Mobility and infectivity of *Meloidogyne javanica* as affected by storage time and temperature in water. *Phytopathology*, 54:192–195.

United States Department of Agriculture. *Foreign Agriculture Service. (1989). World OilseedSituation and Market Highlights*. Circular Series FOP 7–89 P9.

Van der Linde, J. W. (1956). The *Meloidogyne* problem in South Africa. *Nematologica*, 1:177–183.

Van Gundy, S. D. (1985). Ecology of *Meloidogyne* spp. – Emphasis on environmental factors affecting survival and pathogenicity. In: Sasser, J. N. & Carter. C. C. (Eds). *An Advanced Treatise on* Meloidogyne *Biology and Control* Volume I. Raleigh, NC, USA, University of North Carolina Press: 178–182.

Vance, P. N. (1981). Peanut growing in the South Burnett. *Queensland agricultural Journal*, 107:201–213.

Vrain, T. C. (1978). Influence of chilling and freezing temperatures on infestivity of *Meloidogyne incognita* and *M. hapla*. *Journal of Nematology*, 10:177–180.

Wallace, H. R. (1971). Abiotic influences in the soil environment. In: Zuckerman, B. M., Mai, W. F. & Rohde, R. A. (Eds). *Plant Parasitic Nematodes, Volume I.* New York & London Academic Press: 257–280.

Wheeler, T. A. & Starr, J. L. (1987). Incidence and economic importance of plant-parasitic nematodes on peanut in Texas. *Peanut Science*, 14:94–96.

Williams, E. J. & Drexler, J. S. (1981). A non-destructive method for determining peanut pod maturity. *Peanut Science*, 8:134–141.

Wilson, C. (1948). Root-knot nematodes on peanuts in Alabama. *Plant Disease Reporter*, 32:443.

Wittwer, S. H. (1981). The 20 crops that stand between man and starvation. *Farm Chemicals*, 144:17–28.

Yang, B. (1984). The identification of 15 root-knot nematode populations. *Acta Phytopathologica Sinica*, 11:107–112.

Yin, K. C. & Feng, Z. X. (1981). A preliminary survey on the parastic nematodes of Agricultural Crops. *Phytopathologica* 8:111–126.

Zhang, Y. (1985). Occurrence and control of peanut root-knot disease in non-irrigated sloping fields of Zhangjiang District. *Agricultural Science of Guamgdong Province*, 6:48–49.

Chapter 9

Nematode Parasites of Citrus

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Citrus is grown in more than 125 countries in a belt within 35° latitude north or south of the equator. The major limiting factor to citrus production is a requirement that the occurrence of freezing temperatures be of very short duration. Within the family Rutaceae, the genera *Citrus* (oranges, mandarins, pomelos, grapefruit, lemons, limes and citrons), *Fortunella* (kumquats) and *Poncirus* (trifoliate oranges) contain the principal commercial species (Swingle & Reese, 1967). Citrus production worldwide has grown from 24 million tonnes in 1961 to projected levels of 71 million tonnes in 1990 (Wardowski *et al.*, 1986). Approximately 60% of the world's citrus production is consumed as fresh fruits and nearly one-third of total production is used in international trade (Fortucci-Marongiu, 1988).

Citrus spp. are naturally deep rooted plants (Ford, 1954*a, b*) and optimum growth requires deep, well-drained soils because roots will not grow into or remain in saturated zones. Nevertheless, trees can be well-managed in areas with high water tables if grown on beds. Citrus grows well under any rainfall regime provided that adequate soil moisture can be maintained. Irrigation of citrus is commonly practiced by a variety of methods that range from orchard flooding to low-volume drip or microsprinkler systems. In areas with sporadic rainfall, the ability to manage soil moisture is critical for good production, particularly during the period when fruit are set after the first seasonal flower bloom (Sites *et al.*, 1951). There is a tendency at present in the United States and elsewhere to increase early returns by planting higher density orchards with shorter life expectancies due to such diseases as citrus blight, tristeza and greening (Hearn, 1986).

Citrus Nematodes

Numerous nematode species are associated with the citrus rhizosphere (Cohn, 1972). To date, however, relatively few have been shown to be of economic importance. With the notable exception of *Tylenchulus semipenetrans,* most nematode species capable of damaging mature citrus tend to be regional or local problems, due either to edaphic conditions or to the natural distribution of a particular nematode. Because the etiology of specific nematode diseases of citrus affects management recommendations, the recognized nematode pathogens are discussed completely in separate sections.

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

Tylenchulus semipenetrans

The "citrus nematode," *T. semipenetrans,* is aptly named since it occurs in all citrus producing regions of the world and limits production of citrus fruits under a wide range of environmental and edaphic conditions. In the main citrus producing regions of the United States, various surveys estimate that the nematode infests from 50–60% (California, Florida) to as many as 90% (Texas, Arizona) of current orchards. Similar statistics are reported worldwide (Van Gundy & Meagher, 1977 ; Heald & O'Bannon, 1987).

Tylenchulus semipenetrans was first detected on citrus roots in California in 1912 and named and described during the next two years (Cobb 1913, 1914). The nematode causes the disease "slow decline" of citrus. The primary effect of *T. semipenetrans* in newly infested sites is a gradual reduction in tree quality so that over a period of years infested trees are smaller and less productive than normal. The name "slow decline" is less appropriate when young trees are replanted into heavily infested soil where pronounced effects on tree growth may be noted soon after planting.

Symptoms

Symptom development depends on overall orchard conditions. Infested trees growing under otherwise optimum conditions may yield somewhat less fruit while appearing quite healthy. As conditions become less suitable for tree growth, effects of citrus nematode parasitism are more apparent (Van Gundy & Martin, 1961; Van Gundy *et al.,* 1964; Heald & O'Bannon, 1987). In new citrus plantings, symptoms development progresses slowly as nematode populations develop to high levels (Cohn *et al.,* 1965). Symptoms are those associated with poor root development. Leaves are smaller and may become chlorotic. In highly saline conditions, excessive sodium may accumulate in leaves (Van Gundy & Martin, 1961; Heald & O'Bannon, 1987). Wilting occurs earlier during periods of water stress and leaf drop is more pronounced producing exposed branch terminals.

Heavily infected feeder roots are slightly thicker than healthy roots and have a dirty appearance due to soil particles that adhere to gelatinous egg masses on the root surface (Plate 7 A-C). Symptoms may not be apparent on lightly infected root systems so that infected nursery stock may easily go undetected. Feeder roots decay faster due to loss of integrity at the epidermis and at feeding sites in the cortex resulting in invasion by secondary organisms (Schneider & Baines, 1964; Cohn, 1965*b;* Hamid *et al.,* 1985). This may be expressed as lesions on lightly infected roots, while heavy infections result in cortical sloughing and root death.

Biology

The biology of *T. semipenetrans* is described in Chapter 1. The life cycle is regulated by host phenology in addition to seasonal changes in the soil environment. There may be one (Prasad & Chawla, 1965; Bello *et al.,* 1986) or two (Vilardebó, 1964; O'Bannon *et al.,* 1972; Salem, 1980; Baghel & Bhatti, 1982; Duncan & Noling, 1988*a*) distinct periods of active population development per year, although no consistent seasonal periodicity in the number of eggs hatching per gram of root occurred during a survey in Israel (Cohn, 1966). In Florida, populations increase following a large flush of root growth which occurs in the late summer and autumn (July-November) (O'Bannon *et al.,* 1972; Duncan & Noling, 1987). This is often the period of maximum female fecundity. During the spring season (April-May), soil populations continue to increase and reach the highest annual level, even though fecundity may be lower than during the autumn (O'Bannon & Stokes, 1978; Duncan & Noling, 1988*b*). Lowest population levels occur during the summer and, depending on cumulative temperatures, during the winter. Thus, the autumn growth flush of roots may represent a major part of the food source for Florida populations of *T. semipenetrans.* Population growth slows or becomes negative as winter temperatures decline, but continues to increase when spring temperatures again become favourable. Soil temperature and moisture are not unfavourable for nematode development during the summer months. Population decline during this season may be partly due to factors such as increased biological antagonism, reduced availability of young feeder

roots that may be most suitable for penetration and development (Cohn, 1964) or reduced availability of carbohydrates in roots during early fruit set and development. A model of *T. semipenetrans* seasonal populations dynamics was derived from data from a Florida survey (Duncan & Noling, 1988*b*). The model predicts regular, seasonal population changes, the magnitude of which are based primarily on feeder root growth measurements.

Biotypes or races

Physiological races or biotypes of *T. semipenetrans* exist based on host suitability (Baines *et al.*, 1969*a,b*). Since the races vary somewhat by geographic region, so do suitably resistant cultivars. Within citrus, cultivars of *Poncirus trifoliata* are resistant to most populations of *T. semipenetrans*. Several hybrids of *P. trifoliata* and *C. sinensis* such as Troyer citrange and Carrizo citrange are resistant to infection by some, but not all, populations of citrus nematodes (DuCharme, 1948; Cohn, 1965*b* ; Feder, 1968; Baines *et al.*, 1969*b*)and there is evidence from greenhouse trials that they may tolerate infection without significant damage (Kaplan & O'Bannon, 1981). Resistant hybrids of *P. trifoliata* continue to be reported (Gottlieb *et al.*, 1986; Spiegel-Roy *et al.*, 1988) and may provide acceptable rootstocks in the future. Swingle citrumelo (*C. paradisi* x *P. trifoliata*)is a commercially acceptable rootstock with a high degree of resistance to all known populations of *T. semipenetrans*. *Severinia buxifolia* is a citrus relative with a high degree of resistance to the citrus nematode which may become a source of germplasm in intergeneric breeding programs.

Based on a number of reports, four biotypes of the nemtode were proposed (Inserra *et al.*, 1980; Gottlieb *et al.*, 1986). A "Citrus" biotype was described from populations found throughout the United States citrus-growing regions and Italy. It reproduces poorly on *P. trifoliata* but will reproduce on *Citrus* spp. and on the hybrids "Carrizo" and "Troyer" citrange as well as on olive (*Olea europeae*) grape (*Vitis vinifera*) and persimmon (*Diospyros* spp.). The "Poncirus" biotype, found in California, reproduces on most citrus including *P. trifoliata,* and on grape but not olive. A "Mediterranean" biotype is similar to the "Citrus" biotype, except that it does not reproduce on olive. It is found throughout the Mediterranean region, South Africa and perhaps India. A "Grass" biotype was described from Florida, infecting *Andropogon rhizomatus,* but not citrus. "Grass" biotypes have since been reported from a number of non-cultivated hosts in Florida and were recently assigned to the species *Tylenchulus graminis* and *T. palustris* (Inserra *et al.*, 1988).

Factors identified as responsible for resistance of citrus to *T. semipenetrans* population development include host-cell hypersensitivity, wound periderm formation, compounds in root tissues which are toxic to the nematode and unidentified factors which result in low rhizoplane nematode levels early during the infection process (Van Gundy & Kirkpatrick, 1964; Kaplan & O'Bannon, 1981).

Environmental factors affecting parasitism

Factors in addition to host phenology that regulate *T. semipenetrans* populations include host variety, age and quality, and soil texture structure, moisture, pH and nutrient status. Reproductive rates of different races of the nematode obviously vary with rootstock (O'Bannon & Hutchinson, 1974). Even on susceptible commercial rootstocks, reproduction rates may differ considerably (Davide, 1971; O'Bannon *et al.*, 1972). While the scion does not appear to influence resistance or susceptibility of a rootstock, it does influence the general quality of the root system in terms of nematode development (Kirkpatrick & Van Gundy, 1966; Bello *et al.*, 1986). Nematode morphology is also affected to some degree by the host species of citrus (Das & Mukhopadhyaya, 1985). Tree age has a marked affect on population size and distribution (Cohn *et al* ., 1965; Sharma & Sharma, 1981; Bello *et al.*, 1986). In Arizona and Florida, population growth was slow on young trees until canopies developed sufficiently to shade the soil and result in optimum soil temperatures (Reynolds & O'Bannon, 1963*a*). Tree quality also influences rhizosphere conditions such as soil temperature and moisture based on the amount of shade and the transpirational demand.

Tylenchulus semipenetrans is broadly adapted to most edaphic and enviromental conditions common to citriculture. The nematode is sensitive to extreme moisture deficits but population

development occurs across the normal moisture range of agricultural soils (Van Gundy & Martin, 1961; Van Gundy *et al.*, 1964). Similarly, when conditions are otherwise favourable, populations will increase between temperatures of 20–31°C with maximum development at 25°C and very slow development at the extremes (O'Bannon *et al.*, 1966). The nematode will survive in any soil whose texture is suitable to citrus, although unlike many nematode parasites, development is less rapid in sandy soils. Moderate amounts of clay and silt (Van Gundy *et al.*, 1964; Davide, 1971; Bello *et al.*, 1986) and organic matter (O'Bannon, 1968) favour infection and development. Populations develop best at pH 6.0.–8.0; however, at less optimum pH, the nematode is also pathogenic to citrus (Martin & Van Gundy, 1963; Reynolds *et al.*, 1970; Davide, 1971; Bello *et al.*, 1986).

The age structure of a root system is affected by nematode parasitism; as infection rates increase, root systems initiate more new roots in response to increasing damage. Nevertheless, root biomass does not increase due to higher root mortality (Hamid *et al.*, 1985). Thus, infested trees invest proportionately more resources to root turnover. Such qualitative differences in root systems of healthy and declining trees may influence nematode populations directly in terms of food quality and indirectly through changes in the rhizosphere (Duncan & Noling, 1987).

Tree nutrition influences population levels (Martin & Van Gundy, 1963; Mangat & Sharma, 1981). Conversely, reduced mineral content (Zn, Mn and Cu) in leaves of citrus infested with *T. semipenetrans* has been measured along with increases in sodium to toxic levels (Van Gundy & Martin, 1961). However, deficient and excessive mineral levels occurred only when plants were growing in suboptimum conditions. In this regard, populations of *T. semipenetrans* increased on trees irrigated with water whose salinity was moderately toxic to citrus compared with control trees (Machmer, 1958). While there is some evidence that feeder roots of heavily infected trees may accumulate smaller starch reserves (Cohn, 1965*a*), only small differences in carbohydrates concentrations in leaves were measured based on degree of nematode infection (Hamid *et al.*,1985). Carbohydrate reserves in the major roots of infected and non-infected trees have not been reported.

Other hosts

In general, the citrus nematode has a narrow range of host genera. Although 75 rutaceous species (mainly citrus and citrus hybrids) support the nematode, only a few non-rutaceous hosts have been identified, the most important of which are grape, olive and persimmon.

Economic importance and population damage threshold levels

Although *T. semipenetrans* influences citrus yields differently under various circumstances, guidelines have been published to help interpret soil sample results. It was estimated in California that soil stages (juveniles/100 g soil) below 800 represents a non-damaging population level (Van Gundy, 1984). Orchards with levels greater then 1600 may respond economically to nematicide treatment and at levels above 3600 treatments may improve yield substantially. Populations were estimated during the peak growth period of May-July. Females/g root also are used in California to define damage levels, with counts of <300, >700 and >1400 representing low, moderate and high ranges, respectively. In a Florida orchard, it was estimated from samples procured during the peak period of soil population development that yields were not measurably reduced if populations were below 2000 juveniles/100 cm^3 soil (Duncan & Noling, unpubl.). The threshold was approximately 850 juveniles/100 cm^3 soil when populations were measured during periods of low population development. Grapefruit yields in Texas orchards, some of which were treated with nematicides, were according to the equation:

$$\text{yield} = 160.3\ e^{-0.0000429\ \times}$$

where yield is kg/tree and X = nematodes/100 cm^3 soil (Timmer & Davis, 1982). Factors important in determining threshold levels are discussed in the sections on methods of diagnosis below.

Methods of diagnosis

Sampling

Key elements in estimating the level of *T. semipenetrans* in an orchard include the sample size, measurement units, and the procurement location and season. Sample size can be reduced by sampling during seasons of peak population growth and in zones of highest feeder root and nematode concentration (Nigh, 1981*a* ; Duncan, 1986). Stratification of orchards into areas of healthy and unhealthy trees also improves sample precision (Scotto la Massèse, 1980).

Seasonal variation of nematode life stages in the soil and roots during normal conditions in many areas of the world are in the order of 3- to 5-fold (O'Bannon *et al.*, 1972; Salem, 1980; Baghel & Bhatti, 1982; Duncan & Noling, 1988*b*). For comparative purposes, it is important to standardize a sample season, preferably when peak populations are attained. Similarly, feeder roots and nematodes are more abundant beneath the tree canopy than at the dripline or in rows between trees (Nigh, 1981*b*; Davis, 1985; Duncan, 1986). Low volume irrigation systems concentrate root and nematode populations even further in the wetted zones.

Most published work on sample size indicates that accurate estimation of the population level of *T. semipenetrans* is costly. Five samples, each consisting of 15 cores (2.5 x 30 cm) of soil were required to estimate population levels to within 20% of the true mean in a Texas grapefruit orchard (Davis, 1984). In Florida, where population levels are generally lower, between 30–75 cores were necessary to estimate population levels in 2 ha areas of various orchards within 40% of the true mean (McSorley & Parrado, 1982*b* ; Duncan, 1988). Despite a lack of high precision, sampling is valuable since the majority of population estimates are well above or below damage threshold levels. Some laboratories suggest that samples be procured to a depth of at least 60 cm (Van Gundy, 1984), although in a study conducted in a shallow rooted citrus orchard, the population levels in the first 30 cm soil were used to predict the population level in the first 60 cm of the soil horizon (Duncan, 1986).

Laboratories frequently determine infestation levels as nematodes/unit soil weight or volume. A disadvantage to such a method is that a given population level may represent a different parasitic burden depending on whether it is from a healthy or an unhealthy tree (Scotto La Massèse, 1980; Duncan, 1986). If feeder roots are separated from soil samples, soil stage nematode counts can also be expressed as nematodes per root weight in a sample to provide some indication of the number of parasites produced for a given amount of root material. Comparison of such counts may be affected by mortality in the soil and reinvasion of roots, both of which can vary depending on season and edaphic and environmental conditions. Nematodes hatching from root samples are easily obtained (Young, 1954; Cohn *et al.*, 1965; Tarjan, 1972), provide similar information and there is evidence that such counts are less affected by season in some (Cohn, 1966), although not all (O'Bannon *et al.*, 1972) regions. Again, direct comparison of egg hatch data from roots as a measure of parasitic stress can be confounded when roots collected under various soil conditions are processed under uniform, optimum conditions for egg laying and eclosion. Females per unit root can also be determined by extraction (Baines *et al.*, 1969*b*) or direct counts on stained roots (Davis & Wilhite, 1985). Problems with adult female counts are similar to those for comparison of egg hatch data and include the fact that different conditions may result in populations of adult females with different age structure and therefore different fecundity, the main source of metabolite drain to the plant. When sample populations are collected from root material exclusively, it may be difficult to determine whether changes in parasites/root weight is due to changes in nematode level, root levels or both. To overcome this problem, it is necessary to obtain roots from a defined volume of soil rather than selecting a predetermined quantity of roots.

Extraction

Juveniles of *T. semipenetrans* can be separated from soil by most conventional methods. Techniques based on Baermann funnel principles appear to be similar in efficiency to techniques employing

density flotation (Nigh, 1981*b* ; McSorley & Parrado, 1982*a*). A number of methods are used to extract root stages of the nematode, based on maceration (females) (Baines *et al.*, 1969b) or incubation (hatched juveniles) (Young, 1954; Cohn *et al.*, 1965; Tarjan, 1972).

Determination of populations and crop loss

Economic loss assessment in mature, perennial crops is complicated by the fact that the difference in yields between nematode infested and non-infested trees is due to long-term, cumulative stress. The nematodes on the root system affect fruit development, however, infested trees are also smaller and less healthy due to previous effects of parasitism. Factors in addition to nematodes frequently contribute to poor tree conditions and a given number of nematodes/quantity of root system may be more detrimental to unhealthy than to relatively healthy trees (Cohn, 1972; Heald & O'Bannon, 1987). Therefore, efforts to assess regional crop losses must eventually consider orchard condition, tree and rootstock varieties, edaphic, cultural and climatic factors in addition to infestation level of the nematode. Assessment of crop losses in terms of how nematodes affect yields under various conditions can: 1) restrict nematode management to situations for which it is economically justified, and 2) in some cases, result in nematode management programs which profitably focus on orchard improvements that do not aim directly at reducing nematode levels.

Two approaches have been employed for citrus nematode crop loss assessment. Nematode populations have been reduced with nematicides and subsequent yields monitored, or alternatively, the relationship between nematode infestations and yields have been examined. Both techniques have limitations. It is evident from the bulk of experimental evidence that infection by citrus nematodes reduces tree quality and fruit yield and quality. It is generally not clear to what extent other factors may have influenced the results of these studies. When orchards are treated with nematicides, rhizosphere organisms in addition to nematodes are affected (Baines *et al.*, 1962, 1966; Mankau, 1968; Milne & du Toit, 1976; O'Bannon & Nemec, 1978). In the case of systemic chemicals, above-ground pests and other fauna associated with the tree may also be affected (Milne & De Villiers, 1977; Childers *et al.*, 1987). Chemical treatments may also directly affect plant development negatively (Cohn *et al.*, 1968; Timmer, 1977) or positively (Wheaton *et al.*, 1985). Similarly, relating crop yields to nematode infestation levels can be confounded by unmeasured edaphic variables that affect both nematode and tree. No experiments in which mature trees are randomly infested with the nematode have been reported.

Experiments in which nematicide treatments resulted in significant citrus yield increases have been widely reported (Baines, 1964; Yokoo, 1964; Cohn *et al.*, 1965; Oteifa *et al.*, 1965; Philis, 1969; O'Bannon & Tarjan, 1973; Vilardebó *et al.*, 1975; Davide & Dela Rose, 1976; Milne & Willers, 1979; Timmer & Davis, 1982; Childers *et al.*, 1987). Treatment responses in these and other experiments ranged from none to several hundred percent increase in fruit from treated trees in poor quality orchards. Although tree response to nematicide treatment on the average is positive, results have been erratic. Good yield responses have been measured following treatments which did not reduce population levels (Davis *et al.*, 1982) and in some cases, consistent, strong reduction of populations has not resulted in measurable tree response (Davis, 1985). Such results indicate that we do not adequately understand the effects of some nematicide treatments, the damage level of *T. semipenetrans* nor the interaction of the nematode with other debilitating factors under most conditions. On the average, yield increase in response to nematicide treatment has been of the order of 15–30%.

Studies relating tree quality and yield with nematode infestation level report similar findings. Under uniform soil conditions within orchards (Reynolds & O'Bannon, 1963b; Scotto la Massèse, 1980; Coelho *et al.*, 1983) or considering specific varieties between orchards (Davide, 1971), the highest levels of soil stages of *T. semipenetrans* were frequently measured beneath trees with only moderate symptoms. Healthy trees supported smaller populations that had not yet caused significant damage while the reduced root systems of severe decline trees were incapable of supporting high nematode populations. Alternately, it may be possible under such conditions to measure an inverse

relationship between infestation level and tree quality if root abundance is measured along with nematode population level. Figure 1 shows soil-stage population levels of *T. semipenetrans* during a 15-month period in a Florida citrus orchard with slow decline (Duncan & Noling, 1988*a*). The root systems of healthier trees supported higher population levels of *T. semipenetrans* . However, if populations are expressed per gram of feeder roots in the same volume of soil, it is evident that the actual rhizosphere nematode population level increased as tree quality declined. Similarly, in Israel, the average tree quality index declined with nematode infestation level beyond a specific

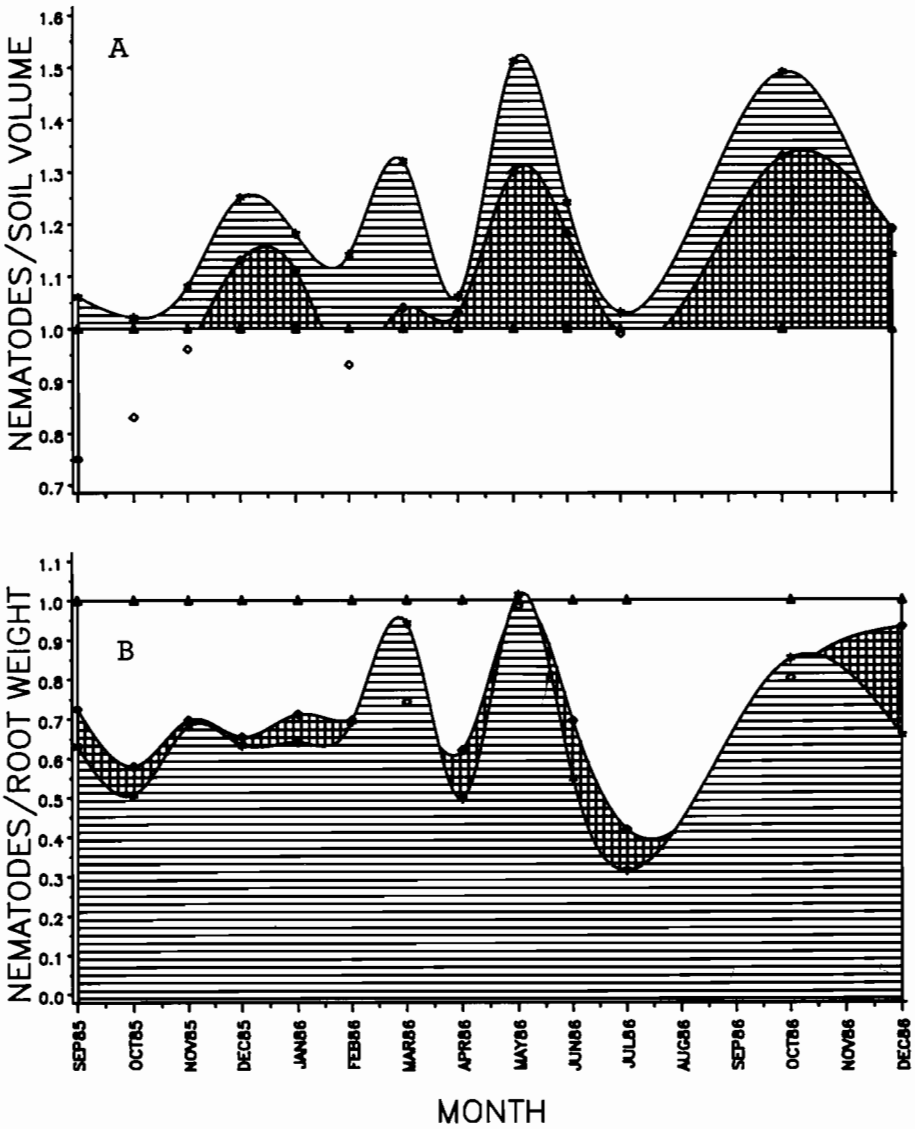

Fig. 1. The relative abundance of migratory stages of *Tylenchulus semipenetrans* under healthy (asterisk, n = 15), moderately declining (diamond, n = 40) and severely declining (triangle, n = 12) citrus trees. Population levels are expressed as (A) nematodes/volume of soil in a sample, or (B) as nematodes/weight of feeder roots in a sample. For each date, the mean population level for each tree category was divided by the mean level from the severely declining trees.

threshold level (40 000 nematodes/g root weight) when numbers of nematodes hatching from feeder roots were used as the unit of measurement (Cohn *et al.*, 1965).

Citrus fruit yield has also been negatively correlated with infestation level (Willers, 1979; Timmer & Davis, 1982; Childers *et al.*, 1987; Noling & Duncan, 1988).

Control

Methods commonly employed to control *T. semipenetrans* depend on local conditions and focus on: 1) excluding the pest, 2) minimizing losses through crop management and 3) reducing population levels of the pest.

Exclusion

Most citrus growing regions have few serious nematode pests so that exclusion of *T. semipenetrans* from orchards is a realistic goal to preclude the perennial expense of nematode management. Occasional introductions of *T. semipenetrans* into non-infested orchards does not negate the value of a conscientious sanitation program, since the nematode migrates very slowly on its own power (Meagher, 1967; Tarjan, 1971; Baines. 1974). In a recent survey of mature orchards in Florida, a large number of *T. semipenetrans* infested orchards appear to have fewer than 10% infested trees (Ferguson & Dunn, unpubl.). In the absence of flooding and particularly with the use of low volume irrigation, trees may remain uninfected for long periods, despite the existence of nematodes on adjacent trees. Exclusion of *T. semipenetrans* is relatively simple in most newly planted orchards and in non-infested existing orchards. Since the host range of the nematode is limited to only a few non-rutaceous plant species, infestation usually results from movement of infected planting stock (Van Gundy & Meagher, 1977) or on contaminated equipment (Tarjan, 1956). Programmes to approve and monitor nursery sites and certify that nursery stock is nematode free have been highly effective in limiting the distribution of *T. semipenetrans* (Milne, 1982). Such programs focus on: 1) continuous monitoring through soil sampling, 2) isolating nursery locations to avoid runoff water from infested orchards and 3) security to prevent contaminated equipment, footwear, etc. from entering the nursery area. Separate equipment for use in infested and non-infested orchards may be feasible in some cases, otherwise equipment must be continually disinfested prior to movement into non-infested orchards (Esser, 1984). Irrigation with some forms of surface water such as canals and rivers has been found to represent a serious source of inter-orchard contamination by *T. semipenetrans* and *Phytophthora parasitica* (Cohn *et al.*, 1976) particularly since pests can be widely spread in a short time. Irrigation water can be decontaminated through the use of settling ponds and filtration systems but the procedures require careful maintenance (Cohn, 1976).

Crop management

The value of optimum cultural practices in relation to the economic and environmental costs associated with many forms of nematode management should be carefully evaluated. A large number of biotic and abiotic forms of stress can damage citrus to a greater degree than *T. semipenetrans*. The effect of the nematodes can be proportionately greater on citrus plants with additional forms of stress than on otherwise healthy plants (Machmer, 1958; Martin & Van Gundy, 1963; Wheaton *et al.*,1985; Labuschagne & Kotze, 1988), although this has not always been reported (O'Bannon *et al.*, 1967). Nevertheless, nematode management can have a limited effect on trees in orchards where tree quality is impaired by other causes. Correcting such factors as poor water drainage, inadeqate bed height for root development, drought stress, excessive salinity, exposure to cold damage, irrigation practices that favour *Phytophthora* root rot, etc. should be considered as important objectives when developing pest management strategies. Subsequently, nematode management may faciliate tree recovery from other forms of stress in addition to nematode parasitism.

Direct management of nematode populations

Direct suppression of citrus nematode populations relies on the use of resistant rootstocks or nematicidal chemicals. While biotypes of *T. semipenetrans* limit the usefulness of some resistant rootstocks such as the Troyer and Carrizo citranges, other commercially acceptable rootstocks such as Swingle citrumelo appear to be very resistant to the known populations of the nematode. Swingle is also resistant to feeder root-rot caused by *Phytophthora parasitica*, Tristeza, and is also reasonably cold-tolerant (Wutscher, 1974). Recently, several selections of Poorman orange (*Citrus* x hybrid of undertermined origin) x *P. trifoliata* hybrids exhibiting combined resistance to *Phytophthora citrophthora* and Tristeza were found to be highly resistant to more than one biotype of the nematode (Gottlieb *et al.*, 1986; Spiegel-Roy *et al.*, 1988).

Nematicides are broadly classified by whether they are used prior to, or following, planting. The most effective preplant nematicides in citrus are fumigants such as methyl bromide, metam sodium and 1,3-dichloropropene. Previously, dibromochloropropane (DBCP) was widely used to control citrus nematodes until it was banned in most countries for health and environmental reasons. The fumigants act directly on nematodes as contact poisons. Preplant fumigation of old orchard sites with histories of citrus nematode infestation is important to prevent the rapid infection of young trees (Baines *et al.*, 1956, 1966; O'Bannon & Tarjan, 1973). Citrus nematodes are well adapted to survive in the absence of plants (Cohn, 1966; Van Gundy *et al.*, 1967) and have been detected in fields for as long as 9 years after the removal of citrus (Baines *et al.*, 1962; Hannon, 1964). Fumigants can adversely effect young tree growth under some conditions (Cohn *et al.*, 1968; Milne, 1974). It is important to observe proper intervals between treatment and planting to avoid phytotoxicity. In nurseries which experience frequent or very thorough fumigation, mycorrhizal fungi may be nearly eradicated (O'Bannon & Nemec, 1978; Timmer & Leyden, 1978). To avoid phosphorus deficiency, replanted nursery stock should be mycorrhizal or seedbeds should be reinoculated with endomycorrhizal fungi. This problem is seldom encountered when replanting orchards since plants in fumigated sites are quickly invaded by fungi from adjacent soil if they are not mycorrhizal at the time of transplanting (Graham, 1988).

Post-plant nematicides in citrus are generally carbamate or organophosphate, acetylcholinesterase inhibitors. Most of the post-plant citrus nematicides such as aldicarb, fenamiphos and oxamyl are translocated systemically within the tree. Aldicarb is used in some citrus areas as a broad spectrum insecticide/nematicide. In others regions, aldicarb is not used because the insecticide/miticide characteristics disrupt biological control in the canopy of the tree. Fenamiphos has a basipetal movement from the point of application which provides a somewhat higher level of nematode control in the deeper soil profiles (O'Bannon & Tarjan, 1979). All of the nematicides used in citrus are incorporated in the soil either mechanically or with irrigation for efficacy and human and wildlife safety. They are inappropriate for small farms that lack proper, safe application equipment.

Three important aspects of treatment with the commonly available post-plant nematicides involve the timing, placement and retention time of the chemical. Where population levels and root growth are seasonally defined, treatment should precede periods when nematodes actively invade new roots. Nematicides in large commercial citrus orchards are often applied in bands down the tree rows or through low volume irrigation systems rather than broadcast. Since the abundance of nematodes and feeder roots in the upper soil horizons decline quickly with distance from the trunk, bands are most effective when they are applied as much as possible beneath the tree canopy (Nigh, 1981*a* ; Duncan, 1986). On grapefruit, nematode control was more effective and yields were increased when the nematicide was applied in a band under the canopy rather than at the dripline (Duncan, unpubl.). When nematicides are applied through low volume irrigation systems they arrive in areas of highest root and nematode abundance.

Retention time in the upper soil horizons affects nematicide efficacy and determines the amount of pesticide that eventually moves below the root system and becomes available as a water pollutant (Thomason, 1987). Precipitation rates and timing have the largest manageable influence on pesticide movement in the soil. Irrigation can be scheduled to prevent free water movement below the rooting

zone. In Florida, aldicarb is applied during the dry spring months in order to have as much control of movement via irrigation as possible.

No systemic citrus nematicide is presently registered for application to the above-ground plant parts, however, a great deal of information supports the efficacy of trunk and foliage applications of some compounds (Zeck, 1971; Tarjan, 1976; O'Bannon & Tomerlin, 1977; Timmer & French, 1979; Anon. 1986). While the cost of above-ground nematicide treatment may be greater or less than soil application, depending on cost of material and labour, the possibility of water pollution is reduced and nematicides are translocated proportionately within the root zone. Because of the small application zone, trunk applications should also reduce the exposure of humans and wildlife to the chemicals.

Consideration of possible environmental effects should be part of a decision on whether to treat the soil with nematicides. As a class of pesticides, nematicides have been heavily restricted in recent years due to environmental contamination and possible health effects (Thomason, 1987). The treatment of nematode pests in citrus orchards has resulted in contamination of large numbers of drinking water wells with several pesticides, some of which (ethylene dibromide and dibromochloropropane) have subsequently been banned for use in the United States and elsewhere (Kaplan, 1988). Under certain conditions of soil type, precipitation rate, and water table level, the potential for groundwater contamination exists for most chemicals that are applied to the soil. Computer models which simulate the movement of agrichemicals in soils are available to assist in determining whether specific nematicides can be used safely (Nofziger & Hornsby, 1987; Duncan & Noling, 1988*a*).

Additional nematode parasites of citrus

Nematodes other than *T. semipenetrans* currently known to be capable of damaging citrus tend to be very limited in distribution. Accordingly, with the exception of burrowing nematodes, considerably less is known about the relationship between other nematode species and citrus. Both migratory endoparasites (lesion and burrowing nematodes) and sedentary endoparasites (root-knot nematodes), as well as a number of species of ectoparasitic nematodes can damage citrus. Additionally, there are nematode species commonly found in the citrus rhizosphere for which insufficient information exists to determine their pathogenic potential.

Radopholus citrophilus

Spreading decline is a severe disease of citrus caused by *Radopholus citrophilus* that is only encountered on Florida's central ridge of deep sandy soils. The nematode is commonly called the burrowing nematode because of its extensive tunneling through root tissue as a migratory endoparasite. The disease was first described in 1928 and the causal organism was identified in 1953 (Suit & DuCharme, 1953). The name of the disease is descriptive of the rapid progression of decline in infested groves which can reach 15m/yr. The nematode was formely known as the citrus race of *R. similis* (Cobb) Thorne, and was distinct from the banana race for which citrus is not a host (DuCharme & Birchfield, 1956). It was renamed as a sibling species to *R. similis* (formerly the banana race of *R. similis*)in 1984 based on differences in chromosome number, isozyme patterns, mating behaviour and host preference (Huettel *et al.*, 1984); small morphological differences have also been detected (Huettel & Yaegashi, 1988). With the new classification, host preference may become a minor species determinant since a population of *R. citrophilus* that attacks *Anthurium* sp. but not citrus has been detected in Hawaii (Huettel *et al.*, 1986). Similarly, a population of *R. similis sensu lato* with five chromosomes (as does *R. citrophilus*)for which citrus is not a host was reported from plantain in Puerto Rico (Rivas & Roman, 1985*a,b*). Because it is presently difficult to identify *R. citrophilus* with certainty, due to the nature of the several criteria which must be considered, governmental

regulatory agencies continue to quarantine "*R. similis*" as the burrowing nematode without regard to the concepts of races biotypes or sibling species (Holdeman, 1986).

Symptoms

Spreading decline is generally distinguishable from other major decline diseases such as citrus blight in that large contiguous groups of trees are affected and expansion of the diseased area is rapid. Forced water uptake in the trunk of the tree (Graham *et al.*, 1983) is indistinguishable from normal trees and is another rapid preliminary method to determine whether a tree may be infected with *R. citrophilus* rather than suffer from citrus blight. Decline trees have sparse foliage, particularly high in the canopy during the early stages of the symptom development. Leaves and fruit are small and fewer mature fruit remain on trees. Branch ends are bare and eventually entire branches die. Affected trees wilt rapidly during periods of low soil moisture particularly during the periods of drought that tend to occur in the winter and spring in Florida. It is during these periods that disease progression is most rapid.

Symptoms on roots are most apparent below 25–30 cm so that evidence of damage to the abundant shallow portion of the root system may be lacking (Ford, 1952, 1953). The most obvious symptom to the root system is the reduction in the quantity of feeder roots in the deeper soil profiles. At depths of 25–50 cm, 75% of the root system may remain, but below this level the root system is almost totally destroyed. Since mature citrus growing on the deep sands of the ridge may establish as much as half of the feeder roots between 1 and 6 m, destruction of the deep root system on a large tree accounts for the drought-related aboveground symptoms during periods of moisture stress. Infected feeder roots develop dark lesions at the points of nematode entry and activity which expand and coalesce as secondary pathogens destroy these tissues. Nematodes may burrow in a section of root for several weeks completely destroying the phloem and much of the cortex (Plate 7E), girdling the central cylinder (DuCharme, 1959). On larger roots, the lesions can form callused margins (Feder & Feldmesser, 1956). The nematode penetrates the region of elongation and root tips can become swollen due to hyperplasia and stubby if terminals are penetrated (Feder & Feldmesser, 1956; DuCharme, 1959, 1968).

Biology

Radopholus citrophilus on citrus has a life cycle of 18–20 days under optimum conditions (DuCharme & Price, 1966) permitting population levels to increase rapidly when conditions are favorable (DuCharme & Suit, 1967). Following root penetration, mature females begin to lay eggs at an average rate of nearly two per day and eggs hatch in 2–3 days. In gnotobiotic culture, colonies initiated with single females attained average population levels of more than 11 000 individuals in less than 3 months, although rhizosphere competitors restrict population growth in orchards far below such a level (DuCharme & Price, 1966). The nematodes can reproduce parthenogenically (Brooks & Perry, 1962) and sexualy (Huettel *et al.*, 1982). Mature males do not feed and comprise 0–40% of the population, averaging about 10% (DuCharme & Price, 1966). The nematode remains within the root until forced by overcrowding and decay to migrate.

Survival and means of dissemination

Radopholus citrophilus does not survive for long periods in the absence of host roots (DuCharme, 1955). In field trials in which root material was excluded, the nematode could not be detected in samples after 6 months (Tarjan, 1961). However, under more natural experimental conditions, the nematode has been detected up to 14 months under bare-fallow conditions (Hannon, 1963) and unconfirmed reports suggest as long as 2 years (Suit *et al.*, 1967). Large root fragments that remain buried in soil after tree removal may help support populations during fallow.

The nematode is spread in contaminated rootstock (Poucher *et al.*, 1967), machinery (Tarjan, 1956), subsoil water (DuCharme, 1955) and it migrates rapidly along developing root systems. In orchards, the spreading decline disease is reported to move as much as 15 m/yr (Poucher *et al.*,

1967), while in greenhouse tests, movement of about a quarter to a third of that rate has been measured (Feldmesser *et al.*, 1960; O'Bannon & Tomerlin, 1969*a*; Tarjan, 1971).

Host range

Radopholus similis sensu lato is remarkably polyphagous, attacking more than 250 plants in 15 families outside of the Rutaceae (Ford *et al.*, 1960). Within the citrus and closely related genera, more than 1200 species, varieties and hybrids have been screened for resistance or tolerance to *R. citrophilus* (Ford & Feder, 1961; O'Bannon & Ford, 1976). Three varieties of citrus, Ridge Pineapple, Estes rough lemon and Milam lemon. and a *P. trifoliata* x *Citrus* hybrid, Carrizo citrange, have been released as rootstocks since 1958. Although data on tolerance under field conditions is very limited, all of the rootstocks have subsequently been shown to support *R. citrophilus* or local biotypes of *R. citrophilus* capable of breaking resistance (Poucher *et al.*, 1967; Kaplan & O'Bannon, 1985). In the case of Carrizo citrange, considerable variability exists within the progeny for susceptibility to burrowing nematodes (Kaplan, 1986).

Environmental factors affecting parasitism

The biology of *R. citrophilus* related to citrus, is stongly influenced by edaphic conditions. The nematode is found in citrus growing regions of Florida other than the ridge but populations do not develop to damaging levels. This is probably related to interactions between soil temperature, moisture and root growth periodicity. The cardinal temperature for *R. citrophilus* is 24°C and development occurs between 12 and 32°C. Optimum temperatures occur for the longest periods each year in the deeper soil horizons where highest reproduction is known to occur. Highest absolute populations in soil samples are found in the late summer-early autumn period when optimum temperatures combine with an annual cycle of root growth to support population increase. As the root-growth cycle declines later in the autumn, infected roots begin to die and soil populations begin to decline even though the nematodes recovered per unit of root tends to be highest in the late autumn (DuCharme, 1967, 1969). The temperature extremes in the in surface soil horizon are nearer the limits for development of *R. citrophilus* during the period of root growth which may partly explain low population development in surface roots. The nematode does not have a known resting stage so that moisture deficits which are more commonly encountered in the shallow horizons may also inhibit development in this zone (Tarjan, 1961).

Soil texture is also an important determinant in the spreading decline disease cycle. The nematode is more pathogenic to citrus in pot studies in sandy than loamy soils (O'Bannon & Tormerlin, 1971). Movement of *R. citrophilus* is highest in light textured soil (Tarjan, 1971).

Disease complexes

Few reports exist of interactions between *R. citrophilus* and other rhizosphere organisms (Feder & Feldmesser, 1961). Feldmesser *et al.*, (1959) obtained indirect evidence that secondary fungal invaders play a key role in the disease complex when they treated infected seedlings with the fungicide captan which increased nematode population levels as well as root and top weights of plants. Root lesions are quickly infected by fungi and other rhizosphere inhabitants (Feder *et al.*, 1956; DuCharme, 1968). *R. citrophilus* population levels declined in the presence of mycorrhizal fungi, probably due to enhanced phosphorus uptake because the effect was also obtained on plants growing with supplemental phosphorus (Smith & Kaplan, 1988). Similarly, citrus plant tolerance to *R. citrophilus* appears to be enhanced by mycorrhizal infection when soils are deficient in phosphorus (O'Bannon & Tomerlin, 1971; O'Bannon & Nemec, 1979).

Biotypes

Two populations have recently been identified as biotypes of *R. citrophilus* (Kaplan & O'Bannon, 1985). Biotype 1 reproduces poorly on Milam lemon and only moderately on Ridge Pineapple, Albritton sweet orange and Carrizo citrange. Biotype 2 reproduces well on all of these rootstocks

and causes significantly more reduction in plant growth than Biotype 1. The pathogenicity of these biotypes on most resistant varieties in the field has not been adequately investigated to date.

Economic importance and damage threshold levels

Radopholus citrophilus and a lesion nematode, *Pratylenchus coffeae*,appear to be the most virulent nematode parasites of citrus worldwide (O'Bannon *et al.*, 1976). However, since *R. citrophilus* distribution on citrus is restricted to Florida, the nematode's economic impact is slight on the world market. In 1972, it was estimated that *R. citrophilus* caused 0.1–0.2% yield losses in the world citrus industry (Cohn, 1972). In infested orchards, the losses have been estimated of the order of 40–70% for oranges and slightly higher for grapefruit (DuCharme, 1968). Although data are unavailable, it is likely that losses to spreading decline are mitigated in recent years by changing management practices described below (O'Bannon, 1977).

Control

Management of spreading decline currently focuses on restricting the spread of the nematode through planting-stock certification, sanitation and physical barriers; cultural management practices; use of resistant and tolerant rootstocks and use of nematicides.

Previous practices in the United States emphasized chemical management of the nematode through state directed efforts known as the "push and treat" and "buffer" programmes. Both programmes relied heavily on intensive sampling to accurately ascertain the limits of infested areas. In the push and treat programme, infested trees and a margin of unifested trees were destroyed, the soil was treated with high rates of DD, EDB or 1,3-D, and prior to replanting on resistant rootstocks, the soil was maintained under bare fallow for at least 6 months (Poucher *et al.*, 1967). Buffers are corridors of land 5–18 m wide created between infested and non-infested locations, in which no plants are permitted to grow. Citrus roots within the buffer zones even at great depth were killed by frequent chemical treatment at high rates (Suit & Brooks, 1957; Poucher *et al.*, 1967). The programmes were expensive and illustrate the damage caused by this disease. The cost incurred to the grower alone when the push and treat method was used to manage spreading decline was estimated to be almost 20 000 dollars/ha in 1977. Nevertheless, it is further estimated that these programmes limited the spread of the nematode by more than 90% (O'Bannon, 1977). In 1983, both programmes were discontinued due to the discovery that the nematicides being used were contaminating and persisting in local drinking water wells. A complete review of the history of these programmes is given by Kaplan (1988).

Based on the potential threat of spreading decline to citrus on Florida's ridge, avoiding infestation by *R. citrophilus* should be a high management priority. Planting stock should always be certified as pest-free. Nurseries are regularly sampled and inspected to remain certified. Commercial movement of soil within and into citrus producing areas requires certification that the site of origin is pest free. Equipment used in infested orchards should be reserved for that purpose when possible or disinfested between operations (Esser, 1984). It has been suggested that buffers between infested and non-infested locations be maintained by mechanically pruning citrus roots on the edge of the buffer zone with trenching machines, that herbicides be used to keep the zone plant free and that nematicides be used on the border of the infested zone to reduce *R. citrophilus* levels. It is critical that proper cleaning and disinfestation of the trenching machines occur prior to use on non-infested buffer margins.

In Florida, with the exception of the ridge area, citrus is commonly grown in shallow soils that permit only limited root development in the surface soil horizons. The fact that *R. citrophilus* damages primarily the deeper (below 45 cm) portion of the citrus root system, provides the opportunity to manage spreading decline with cultural or management practices designed to support a healthy, shallow root system. Infested orchards in which sound practices are employed have remained economically viable (Tarjan & O'Bannon, 1977), and may out-produce annual state production averages (Bryan, 1966). Practices which have been suggested include: use of herbicides rather than cultivation

for weed management to avoid cutting surface roots (Tarjan & Simmons, 1966); use of supplemental irrigation, particularly frequent short irrigation cycles rather than less frequent long cycles to provide sufficient water primarily to the surface root system (Bryan, 1966, 1969); use of optimum fertility schedule. It is likely that the use of management practices to maintain a vigorous, shallow root system will be more successful if young trees are permitted during growth to attain an optimum shoot to root ratio under such practices, than if large mature trees must adapt to new conditions.

There are currently two rootstocks recommended for use against spreading decline, Milam lemon and Ridge Pineapple sweet orange. Both have resistance to biotype 1 of *R. citrophilus*. A second biotype of the nematode has been isolated that reproduces well on both rootstocks and is capable of damaging seedlings in pots (Kaplan & O'Bannon, 1985). The distribution and abundance of *R. citrophilus* capable of breaking resistance to these rootstocks is unknown.

The use of systemic nematicides to suppress *R. citrophilus* in deeper roots has been effective and resulted in increased yield (O'Bannon & Tomerlin, 1977; O'Bannon & Tarjan, 1979). Fenamiphos is currently registered for use against burrowing nematodes in Florida citrus.

Diagnosis and sampling

In Florida, root samples are commonly processed to ascertain whether *R. citrophilus* is present in an orchard because the nematode is highly endoparasitic. The samples are procured to depths of 120 cm to obtain roots most likely to contain high populations of the nematode. Therefore, sampling to determine the distribution of the nematode in an infested orchard is expensive. Visual stratification of orchards based on tree decline symptoms is important in sampling for *R. citrophilus*. Random sampling is inappropriate because determination of population levels is generally not the goal of sampling for burrowing nematodes but rather delimiting an area of infestation. Intensive sampling (three samples/tree) of suspicious trees increases the chance of detecting the nematode whose population level can be quite low during some periods.

Pratylenchus

Three species of lesion nematodes, *Pratylenchus coffeae, P. brachyurus* and *P. vulnus* have been demonstrated to damage citrus. *P. coffeae* is easily the most pathogenic (Plate 7 G, H). It is widespread having been reported on citrus in the United States (O'Bannon *et al.*, 1972), India (Siddiqi, 1964), Japan (Yokoo & Ikegemi, 1966), South Africa (Milne, 1982) and Taiwan (Huang & Chang, 1976). In the United States, damage by *P. coffeae* has been observed in Florida where the nematode has been detected in only a few groves (O'Bannon & Tarjan, 1985). In South Africa, the nematode has not been associated with economic problems (Milne, 1982) as it has in other regions where it is found. Infection occurs primarily in the feeder roots where all motile stages of the nemtode penetrate cortical tissue both inter and intracellularly. If penetration of the root tip occurs, the meristem is destroyed and lateral roots are often initiated. The nematodes can be found in vascular tissues only when localized populations are unusually high. Cortical invasion results in extensive cavities, but vascular tissues remain intact until invaded by secondary organisms.

Pratylenchus coffeae appears to be obligatorily amphimictic with males feeding in the roots and comprising 30–40% of the population (Radewald *et al.*, 1971*b*). Reproduction of *P. coffeae* is highest when soil temperatures are relatively high (26–30°C). At these temperatures, populations complete the life cycle in less than one month and may reach levels as high as 10 000 nematodes/g root (O'Bannon & Tomerlin, 1969*b*; Radewald *et al.*, 1971*a*). The nematode can survive in roots in soil for at least 4 months (Radewald *et al.*, 1971*a*).

In pot studies, *P. coffeae* reduced root weights by as much as half and plant growth by 38% (Siddiqi, 1964; O'Bannon & Tomerlin, 1969*b*; Radewald *et al.*, 1971*a*). In the field, damage by *P. coffeae* can be severe. Growth reduction of young trees during 4 years in the field ranged from 49–80% depending on the rate of growth of the nematode on different rootstocks. Again, depending on the rootstock, numbers of fruits during the first bearing years ranged from threefold to twentyfold

differences between infected and non-infected trees (O'Bannon & Tomerlin, 1973). Soil types ranging from sands to sandy loams did not affect the pathogenicity of *P. coffeae* to rough lemon roots (O'Bannon *et al.*, 1976). Migration of the nematode through soil appears to be relatively slow, of the order one m/year (Tarjan, 1971; O'Bannon & Tomerlin, 1973; O'Bannon, 1980). The limited distribution of *P. coffeae* in Florida citrus is partly due to a rootstock certification program and may also be due to competition with the more widespread *T. semipenetrans*. In a survey within a grove, the two species appeared to be mutually exclusive although exclusion of one species by the other was not observed in experiments (Kaplan & Timmer, 1982). No commerical rootstocks resistant to the nematode are available, although some selections of a Microcitrus hybrid and perhaps of *Poncirus trifoliata* appear to have some resistance (O'Bannon & Esser, 1975).

Pratylenchus brachyurus has a biology similar to *P. coffeae*. Although well distributed worldwide, *P. brachyurus* varies in its distribution in citrus. In Florida, the nematode was present in 90% of groves sampled (Tarjan & O'Bannon, 1969) while it has not been reported from citrus groves in South Africa, even though it is widespread in that country (Milne, 1982). It is a proven pathogen of seedlings in greenhouse trials (Brooks & Perry, 1967; Tarjan & O'Bannon, 1969; Radewald *et al.*, 1971*a* ; Tomerlin & O'Bannon, 1974; Frederick & Tarjan, 1975), and on young trees in the field (O'Bannon *et al.*, 1974). It is generally not considered to be a problem on mature citrus, although it was suggested that other sources of plant stress such as severe drought may exacerbate damage by this species to mature trees (O'Bannon *et al.*, 1974). When populations of *P. brachyurus* in mature Valenica orange trees on rough lemon rootstock were controlled with aldicarb, trees suffered less frost damage during a severe winter and subsequent yields were increased (Wheaton *et al.*, 1985; Childers *et al.*, 1987). It is unclear, however, what other factors may have been affected by the systemic pesticide.

Like *P. coffeae, P. brachyurus* reproduces best at temperatures above 25°C and can affect seedling growth in light and medium texture soils. Movement of *P. brachyurus* through soil is not as rapid as that of *P. coffeae* (O'Bannon, 1980) and citrus is not as good a host for this nematode; populations in roots are frequently a tenth of those of *P. coffeae* (Radewald *et al.*, 1971*a*).

To date, *Pratylenchus vulnus* has been found associated with citrus in Italy (Inserra & Vovlas, 1974) and California (Siddiqui *et al.*, 1973) and was shown to be capable of causing severe damage to nursery seedlings (Inserra & Vovlas, 1977*a*). As with other species of *Pratylenchus,* the nematode is pathogenic in a range of soils from sand to sandy clay loam. Biology, population growth rates and root damage are similar to those described for *P. coffeae*. Since the nematode does not appear to be widespread in citrus orchards in Italy, certification of nursery stock to be free of the pathogen has been suggested.

Belonolaimus longicaudatus

Belonolaimus longicaudatus, the "sting nematode" which occurs in about 5% of Florida citrus orchards, can damage citrus by greatly reducing the fibrous root abundance of trees (Plate 7F). Sting nematodes are widely distributed on a number of cultivated and non-cultivated host plants in the southeastern United States. They are intimately associated with the citrus root system, and can be spread on infested planting stock, even when the roots are devoid of soil (Kaplan, 1985).

In nurseries, relatively low populations (40 nematodes/dm^3 soil) can cause aboveground symptoms of stunted, chlorotic plants (Kaplan, 1985). The nematode is ectoparasitic, feeding on root tips of citrus. Root systems of infested trees appear very coarse due to a reduction in the number of lateral roots and swollen fibrous roots. Fibrous roots also have swellings at or near terminals as well as multiple apices. The epidermis may slough easily due to secondary infection. Histological examination has shown several meristematic zones at root tips with tissue disorganization that includes hyperplastic tissue, cavities and extensive vascular formation. Cell disruption at the cavity borders results in cytoplasm leakage into these spaces and suggests them to be the possible site of feeding (Standifer & Perry, 1960; Kaplan, 1985).

Sting nematodes have been associated with severe stunting of a number of rootstocks in the field (Standifer & Perry, 1960; Esser & Simpson, 1984; Kaplan, 1985), and cause similar symptoms in pot experiments (Standifer & Perry, 1960; Abu-Garbieh & Perry, 1970). Preplant soil fumigation and post-plant nematicide treatments have alleviated symptoms of sting nematode parasitism (Bistline *et al.*, 1967; Kaplan. pers. comm.). Hot water treatment for 5 min at 49°C was sufficient to kill *B. longicaudatus* and has been suggested as an eradication method for bare-root seedlings (Kaplan, 1985).

Meloidogyne

Root-knot nematodes (*Meloidogyne* spp.) capable of attacking citrus are very limited in distribution. These nematodes are endoparasites, causing root galls. Although there have been several reports of the common species of root-knot nematodes (*M. incognita, M. javanica* and *M. arenaria*) developing or reproducing on citrus (Minz, 1956; Den Ouden, 1965; Whitehead, 1968; Scotto la Massèse, 1969; Gill, 1971), they appear to be problems in only a few localized regions. An apparently pathogenic species of root-knot nematode was reported from Taiwan and New Delhi where it caused elongated galls on citrus roots. The nematode was given the common name "Asiatic pyroid citrus nematode" and was found to be able to complete its life cycle on several citrus and other plant species including corn and sweet potato. Control measures suggested at the time focused on the use of a number of trap crops as cover crops since *Crotalaria* sp., strawberry, peanut and soybean were found to be non-hosts even though the nematode invades the roots (Chitwood & Toung, 1960). *Meloidogyne fujianensis* (Pan, 1985) and *M. oteifae* (Pan, 1984) have been reported from China on *C. reticulata* with the former species parasitizing up to 60% of citrus trees surveyed.

A more common situation in which root-knot nematodes may cause problems in citrus was reported by Van Gundy *et al.* (1959) who found that *M. incognita, M. javanica* and M. *arenaria* infected roots of Troyer citrange and sour orange causing small galls but without reproducing. Galls on plants in the field were associated with unthrifty plant growth but were found to be due to infection by populations that were supported on weed hosts. This work was later supported by that of Inserra *et al.* (1978) who observed extensive root damage due to invasion of citrus roots by *M. javanica* even though no reproduction occurred, and in Israel (Orion & Cohn, 1975) where potted citrus responded to a specialized *M. javanica* race with hypersensitivity and failure of giant cell information. Nevertheless, the threat posed to citrus production by races of the nematode capable of reproducing on citrus was sufficient to warrant an eradication effort in California of a population of *M. javanica* found to be supported by a dooryard citrus tree (Gill, 1971).

Xiphinema

A large number of nematode species of the genus *Xiphinema* (dagger nematodes) have been reported from the citrus rhizosphere (Baines *et al.*, 1978). These nematodes are all ectoparasitic. Very little research has been done regarding the pathogenicity of these nematodes to citrus even though high populations of some species have been consistently associated with citrus in California, South Africa and Sudan (Yassin, 1974; Cohn, 1976; Baines *et al.*, 1978; Milne, 1982). Most species of *Xiphinema* predominate in lighter textured soils (Cohn, 1969). In South Africa, control of *X. brevicolle* with DBCP did not result in marked tree quality improvement (Milne, 1982). In Sudan, high populations of *X. brevicolle* were associated with declining grapefruit trees. Subsequent pot studies resulted in similar root symptoms of stubby, swollen roots and root abundance was greatly reduced by the nematode (Yassin, 1974). *Xiphinema brevicolle* and *X. index* reduced sour orange seedling size by nearly half in pot studies in Israel (Cohn & Orion, 1970). Feeder root abundance on infested plants is severely reduced. Damage is primarily to epidermal and outer cortical cells which become necrotic and give a typically dark appearance to damaged roots (Cohn, 1970; Cohn & Orion, 1970; Baines *et al.*, 1978).

Trichodorus and *Paratrichodorus*

Low levels of *Trichodorus* and *Paratrichodorus* spp. (stubby root nematodes) are often encountered in soil samples from citrus (Baines *et al.*, 1959; Malo, 1961; Colbran, 1965). There is some indication that population levels may increase above the normal levels in recently fumigated soil (Perry, 1953; Standifer & Perry, 1960). *Paratrichodorus lobatus* has also been found at high levels in citrus nurseries in Australia where it is widespread in nurseries and orchards (Stirling, 1976). *Paratrichodorus porosus, P. lobatus* and *P. minor* have been reported to reduce root elongation and cause stubby root symptoms without evidence of necrosis on citrus in pot studies (Baines *et al.*, 1978; Standifer & Perry, 1960; Stirling, 1976). Despite decreasing feeder root weight in a pot study, *P. lobatus* did not affect taproot or seedling weights, nor were population levels in a nursery correlated with tree size (Stirling, 1976). However, nursery trees infested with the nematode at levels of 1500/500 cm^3 soil had reduced root systems, poor leaf colour and tended to wilt during the day. Only one other report, based on the response of young trees to soil fumigation, implicates stubby root nematodes as possible pathogens of consequence in the field (Meagher, 1969).

Many dorylaimid nematode species are vectors of plant viruses. Despite a number of attempts, no nematode transmission of citrus viruses has yet been demonstrated.

Hemicycliophora

A number of species of *Hemicycliophora* have been identified from the citrus rhizosphere. *H. arenaria* is a species native to plants in the desert valleys of southern California that causes damage in citrus nurseries (McElroy *et al.*, 1966). The nematode was closely studied (Van Gundy, 1959) and quarantined to prevent its spread to other areas of that state. It appears to have a wide host range (ten of nineteen hosts tested) although the rutaceous host status is variable. *Citrus limon, C. aurantifolia, C. reticulata* and *Severinia buxifolia* are susceptible, while *Poncirus trifoliata, C. aurantium, C. paradisi* and *C. sinensis* are resistant (Van Gundy & Rackham, 1961). The nematode feeds in large numbers at root tips whose roots typically develop round galls arising from hyperplasia. Seedling growth in pot studies was reduced by 35%. *Hemicycliophora nudata* causes similar symptoms on citrus in Australia (Colbran, 1963). *H. arenaria* can be eradicated from root systems with hot water dips (10 min 46°C), preplant soil fumigation with methyl bromide or DD is very effective and a number of rootstocks resistant to the nematode are available (Van Gundy & McElroy, 1969).

References

Abu-Gharbieh, W. I. & Perry, V. G. (1970). Host differences among Florida populations of *Belonolaimus longicaudatus* Rau. *Journal of Nematology*, 2:209–216.

Anonymous. (1986). Agrichemical Briefing. The industry's biweekly issue and research update. *An Agricultural Age Publication* Vol. 4, 4p.

Baghel, P. P. S. and Bhatti, D. S. (1982). Vertical and horizontal distribution of phytonematodes associated with citrus. *Indian Journal of Nematology*, 12:339–344.

Baines, R. C. (1964). Contolling citrus nematode with DBCP increases yields. *California Citrograph*, 49:222,233.

Baines, R. C. (1974). The effect of soil type on movement and infection rate of larvae of *Tylenchulus semipenetrans*. *Journal of Nematology*, 6:60–62.

Baines, R. C., Foote, F. J., & Martin, J. P. (1956). Fumigate soil before replanting citrus for control of the citrus nematode. *Citrus Leaves*, 36:6–8, 24, 27.

Baines, R. C., Klotz, L. J. DeWolfe, T. A., Small, R. H., & Turner, G. O. (1966). Nematocidal and fungicidal properties of some soil fumigants. *Phytopathology*, 56:691–698.

Baines, R. C., Martin, J. P., DeWolfe, T. A., Boswell, S. B., & Garber, M. J. (1962). Effect of high doses of D-D on soil organisms and the growth and yield of lemon trees. *Phytopathology*, 52:723.

Baines, R. C., DeWolfe, T. A., Klotz, L. J., Bitters, W. P., Small, R. H., & Garber, M. J. (1969*a*). Susceptibility

of six *Poncirus trifoliata* selections and Troyer citrange to a biotype of the citrus nematode and growth response on fumigated soil. *Phytopathology*, 59:1016–1017.

Baines, R. C., Miyakawa, T., Cameron, J. W., & Small, R. H. (1969*b*). Biotypes of the citrus nematode. *Prodeedings of the 1st International Citrus Symposium, Riverside, California* 2:955–956.

Baines, R. C., Van Gundy, S. D., & DuCharme, E. P. (1978). Nematodes attacking citrus. Chapter 7. In: Reuther, W. Calavan, E. C. & Carman G. E. (Eds). *The Citrus Industry Volume IV*. University of California, Division of Agricultural Science: 321–345.

Baines, R. C., Van Gundy, S. D., & Sher, S. A. (1959). Citrus and avocado nematodes. *California Agriculture*, 13:16–18.

Bello, A., Navas, A., & Belart, C. (1986). Nematodes of citrus-groves in the Spanish Levante Ecological study focused to their control. Proceedings of the Expert's Meeting, Acireale, March 26–29, 1985. In: Cavalloro, R., & Di Martino, E. (Eds). *Integrated Pest Control in Citrus-Groves*. A. A. Balkema Publ. Cp., Rotterdam, Boston: 217–226.

Bistline, F. W., Collier, B. L., & Dieter, C. E. (1967). Tree and yield response to control of a nematode complex including *Belonolaimus longicaudatus* in replanted citrus. *Nematologica*, 13:137–138.

Brooks, T. L. & Perry. V. G. (1962). Apparent parthenogenetic reproduction of the burrowing nematode *Radopholus similis. Soil Crop Science Society of Florida Proceedings*, 22:160–162.

Brooks, T. L. & Perry. V. G. (1967). Pathogenicity of *Pratylenchus brachyurus* to citrus. *Plant Disease Reporter*, 51:569–573.

Bryan, O. C. (1966). Soil moisture – the key factor in the production of nematode-infested groves. *Citrus and Vegetable Magazine*, 29:39–40

Bryan, O. C. (1969). Living with the burrowing nematode. *Citrus and Vegetable Magazine*, 33:29,38.

Childers, C. C., Duncan, L. W., Wheaton, T. A., & Timmer, L. W. (1987). Arthropod and nematode control with Aldicarb on Florida citrus. *Journal of Economic Entomology*, 80:1064–1071

Chitwood, B. G. & Toung, M. C. (1960). Host-parasite interactions of the Asiatic pyroid citrus nema. *Plant Disease Reporter*, 44:848–854.

Cobb, N. A. (1913). Notes on *Mononchus* and *Tylenchulus. Journal of the Washington Academy of Science*, 3:287–288.

Cobb, N. A. (1914). Citrus-root nematode. *Journal of Agricultural Research*, 2:217–230.

Coelho, Y. D. S., Paguio, O. D. L. R., Zem, A. C., & Filho, H. P. S. (1983). Citrus decline and nematode population on citrus. *Fitopatologia Brasileira*, 8:367–370.

Cohn, E. (1964). Penetration of the citrus nematode in relation to root development. *Nematologica*, 10:594–600.

Cohn, E. (1965*a*). On the feeding and histopathology of the citrus nematode. *Nematologica*, 11:47–54.

Cohn, E. (1965*b*). The development of the citrus nematode on some of its hosts. *Nematologica*, 11:593–600.

Cohn, E. (1966). Observations on the survival of free-living stages of the citrus nematode. *Nematologica*, 12:321–327.

Cohn, E. (1969). The occurrence and distribution of species of *Xiphinema* and *Longidorus* in Israel. *Nematologica*, 15:179–192.

Cohn, E. (1970). Observations on the feeding and symptomatology of *Xiphinema* and *Longidorus* on selected host roots. *Journal of Nematology*, 2:167–173.

Cohn, E. (1972). Nematode diseases of citrus. In: Webster, J. M. (Ed). *Economic Nematology*, Academic Press, London: 215–244.

Cohn, E. (1976). *Report of investigations on nematodes of citrus and subtropical fruit crops in South Africa.* Citrus and Subtropical Fruit Research Institute, Nelspruit. 41 p.

Cohn, E., Feder, W. A., & Mordechai, M. (1968). The growth response of citrus to nematicide treatments. *Israel Journal of Agricultural Research*, 18:19–24.

Cohn, E., Hough, A., & Mulder, N. (1976). Elimination of nematodes and other plant pathogens from irrigation water by filtration techniques. *13th International Nematology Symposium, Dublin, Ireland, Sept. 5–11:*16–17.

Cohn, E., Minz, G., & Monselise, S. P. (1965). The distribution, ecology and pathogenicity of the citrus nematode in Israel. *Israel Journal of Agricultural Research*, 15:187–200.

Cohn, E. & Orion, D. (1970). The pathological effect of representative *Xiphinema* and *Longidorus* species on selected host plants. *Nematologica*, 16:423–428.

Colbran, R. C. (1963). Studies of plant and soil nematodes. 6. Two new species from citrus orchards. *Queensland Journal of Agricultural Science*, 20:469–474.

Colbran, R. C. (1965). Studies of plant and soil nematodes. 9. *Trichodorus lobatus* n. sp. (Nematoda: Trichodoridae), a stubby-root nematode associated with citrus and peach trees. *Queensland Journal of Agricultural and Animal Science*, 22:273–276.

Das, T. K. & Mukhopadhyaya, M. C. (1985). Influence of citrus species on the morphological variations of *Tylenchulus semipenetrans*. *Indian Journal of Nematology*, 15:114–116.

Davide, R. G. (1971). *Survey of the distribution of different plant parasitic nematodes associated with the citrus decline in the Philippines.* A report of NSDB project No. 2203, University of Philippines, College of Agriculture, Laguna. 73 p.

Davide, R. G. & Dela Rose, A. G. (1976). Host-parasite relationships and control of the citrus nematode in the Philippines. II. Evaluation of nematode damage on citrus. University of Philippines, College of Agriculture, Laguna, *NSDB Technical Journal*, 1:8–15.

Davis, R. M. (1984). Distribution of *Tylenchulus semipenetrans* in a Texas grapefruit orchard. *Journal of Nematology*, 16:313–317.

Davis, R. M. (1985). Citrus nematode control in Texas. *Citrograph*, July, 1985:212–213.

Davis, R. M., Heald, C. M. & Timmer, L. W. (1982). Chemical control of the citrus nematode on grapefruit. *Journal of the Rio Grande Valley Horticultural Society*, 35:59–63.

Davis, R. M. & Wilhite, H. S. (1985). Control of *Tylenchulus semipenetrans* on citrus with fenamiphos and oxamyl. *Plant Disease*, 69:974–976.

Den Ouden, H. (1965). [An infestation on citrus in Surinam caused by *Meloidogyne exigua*]. *Surinamese Landbouw*, 13:34.

DuCharme, E. P. (1948). Resistance of *Poncirus trifoliata* rootstock to nematode infestation in Argentina. *The Citrus Industry*, 29:9, 15.

DuCharme, E. P. (1955). Sub-soil drainage as a factor in the spread of the burrowing nematode. *Proceedings of the Florida State Horticultural Society*, 68:29–31.

DuCharme, E. P. (1959). Morphogenesis and histopathology of lesions induced on citrus roots by *Radopholus similis*.. *Phytopathology*, 49:388–395.

DuCharme, E. P. (1967). Annual population periodicity of *Radopholus similis* in Florida citrus goves. *Plant Disease Reporter*, 51:1031–1034.

DuCharme, E. P. (1968). Burrowing nematode decline of citrus, a review. In: Smart, G. C. and Perry, V. G. (Eds) *Tropical Nematology*. University of Florida Press, Gainesville :20–37.

DuCharme, E. P. (1969). Temperature in relation to *Radopholus similis* (Nematoda) spreading decline of citrus. *Proceedings of the 1st International Citrus Symposium*, 2:979–983.

DuCharme, E. P. & Birchfield, W. (1956). Physiologic races of the burrowing nematode. *Phytopathology*, 46:615–616.

DuCharme, E. P. & Price, W. C. (1966). Dynamics of multiplication of *Radopholus similis*. *Nematologica*, 12:113–121.

DuCharme, E. P. & Suit, R. F. (1967). Population fluctuations of burrowing nematodes in Florida citrus groves. *Proceedings of the Florida State Horticultural Society*, 80:63–67.

Duncan, L. W. (1986). The spatial distribution of citrus feeder roots and of the citrus nematode, *Tylenchulus semipenetrans*. *Revue de Nématologie*, 9:233–240.

Duncan, L. W. (1988). Citrus fibrous roots and *Tylenchulus semipenetrans* sample optimization in Florida flatwoods citrus orchards. *Journal of Nematology*, 20:633.

Duncan, L. W. & Noling, J. W. (1987). The relationship between development of the citrus root system and infestation by *Tylenchulus semipenetrans*. *Revue de Nématologie*, 10:61–66.

Duncan, L.W. & Noling, J. W. (1988*a*). Computer simulated management of *Tylenchulus semipenetrans* on citrus. *International Citrus Congress Middle East*, Book of Abstracts:262.

Duncan, L. W. & Noling, J. W. (1988*b*). Modeling population dynamics of *Tylenchulus semipenetrans* in a flatwoods citrus grove. *Soil and Crop Science Society of Florida Proceedings*, 47:250.

Esser, R. P. (1984). How nematodes enter and disperse in Florida nurseries via vehicles. *Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Nematology Circular No. 109*. 2 p.

Esser, R. P. & Simpson, S. E. (1984). Sting nematode on citrus. *Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Nematology Circular No. 106*. 2 p.

Feder, W. A. (1968). Differential susceptibility of selections of *Poncirus trifoliata* to attack by the citrus nematode, *Tylenchulus semipenetrans*. *Israel Journal of Agricultural Research*, 18:175–179.

Feder, W. A. & Feldmesser, J. (1956). Root abnormalities caused by burrowing nematode infections. *Pythopathology*, 46:11.

Feder, W. A. & Feldmesser, J. (1961). The spreading decline complex: the separate and combined effects of *Fusarium* spp. and *Radopholus similis* on the growth of Duncan grapefruit seedlings in the greenhouse. *Phytopathology*, 51:724–726.

Feder, W. A., Feldmesser, J., & Walkinshaw, C. H. (1956). Microorganisms isolated from feeder roots of citrus seedlings affected by spreading decline. *Soil Crop Science Society of Florida Proceedings*, 16:127–129.

Feldmesser, J, Rebois, R. V. & Taylor, A. L. (1959). Progress report on growth response of burrowing nematode infected citrus following chemical treatments under greenhouse conditions. *Plant Disease Reporter*, 43:261–263.

Feldmesser, J., Cetas, R. C., Grimm, G. R. Rebois, R. V., & Widden, R. (1960). Movement of *Radopholus similis* into rough lemon feeder roots and in soil, and its relation to *Fusarium* in the roots. *Phytopathology*, 50:635.

Ford, H. W. (1952). The effect of spreading decline on the root distribution of citrus. *Proceedings of the Florida State Horticultural Society*, 65:47–50.

Ford, H. W. (1953). Effect of spreading decline disease on the distribution of feeder roots of orange and grapefruit trees on rough lemon rootstocks. *Journal of the American Society for Horticultural Science*, 61:68–72.

Ford, H. W. (1954*a*). The influence of rootstock and tree age on root distribution of citrus. *Proceedings of the American Society for Horticultural Science*, 63:137–172.

Ford, H. W. (1954*b*). Root distribution in relation to the water table. *Proceedings of the Florida State Horticultural Society* 67:30–33.

Ford, H. W. & Feder, W. A. (1961). Additional citrus rootstock selections that tolerate the burrowing nematode. *Proceedings of the Florida State Horticultural Society*, 74:50–53.

Ford, H. W., Feder, W. A., & Hutchins, P. C. (1960). Citrus varieties, hybrids, species, and relatives evaluated for resistance to the burrowing nematode *Radopholus similis*. *Citrus Experiment Station Mimeo Series 60–13*, 26 p.

Fortucci-Marongiu, P. (1988). *Three decades of the world citrus economy*. Intergovernmental Group on Citrus Fruit, Commodities and Trade Division, FAO, Rome, Italy, 9 p.

Frederick, J. J. & Tarjan. A. C. (1975). Control of *Pratylenchus brachyurus* in rough lemon seedlings with Dowco 275 (Diethylfluropyridyl phosphorothioate). *Nematropica*, 5:10–13.

Gill, H. S. (1971). Occurrence and reproduction of *Meloidogyne javanica* on three species of citrus in California. *Plant Disease Reporter*, 55:607–608.

Gottlieb, Y., Cohn, E., & Spiegel-Roy, P. (1986). Biotypes of the citrus nematode (*Tylenchulus semipenetrans* Cobb) in Israel. *Phytoparasitica* 14:193–198.

Graham, J. H. (1988). Fumigation induced stunting. In: Whiteside, J. O. Garnsey, S. M. & Timmer, L. W. [Eds.] *Compendium of Citrus Diseases*. (in press).

Graham, J. H., Timmer, L. W., & Lee, R. F. (1983). Comparison of zinc, water uptake by gravity infusion and syringe injection tests for diagnosis of citrus blight. *Proceedings of the Florida State Horticultural Society*, 96:45–47.

Hamid, G. A., Van Gundy, S. D. & Lovatt, C. J. (1985). Citrus nematode alters carbohydrate partitioning in

the "Washington" navel orange. *Journal of the American Society for Horticultural Science* 110:642–646.

Hannon, C. I. (1963). Longevity of *Radopholus similis* under field conditions. *Plant Disease Reporter*, 47:812–816.

Hannon, C. I. (1964). Longevity of the citrus-root nematode in Florida. *Soil Crop Science Society of Florida Proceedings*, 24:158–161.

Heald, C. M. & O'Bannon, J. H. (1987). Citrus declines caused by nematodes. V. Slow decline. *Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Nematology Circular No. 143*. 4 p.

Hearn, C. Jack. (1986). Production trends around the world. In: Wardowski, W. F., Nagy, S. and Grierson, W. [Eds.]. *Fresh Citrus Fruits*. The AVI Publ. Co., Westport, CT:127–132.

Holdeman. Q. L. [Ed.] (1986). *The burrowing nematode: The citrus pathotype*. Division of Plant Industry, California Department of Food and Agriculture, 70 p.

Huang, C. S. & Chang, Y. C. (1976). Pathogenicity of *Pratylenchus coffeae* on sunki orange. *Plant Disease Reporter*, 60:957–960.

Huettel, R. N., Dickson, D. W., & Kaplan, D. T. (1982). Sex attractants and behavior in the two races of *Radopholus similis*. *Nematologica*, 28:360–369.

Huettel, R. N. Dickson, D. W. & Kaplan, D. T. (1984). *Radopholus citrophilus* n. sp. (Nematoda), a sibling species of *Radopholus similis*. *Proceedings of the Helminthological Society of Washington*, 51:32–35.

Huettel, R. N., Kaplan, D. T. & Dickson, D. W. (1986). Characterization of a new burrowing nematode population, *Radopholus citrophilus*, from Hawaii. *Journal of Nematology* 18:50–54.

Huettel, R. N. & Yaegashi, T. (1980). Morphological differences between *Radopholus citrophilus* and *similis*. *Journal of Nematology*, 20:150–157.

Inserra, R. N. & Vovlas, N. (1974). Dannida *Pratylenchus vulnus* su arancio amaro in Puglia. *Nematologia mediterranea*, 2:183–185.

Inserra, R. N. & Vovlas, N. (1977*a*). Effects of *Pratylenchus vulnus* on the growth of sour orange. *Journal of Nematology*, 9:154–157.

Inserra, R. N. & Vovlas, N. (1977*b*). Nematodes other than *Tylenchulus semipenetrans* pathogenic to citrus. *Proceedings of the International Society of Citriculture*, 3:826–831.

Inserra, R. N., Perotta, G., Vovlas, N., & Catara, A. (1978). Reaction of citrus rootstocks to *Meloidogyne javanica*. *Journal of Nematology*, 10:181–184.

Inserra, R. N., Vovlas, N., O'Bannon, J. H., & Esser, R. P. (1988). *Tylenchulus graminis* n. sp. and *T. palustris* n. sp. (Tylenchulidae), from native flora of Florida, with notes on *T. semipenetrans* and *T. furcus*. *Journal of Nematology*, 20:266–287.

Inserra, R. N., Vovlas, N., & O'Bannon, J. H. (1980). A classification of *Tylenchulus semipenetrans* biotypes. *Journal of Nematology*, 12:283–287.

Kaplan, D. T. (1985). Influence of the sting nematode, *Belonolaimus longicaudatus*, on young citrus trees. *Journal of Nematology*, 17:408–414.

Kaplan, D. T. (1986). Variation in *Radopholus citrophilus* population densities in the citrus rootstock Carrizo citrange. *Journal of Nematology*, 18:31–34.

Kaplan, D. T. (1988) Future considerations for nematode management in citrus. *Proceedings of the International Society of Citriculture* 11 p (in press).

Kaplan, D. T. & O'Bannon, J. H. (1981). Evaluation and nature of citrus nematode resistance in Swingle citrumelo. *Proceedings of the Florida State Horticultural Society*, 94:33–36.

Kaplan, D. T. & O'Bannon, J. H. (1985). Occurrence of biotypes in *Radophlus citrophilus*. *Journal of Nematology*, 17:158–162.

Kaplan, D. T. & Timmer, L. W. (1982). Effects of *Pratylenchus coffeae-Tylenchulus semipenetrans* interactions on nematode population dynamics in citrus. *Journal of Nematology*, 14:368–373.

Kirkpatrick, J. C. & Van Gundy, S. D. (1966). Scion and rootstock as factors in the development of citrus nematode populations. *Phytopathology*, 56:438–441.

Labuschagne, N. & Kotze, J. M. (1988). Factors affecting feeder root rot of citrus caused by *Fusarium solani*. *Proceedings of the International Society of Citriculture*, Tel-Aviv, Israel, March 1988:120.

Machmer, J. H. (1958). Effect of soil salinity on nematodes in citrus and papaya plantings. *Journal of the Rio Grande Valley Horticultural Society, 12:57–60.*

Malo, S. E. (1961). Nematode populations associated with citrus roots in central Florida. *Plant Disease Reporter*, 45:20–23.

Mangat, B. P. S. & Sharma, N. K. (1981). Influence of host nutrition on multiplication and development of citrus nematode. *Indian Phytopathology*, 34:90–91.

Mankau, R. (1968). Effect of nematocides on nematode-trapping fungi associated with the citrus nematode. *Plant Disease Reporter*, 52:851–855.

Martin, J. P. & Van Gundy, S. D. (1963). Influence of soil phosphorous level on the growth of sweet orange seedlings and the activity of the citrus nematode (*Tylenchulus semipenetrans*). *Soil Science*, 96:128–135.

McElroy, F. D., Sher, S. A. & Van Gundy, S. D. (1966). The sheath nematode *Hemicycliophora arenaria* a native to California soils. *Plant Disease Reporter*, 40:581–583.

McSorley, R & Parrado, J. L. (1982*a*). Relationship between two nematode extraction techniques on two Florida soils. *Soil Crop Science Society of Florida Proceedings*, 41:30–36.

McSorley, R & Parrado, J. L. (1982*b*). Plans for the collection of nematode soil samples from fruit groves. *Nematropica*, 12:257–267.

Meagher, J. W. (1967). Observations on the transport of nematodes in subsoil drainage and irrigation water. *Australian Journal of Experimental Agricultural Animal Husbandry*, 7:577–579.

Meagher, J. W. (1969). Nematodes as a factor in citrus production in Australia. *Proceedings of the 1st International Citrus Symposium*, Riverside, CA., 2:999–1006.

Milne, D. L. (1974). Citrus seedbeds: methyl bromide and mycorrhizae. Citrus and Subtropical Fruit Research Institute, Nelspruit:9–11.

Milne, D. L. (1982). Nematode pests of citrus. In: Keetch, D. P., & Heyns, J. (Eds). *Nematology in Southern Africa*. Republic of South Africa, Department of Agriculture and Fisheries Science Bulletin No. 400:12–18.

Milne, D. L. & De Villiers, E. A. (1977). Soil application of systemic pesticides for control of thrips and nematodes on citrus. *Citrus and Subtropical Fruit Journal,* 518:9, 18.

Milne, D. L. & du Toit, W. (1976). The effect of citrus nematicides on the earthworm population in the soil. Citrus and Subtropical Fruit Research Institute, Nelspruit. p. 13–15.

Milne, D. L. & Willers, P. (1979). Yield and nutritional responses to phenamiphos treatment of citrus infested with citrus nematodes. *Subtropica*, 1:11–14.

Minz, G. (1956). The root-knot nematode, *Meloidogyne* spp. in Israel. *Plant Disease Reporter*, 40:798–801.

Nigh, E. L., Jr. (1981*a*). Relation of citrus nematode to root distribution in flood irrigated citrus. *Journal of Nematology* 13:451–452.

Nigh, E. L., Jr. (1981*b*). Evaluation of sampling and extraction techniques to determine citrus nematode. *Tylenchulus semipenetrans*, populations. *Journal of Nematology*, 13:451.

Nofziger, D. L. & Hornsby, A. G. (1987). Chemical movement in layered soils: User's manual. *Florida Cooperative Extension Service Circular 780* University of Florida, Gainesville. 43 p.

Noling, J. W. & Duncan, L. W. (1988). Estimation of citrus nematode stress and yield losses in a mature citrus grove. *Journal of Nematology*, 20:653.

O'Bannon, J. H. (1968). The influence of an organic soil amendment on infectivity and reproduction of *Tylenchulus semipenetrans* on two citrus rootstocks. *Phytopathology*, 58:597–601.

O'Bannon, J. H. (1977). Worldwide dissemination of *Radopholus similis* and its importance in crop production. *Journal of Nematology*, 9:16–25.

O'Bannon, J. H. (1980). Migration of *Pratylenchus coffeae* and *P. brachyurus* on citrus and in soil. *Nematropica*, 10:70.

O'Bannon, J. H. & Esser, R. P. (1975). Evaluation of citrus, hybrids, and relatives as hosts of the nematode *Pratylenchus coffeae*, with comments on other hosts. *Nematologia mediterranea*, 3:113–122.

O'Bannon, J. H. & Esser, R. P. (1985). Citrus declines caused by nematodes in Florida. I. Soil factors. Florida *Department of Agriculture and Consumer Services, Division of Plant Industry, Nematology Circular No. 114.* 4 p.

O'Bannon, J. H. & Ford, H. W. (1976). An evaluation of several *Radopholus similis*-resistant or -tolerant citrus rootstocks. *Plant Disease Reporter*, 60:620–624.

O'Bannon, J. H. and Hutchinson, D. H. (1974). Development of rootstocks resistant to the citrus nematode, *Tylenchulus semipenetrans*. In: Jackson, L. K. Krezdorn, A. H. & Soule, J. (Eds). *Proceedings of the 1st International Citrus Short Course* (Sept. 24–29, 1973), Gainesville, Florida: 22–29.

O'Bannon, J. H. Leather, C. R., & Reynolds, H. W. (1967). Interactions of *Tylenchulus semipenetrans* and *Fusarium* species on rough lemon (*Citrus limon*). *Phythopathology*, 57:414–417.

O'Bannon, J. H. & Nemec, S. (1978). Influence of soil pesticides on vesicular-arbuscular mycorrhizae in a citrus soil. *Nematropica*, 8:56–61.

O'Bannon, J. H. & Nemec, S. (1979). The response of *Citrus limon* seedlings to a symbiont, *Glomus etunicatus*, and a pathogen, *Radopholus similis*. *Journal of Nematology*, 11:270–274.

O'Bannon, J. H., Radewald, J. D., & Tomerlin, A. T. (1972). Population fluctuation of three parasitic nematodes in Florida citrus. *Journal of Nematology*, 4:194–199.

O'Bannon, J. H., Radewald, J. D., Tomerlin, A. T., & Inserra, R. N. (1976). Comparative influence of *Radopholus similis* and *Pratylenchus coffeae* on citrus. *Journal of Nematology*, 8:58–63.

O'Bannon, J. H., Reynolds, H. W., & Leathers, C. R. (1966). Effects of temperature on penetration, development, and reproduction of *Tylenchulus semipenetrans*. *Nematologica*, 12:483–487.

O'Bannon, J. H. & Stokes, D. E. (1978). An ecological study of a nematode complex in a Florida citrus grove. *Nematologia mediterranea*, 6:57–65.

O'Bannon, J. H. & Tarjan, A. C. (1973). Preplant fumigation for citrus nematode control in Florida. *Journal of Nematology*, 5:88–95.

O'Bannon J. H. & Tarjan A. C. (1979). Management of *Radopholus similis* infecting citrus with DBCP or phenamiphos. *Plant Disease Reporter*, 63:456–460.

O'Bannon, J. H. & Tarjan, A. C. (1985). Citrus declines caused by nematodes in Florida. III. Citrus slump. *Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Nematology Circular No. 117.* 3 p.

O'Bannon, J. H., Tarjan, A. C., & Bistline, F. W. (1974). Control of *Pratylenchus brachyurus* on citrus and tree response to chemical treatment. *Soil Crop Science Society of Florida Proceedings*, 33:65–67.

O'Bannon, J. H. & Tomerlin, A. T. (1969a). Movement of *Radopholus similis* on a weed host (*Solanum nigrum*). *Journal of Nematology*, 1:21.

O'Bannon, J. H. & Tomerlin, A. T. (1969b). Population studies on two species of *Pratylenchus* on citrus. *Journal of Nematology*, 1:299–300.

O'Bannon, J. H. & Tomerlin, A. T. (1971). Response of citrus seedlings to *Radopholus similis* in two soils. *Journal of Nematology*, 3:255–259.

O'Bannon, J. H. & Tomerlin, A. T. (1973). Citrus tree decline caused by *Pratylenchus coffeae*. *Journal of Nematology*, 5:311–316.

O'Bannon, J. H. & Tomerlin, A. T. (1977). Control of the burrowing nematode, *Radopholus similis*, with DBCP and oxamyl. *Plant Disease Reporter*, 61:450–454.

Orion, D. & Cohn, E. (1975). A resistant response of citrus roots to the root-knot nematode, *Meloidogyne javanica*. *Marcellia*, 38:327–328.

Oteifa, B. A., Shafiee, V. A., & Eissa, F. M. (1965). Efficacy of DBCP flood irrigation in established citrus. *Plant Disease Reporter*, 49:598–599.

Pan, C. (1984). [Studies on plant-parasitic nematodes on economically important crops in Fujian. I. Species of root-knot nematodes (*Meloidogyne* species) and their host-plants.] *Acta Zoologica Sinica*, 30:159–167.

Pan, C. (1985). [Studies on plant-parasitic nematodes on economically important crops in Fujian. III. Description of *Meloidogyne fujianensis* n. sp. (Nematoda: Meloidogynidae) infesting Citrus in Najing County.] *Acta Zoologica Sinica*, 31:263–268.

Perry, V. G. (1953). Return of the nematodes following fumigation of Florida soils. *Proceedings of the Florida State Horticultural Society*, 66:112–114.

Philis, J. (1969). Control of citrus nematode, *Tylenchulus semipenetrans*, with DBCP in established Cyprus citrus groves. *Plant Disease Reporter*, 53:804–806.

Poucher, C., Ford, H. W., Suit, R. F. & DuCharme, E. P. (1967). Burrowing nematode in citrus. *Florida Department of Agriculture, Division of Plant Industry Bulletin No. 7.* 63 p.

Prasad, S. K. & Chawla, M. L. (1965). Observations on the population fluctuations of citrus nematode, *Tylenchulus semipenetrans* Cobb, 1913. *Indian Journal of Entomology*, 27:450–454.

Radewald, J. D., O'Bannon, J. H., & Tomerlin, A. T. (1971*a*). Temperature effects on reproduction and pathogenicity of *Pratylenchus coffeae* and *P. brachyurus* and survival of *P. coffeae* in roots of *Citrus jambhiri*. *Journal of Nematology*, 3:390–394.

Radewald, J. D., O'Bannon, J. H., & Tomerlin, A. T. (1971*b*). Anatomical studies of *Citrus jambhiri* roots infected by *Pratylenchus coffeae*. *Journal of Nematology*, 3:409–416.

Reynolds, H. W. & O'Bannon, J. H. (1963a). Factors influencing the citrus replants in Arizona. *Nematologica*, 9:337–340.

Reynolds, H. W. & O'Bannon, J. H. (1963b). Decline of grapefruit trees in relation to citrus nematode populations and tree recovery after chemical treatment. *Phytopathology*, 53:1011–1015.

Reynolds, H. W., O'Bannon, J. H., Tomerlin, A. T., Nigh, E. L., Jr., & Rodney, D. R. (1970). The influence of various ecological factors on survival of *Tylenchulus semipenetrans*. *Soil Crop Science Society of Florida Proceedings*, 30:366–370.

Rivas, X. & Roman, J. (1985*a*). Oogenesis y reproduccion de una poblacion de *Radopholus similis* de Puerto Rico. *Nematropica*, 15:19–25.

Rivas, X. & Roman, J. (1985*b*). Estudio sobre la gama de hospederos de una poblacion de *Radopholus similis* de Puerto Rico. *Nematropica*, 15:165–170.

Salem, Ahmed Abdul-Magid. (1980). Observations on the population dynamics of the citrus nematode, *Tylenchulus semipenetrans* in Sharkia Governorate. *Egypt Journal of Phytopathology*, 12:31–34.

Schneider, H & Baines, R. C. (1964). *Tylenchulus semipenetrans:* parasitism and injury to orange tree roots. *Phytopathology*, 54:1202–1206.

Scotto la Massèse, C. (1969). The principal plant nematodes of crops in the French West Indies. In: Peachey, J. E. [Ed.]. *Nematodes of Tropical Crops.* Commonwealth Bureau of Helminthology (Great Britain) Technical Communication, 40:168–169.

Scotto la Massèse, C. (1980). Possibilités offertes par les "courbes isopathologiques" dans l'appréciation de la pathogénie des parasites illustrées par deux exemples en nématologie fruitière. *Revue de Zoologie Agricole*, 78:97–113.

Sharma, N. K. & Sharma, S. K. (1981). Spatial distribution of soil stages of citrus nematode *Tylenchulus semipenetrans* in relation to tree age. *Indian Journal of Nematology*, 11:226–228.

Siddiqi, M. R. (1964). Studies on nematode root-rot of citrus in Uttar Pradesh, India. *Proceedings of the Zoological Society* (Calcutta), 17:67–75.

Siddiqui, I. A., Sher, S. A., & French, A. M. (1973). *Distribution of plant parasitic nematodes in California.* State of California, Department of Food and Agriculture, Division of Plant Industry. 324 p.

Sites, J. W., Reitz, H. J., & Deszyck, E. J. (1951). Some results of irrigation research with Florida citrus. *Proceedings of the Florida State Horticultural Society*, 64:71–79.

Smith, G. & Kaplan, D. T. (1988). Phosphorus and burrowing nematode interactions on growth of rough lemon citrus seedlings. *Journal of Nematology*, 20:539–544.

Spiegel-Roy, R., Vardi, A., Elhanati, A., Solel, Z., & Bar-Joseph, M. (1988). Rootstock selection from a Poorman orange x *Poncirus trifoliata* cross. *Proceedings of the International Society of Citriculture* (in press).

Standifer, M. S. & Perry, V. G. (1960). Some effects of sting and stubby root nematodes on grapefruit roots. *Phytopathology*, 50:152–156.

Stirling, G. R. (1976). *Paratrichodorus lobatus* associated with citrus, peach and apricot trees in South Australia. *Nematologica*, 22:138–144.

Suit, R. F. (1947). Spreading decline of citrus in Florida. *Proceedings of the Florida State Horticultural Society*, 60:17–23.

Suit, R. F. & Brooks, T. L. (1957). Current information relating to barriers for the burrowing nematode. *Proceedings of the Florida State Horticultural Society*, 70:55–57.

Suit, R. F. & Ducharme, E. P. (1953). The burrowing nematode and other parasitic nematodes in relation to spreading decline. *Citrus Leaves*, 33:8–9, 32–33.

Suit, R. F., Hanks, R. W., Tarjan, A. C., Feldman, A. W., & Ducharme, E. P. (1967). Control of spreading decline of citrus. State Project 773. *Florida Agricultural Experiment Station Annual Report:* 228–229.

Swingle, Walter T. & Reese, R. (1967). The botany of citrus and its wild relatives. Chapter 3. In: Reuther, W., Webber, H. J., and Batchelor, L. D., (Eds). *The Citrus Industry*, University of California, Division of Agricultural Science: 190–430.

Tarjan, A. C. (1956). The possibility of mechanical transmission of nematodes in citrus groves. *Proceedings of the Florida State Horticultural Society*, 69:34–37.

Tarjan, A. C. (1961). Longevity of *Radopholus similis* (Cobb) in host-free soil. *Nematologica*, 6:170–175.

Tarjan, A. C. (1971). Migration of three pathogenic citrus nematodes through two Florida soils. *Soil Crop Science Society of Florida Proceedings*, 31:253–255.

Tarjan, A. C. (1972). Observations on extracting citrus nematodes, *Tylenchulus semipenetrans*, from citrus roots. *Plant Disease Reporter*, 56:186–188.

Tarjan, A. C. (1976). Application of systemic nematicides to trunks of trees. *Journal of Nematology*, 8:303.

Tarjan, A. C. & O'Bannon, J. H. (1969). Observations on meadow nematodes (*Pratylenchus* spp.) and their relation to decline of citrus in Florida. *Plant Disease Reporter*, 53:683–686.

Tarjan, A. C. & O'Bannon, J. H. (1977). Nonpesticidal Approaches to Nematode Control. *Proceedings of the international Society of Citriculture*, 3:848–853.

Tarjan, A. C. & Simmons, P. N. (1966). The effect of interacting cultural practices of citrus trees with spreading decline. *Soil Crop Science Society of Florida Proceedings*, 26:22–31.

Thomason, I. J. (1987). Challenges facing nematology: environmental risks with nematicides and the need for new approaches. In: Veech, J. A. and Dickson, D. W., (Eds). *Vistas on Nematology* E. O. Painter Printing Company, Deleon Springs, Florida: 469–476.

Timmer, L. W. (1977). Control of citrus nematode *Tylenchulus semipenetrans* on fine-textured soil with DBCP and oxamyl. *Journal of Nematology*, 9:45–50.

Timmer, L. W. & Davis, R. D. (1982). Estimate of yield loss from the citrus nematode in Texas grapefruit. *Journal of Nematology*, 14:582–585.

Timmer, L. W. & French, J. V. (1979). Control of *Tylenchulus semipenetrans* on citrus with aldicarb, oxamyl, and DBCP. *Journal of Nematology*, 11:387–394.

Timmer, L. W. & Leyden, R. F. (1978). Stunting of citrus seedlings in fumigated soils in Texas and its correction by phosphorus fertilization and inoculation with mycorrhizal fungi. *Journal of the American Society for Horticultural Science*, 103:533–537.

Timmer, L. W. & Leyden, R. F. (1978). Relationship of seedbed fertilization and fumigation to infection of sour orange seedlings by mycorrhizal fungi and *Phytophthora parasitica*. *Journal of the American Society for Horticultural Science*, 103:537–541.

Tomerlin, A. T. & O'Bannon, J. H. (1974). Effect of *Radopholus similis* and *Pratylenchus brachyurus* on citrus seedlings in three soils. *Soil Crop Science Society of Florida Proceedings*, 33:95–97.

Van Gundy, S. D. (1959). The life history of *Hemicycliophora arenaria* Raski (Nematoda: Criconematidae). *Proceedings of the helminthology Society of Washington*, 26:67–72.

Van Gundy, S. D. (1984). Nematodes. In: *Intergrated pest mangement for citrus*. University of California, Riverside: 129–131.

Van Gundy, S. D., Bird, A. F., & Wallace, H. R. (1967). Aging and starvation in larvae of *Meloidogyne javanica* and *Tylenchulus semipenetrans*. *Phytopathology*, 57:599–571.

Van Gundy, S. D. & Kirkpatrick, J. D. (1964). Nature of resistance in certain citrus rootstocks to citrus nematodes. *Phytopathology*, 54:419–427.

Van Gundy, S. D. & Martin, J. P. (1961). Influence of *Tylenchulus semipenetrans* on the growth and chemical composition of sweet orange seedlings in soils of various exchangeable cation ratios. *Phytopathology*, 51:146–151.

Van Gundy, S. D. & Martin, J. P. (1962). Soil texture, pH and moisture effects on the development of citrus nematode (*Tylenchulus semipenetrans*). *Phytopathology*, 52:31.

Van Gundy, S. D., Martin, J. P., & Taso, P. H. (1964.) Some soil factors influencing reproduction of the citrus nematode and growth reduction of sweet orange seedlings. *Phytopathology*, 54:294–299.

Van Gundy, S. D. & McElroy, F. D. (1969). Sheath nematode: its biology and control. *Proceedings of the 1st International Citrus Symposium, Riverside, California* 2:985–989.

Van Gundy, S. D. & Meagher, J. W. (1977). Citrus nematode (*Tylenchulus semipenetrans*) problems worldwide. *1977 International Citrus Congress, Orlando, Florida*: 7.

Van Gundy, S. D. & Rackham, R. L. (1961). Studies on the biology and pathogenicity of *Hemicycliophora arenaria*. *Phytopathology*, 51:393–397.

Van Gundy, S. D., Stolzy, L. H., Szuszkiewicz, T. E. & Rackham, R. L. (1962). Influence of oxygen supply on survival of plant parasite nematodes in soil. *Phytopathology*, 52:628–632.

Van Gundy, S. D., Thomason, I. J., & Rackham, R. L. (1959). The reaction of three *Citrus* spp. to three *Meloidogyne* spp. *Plant Disease Reporter*, 43:970–971.

Vilardebo, A. (1964). Etude sur *Tylenchulus semipenetrans* Cobb au Maroc II. *Al Awamia, Rabat*, 11:31–49.

Vilardebo, A., Sqalli, A., & Devaux, R. (1975). Utilisation du DBCP, du phenamiphos et du prophos contre *Tylenchulus semipenetrans* dans les vergers du Maroc. *Fruits*, 30:313–317.

Wardowski, W. F., Nagy, S. & Grierson, W. (Eds). (1986). *Fresh Citrus Fruits*. The AVI Publishing Company, Westport, CT. 571 p.

Wheaton, T. A., Childers, C. C., Timmer, L. W., Duncan, L. W., & Nikdel, S. (1985). Effects of aldicarb on yield, fruit quality, and tree condition on Florida citrus. *Proceedings of the Florida State Horticultural Society*, 98:6–10.

Whitehead, A. G. (1968). Taxonomy of *Meloidogyne* (Nematodea: Heteroderidae) with descriptions of four new species. *Transactions of the Zoological Society of London*, 31:263–401.

Willers, P. (1979). Influence of citrus nematode, *Tylenchulus semipenetrans*, on Navel yield in Sundays River Valley orchard. *Citrus and Subtropical Fruit Research Institute, Nelspruit*: 9–10

Wutscherr, H. K. (1974). Swingle citrumelo: An ultraresistant rootstock. *Citrograph*, 59:387–388, 391.

Yassin, A. M. (1974). A note on *Longidorus* and *Xiphinema* species from the Sudan. *Nematologia mediterranea*, 2:141–147.

Yokoo, T. (1964). [Studies on the citrus nematode (*Tylenchulus semipenetrans* Cobb, 1913) in Japan.] *Agricultural Bulletin, Saga University*, 20:71–109.

Yokoo, T. and Ikegemi, Y. (1966). Some observations on growth of the new host plant, snapdragon (*Antirrhinum majus* L.) attacked by root lesion nematode, *Pratylenchus coffeae* and control effect of some nematicides. *Agricultural Bulletin, Saga University*, 22:83–92.

Young, T. W. (1954). An incubation method for collecting migratory endoparasitic nematodes. *Plant Disease Reporter*, 38:794–795.

Zeck, W. M. (1971). The systemic nematicidal potential of Nemacur. *Pflanzenschutz-Nachichten*, 24:114–118.

Chapter 10

Nematode Parasites of Subtropical and Tropical Fruit Trees

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This chapter covers tropical and subtropical fruit tree crops, for many of which detailed information concerning nematode damage is relatively scarce. We have included here eleven tree crops, which largely by virtue of their production value on a world basis or their importance in world trade, may be regarded in this context as major crops among the long list of tropical and subtropical fruits which are cultivated worldwide. These include eight fruit, three nut and two vine crops. We also treat here eight additional fruit crops which, by the same measure, may be considered to be of more local significance at the present time, although several of them are attracting increasing attention and hold definite economic potential. We have attempted to emphasize those nematode pests for which some evidence of economic impact exists; a literature review – up to 1980 – of nematodes associated with several tropical and subtropical fruits, is also available (McSorley, 1981).

The fruit trees are herein reviewed in alphabetical order of their common names within each section.

FRUIT CROPS

Avocado

The avocado tree (*Persea americana* Mill.) originates from Central America and its fruit is consumed primarily as a fresh product. The major areas of commercial production today are regions in north, central and south America (Mexico, Brazil, USA, the Caribbean Islands) and some Asian (Philippines, Indonesia, Israel) and African (Zaire, Cameroon, South Africa) countries (Ahmed & Barmore, 1980; Knight, 1980). Total world production in 1985 was reported to be 1 603 000 t of which 82% was produced in the Americas, 9.4% in Asia, and about 8% in Africa (FAO, 1986).

Avocado, in comparison with other tree crops, appears to be relatively free of aggressive nematode pests, and it is difficult to determine the economic importance of the identified nematode parasites to avocado production. Nevertheless, Sher (1955) attributed plant damage in California to *Pratylenchus vulnus*, and reduced tree growth was shown to be caused by this nematode, both in greenhouse inoculation experiments, as well as in preplant fumigation trials with DD (Sher *et al.*, 1959). However, practical nematode control recommendations to growers did not emerge in the years

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following these studies. Work done in Florida during the mid–1950s also implicated *P. brachyurus* and *Radopholus similis* in reduced performance of avocado trees (Young & Ruehle, 1955), and Ducharme and Suit (1953) demonstrated their capacity to create root lesions. Again, however, it appears in retrospect that much of this and other contemporary work in Florida (McSorley, 1981) was related to surveys carried out in areas of citrus spreading decline, which at that time was a major economic disaster. No practical conclusions or recommendations regarding these nematode species in commercial avocado orchards have since been developed.

In Israel populations of *Xiphinema brevicolle*, sometimes as high as 500 per 100 g soil, are often recovered from around avocado roots, and reduced seedling growth in pots as a result of inoculation with this nematode has been demonstrated (Cohn, 1968). However, postplant DBCP treatment in orchards did not consistently improve tree performance.

Interestingly, most of the economically important sedentary plant nematodes do not even infect avocado; only one of them (*Rotylenchulus reniformis*) has been observed on avocado roots in West Africa (Peacock, 1956), where Caveness (1967) found avocado to be a good host, and in Brazil (Sharma, 1978). There is no evidence that *R. reniformis* causes economic damage to avocado plants.

Possibly, the role of nematodes in damaging avocado roots has been overshadowed by the attention aroused by the severe avocado root disease caused by the soil fungus *Phytophthora cinnamomi* and as suggested by Milne (1982*a*), it would be interesting to establish whether plant parasitic nematodes are capable of affecting the severity of this disease or the susceptibility to it of avocado trees.

Fig

The fig, *Ficus carica* L., one of the oldest fruits known to man, originates from the Mediterranean region, and is consumed mainly as a dried fruit (approximately 90%), although some are marketed fresh, and a few are canned or made into preserves (Bolin & King, 1980). The Mediterranean countries still produced more than 85% of the estimated 120 000 t total annual world production during the late 1970s (Turkey and Greece being the largest producers with 60 000 t and 22 000 t respectively, in 1976), while other smaller fig producers included California, Texas, Australia and South Africa (Knight, 1980).

The root-knot nematode is probably the most severe nematode problem in fig cultivation (Plate 8E), and certainly the best documented. Numerous reports of root-knot damage to fig exist from Mediterranean, north and south American countries, as well as from southern Africa, and among the identified species are *Meloidogyne arenaria, M. incognita, M. incognita acrita* and *M. javanica* (McSorley, 1981). The problem is recognized as a major limiting factor in commercial fig production in the USA (Knight, 1980), in France (Scotto La Massèse *et al.*, 1984) and in Brazil (Ferraz *et al.*, 1982). Several measures have been recommended to reduce the damage. Preplant fumigation permits better establishment of newly planted trees (Krezdorn & Adriance, 1961). Nematode populations were considerably reduced in young trees by stem treatments with an experimental paste formulation of phenamiphos (Inserra & O'Bannon, 1974). Partial nematode control and improved rooting on cuttings under nursery conditions were also attained by application of the systemic compounds aldicarb, carbofuran, ethoprop and phenamophos (Ferraz *et al.*, 1982). Work has also been carried out to develop root-knot resistant rootstocks for fig. Tests in California revealed that while all *Ficus carica* specimens examined were susceptible to *Meloidogyne*, four other *Ficus* species (*F. racemosa* L., *F. cocculifolia* Baker, *F. gnaphalocarpa* Steud. ex Miquel., and *F. palmata* Forsk.) showed a high degree of resistance to unidentified species of root-knot nematodes, as well as good graft compatibility with *F. carica* (Krezdorn & Glasgow, 1970).

In Israel, root-knot resistance was recognized as the most effective measure to combat the nematode; the fig varieties "Celeste" and "Poulette" were considered resistant to the nematode, while the species *Ficus glomerata* Roxb. was found to exhibit a high degree of tolerance, but showed other unsatisfactory qualities as a rootstock (Gur, 1955).

Heterodera fici is another nematode pest of fig, which is fairly widely distributed throughout the world, having been reported infesting trees in several Mediterranean countries, including France (Scotto La Massèse *et al.*, 1984), Spain (Bello-Perez & Jimenez-Millan, 1963), Italy (Di Vito, 1976) and Turkey (Yuksel, 1981), as well as in California (Sher & Raski, 1956), Brazil (Brancalion *et al.*, 1981) and Soviet Asia (Narbaev & Sidikov, 1985). The potential pathogenicity of *H. fici* on fig seedlings was demonstrated in pot trials by Di Vito and Inserra (1982), who reported 30% death of plants with an initial nematode population of 8/cm^3, and 100% plant mortality with an initial nematode density of 64/cm^3 and larger. Thus, while field populations of *H. fici* do not generally appear to attain such damaging levels in orchards, the nematode can be considered a potential threat in fig nurseries, where fig rootstocks are often obtained from seeds. It is also noteworthy that the nematode has caused considerable damage to potted plants of the related *F. elastica* Roxb. (Scotto La Massèse *et al.*, 1984; Narbaev & Sidikov, 1985).

Ficus carica is the type host of *Xiphinema index* (Thorne & Allen, 1950), and this nematode attains extremely large populations around fig trees in the Mediterranean region. The anatomical changes caused by the nematode on fig roots – in the form of terminal galls and modified cells – as well as the associated biochemical changes, have been studied in great detail and have been fully described (Poehling *et al.*, 1980; Wyss *et al.*, 1980); so, too, has the feeding behaviour of the nematode on fig roots (Wyss, 1987). Although fig has been shown to be a more favourable host of *X. index* than grapevine (Coiro & Lamberti, 1978), there does not appear to be as much damage to plant growth. Similarly, there is no known virus transmission in fig by this nematode, which is the vector of fanleaf virus disease in grapevine.

The only other nematode species possibly associated with injury to fig roots are *Paratylenchus hamatus* in California (Thorne & Allen, 1950) and *Pratylenchus vulnus*, which has been implicated as a possible pathogen of fig in California (McSorley, 1981) and in France (Scotto La Massèse *et al.*, 1984).

Guava

The common guava (*Psidium guajava* L.) is indigenous to tropical America. It is consumed as fresh fruit and also in processed form as jelly, paste, puree, canned shells and juice. It is grown today throughout the tropics and subtropics and is of commercial importance in India, the West Indies, Hawaii, Florida, South Africa, Brazil, Mexico and Egypt. Accurate statistics on production are not available, but an estimate of the annual world total for the early seventies was approximately 430 000 t, of which more than half was from India and Mexico – largely as fresh fruit – with Brazil as a leader of the processed producers with 33 000 t in 1972 (Wilson, 1980).

The best documented nematode problem affecting guava is that created by the root-knot nematode (*Meloidogyne* spp.) which is a recognized limiting factor in commercial guava production in central American countries, notably in Cuba (Anorga Morales & Rodriguez Fuentes, 1978), Puerto Rico (Ayala, 1969) and Florida (Ruehle, 1959). Workers from Cuba have reported severe damage to guava, attributed to high levels of infestation with *M. arenaria, M. incognita, M. hapla, M. javanica* and other species of root-knot nematodes (Cuadra & Quincosa, 1982). Shesteperov (1979) reported much reduced guava tree development and yields, as well as total elimination of a second annual harvest, due to root-knot infections. Rodriguez Fuentes and Landa Balanos (1977) reported reduced levels of *Meloidogyne* and *Pratylenchus* in guava nurseries as a result of preplant soil treatment with metham sodium and DBCP. The problem in Cuba was addressed by screening other *Psidium* species for possible resistant rootstocks, and resulted in the commercial use of a rootstock of *P. friedrichstalianum* (Berg.) Nied., which evidently shows a high degree of resistance to *Meloidogyne* spp. (Fernandez Diaz-Silveira, 1975). However, Gonzales and Sourd (1982) found *P. friedrichstalianum* to show only moderate tolerance to *Meloidogyne* and recommended interspecific and intergeneric hybridization to obtain a rootstock with nematode tolerance and compatibility with *P.*

guajava. Other *Psidium* species – among them *P. cattleianam* Sabine, *P. molle* Bertol., *P. guineensis* and *P. guayabita* – were highly susceptible to the nematode (Cuadra & Quincosa, 1982).

It is noteworthy that there are far fewer reports of outstanding damage to guava by root-knot nematodes, outside of the Caribbean and America. Although a case of slight root galling by *M. arenaria* was reported by Martin (1959) from central Africa, occurrence of root-knot nematodes on guava in southern Africa and the Mediterranean region seems to be fairly rare. Sikora (1988) reported heavy galling of guava roots – with associated tree decline – in two isolated regions in Niger (Plate 8 A, B), evidently involving a nematode species not found on any vegetable crop in the vicinity. It is, therefore, possible that the severe root-knot problem in Cuba and Puerto Rico and the isolated cases in Africa involve specialized and particularly virulent races of *Meloidogyne*.

Three other plant parasitic nematodes attacking guava warrant mention: *Helicotylenchus dihystera* was found consistently associated with guava plantations in South Africa and was shown to reduce height and leaf size of guava seedlings in inoculation trials (Willers & Gretch, 1986). *Hoplolaimus indicus* was shown in pot experiments to be a pathogen of guava in India (Mahto & Edward, 1979), and *Tylenchorhynchus cylindricus* in numbers of up to 2000/100 cm^3 of soil was found associated with damaged guava trees in Iran (Abivardi, 1973).

Lychee

The lychee (*Litchi chinensis* Sonn.) – also spelled litchee, litchi, and its dried fruit form, "litchi nut" – is indigenous to southern China and is marketed as fresh, dried and canned fruit. China is still probably the world's largest producer, followed by India, with smaller plantations in Burma, South Africa, West Indies, New Zealand, Brazil, Australia, Madagascar, Florida and Hawaii (Cavaletto, 1980). World production figures are unavailable, but it has been estimated that South Africa has an annual production of about 1000 t (Milne, 1982). It seems that world production would hardly exceed several tens of thousand tons.

Detailed information on economic nematode damage to lychee is available only from South Africa. Milne (1982) recognized *Xiphinema brevicolle* and *Hemicriconemoides mangiferae* as major nematode pests of lychee, causing a severe tree decline syndrome. Typical above-ground symptoms were the presence of many bare twigs and branches, leaf chlorosis, leaf-tip burn, poor flowering and excessive fruit drop, and in some orchards up to 40% of the trees died. Root symptoms were severe stubby root and darkening of the roots, leading eventually to loss of a large proportion of the feeder root mass and consequent interference in the uptake of nutrients and water. *X. brevicolle* feeds more superficially, while *H. mangiferae*, which causes extensive destruction of the cortical tissue, is considered the more severe pathogen. Populations as high as 20 000 *H. mangiferae*/0.5 litre soil and roots and 10 000 *X. brevicolle*/0.5 litre soil and roots were recorded.

Preplant soil fumigation with Telone or methyl bromide effectively improved performance of replants in infested areas. DBCP treatment of established trees induced a favourable growth response and attained good nematode control.

Meloidogyne javanica infection of lychee roots in orchards – confirmed by inoculations – was encountered, but galls are generally inconspicuous. *Trichodorus* spp., have also been found associated with nursery seedlings.

Mango

The mango (*Mangifera indica* L.), the most important and most widely grown tropical fruit, originates from the Indo-Malaysian region and is today cultivated in most tropical and subtropical countries. It is marketed largely as fresh fruit, but also processed as juice, puree, chutney and pickle (Knight, 1980). Total world production in 1985 was reported as 14 440 000 t (FAO, 1986), of which 64% was from India, 16% from other Asian countries (largely Pakistan, Philippines, Indonesia, China,

Bangladesh and Sri Lanka), 14% from Central and South America (primarily Mexico, Brazil, Haiti and Dominican Republic) and 6% from Africa (mainly, Tanzania, Zaire, Madagascar and Egypt).

Like avocado, mango appears to be relatively free from severe nematode damage, despite the fairly long list of nematode species associated with it. Probably the most widely distributed nematode associated with mango is *Hemicriconemoides mangiferae* (Plate 8F) (McSorley, 1981), which has also been shown in inoculation trials to be potentially damaging to mango seedlings at a population level of six nematodes per cm^3 of soil (Saeed, 1974). This nematode species has also been observed feeding on mango roots together with *Xiphinema brevicolle* in South Africa, although chemical treatment of existing trees, while reducing nematode populations, failed to induce a favourable tree response (Milne, 1982*a*). Economic responses to chemical treatment in mango have, however, been reported when using DBCP to control *Hoplolaimus columbus* and a *Xiphinema* species in Egypt (Shafiee & Osman, 1971) and phenamiphos applications were found effective in controlling *Pratylenchus brachyurus*, but not *Rotylenchulus reniformis* in Florida (McSorley & Parrado, 1983). *Rotylenchulus reniformis* appears to be the only sedentary nematode affecting mango (McSorley & Parrado, 1983), and, interestingly, soil and root populations on seedlings were effectively reduced by application of the growth regulant ethephon (Badra & Khattab, 1982).

Olive

The olive tree, *Olea europaea* L., is apparently a native of Western Asia, and is cultivated primarily in the Mediterranean Basin – largely (about 75%) for oil extraction. Total world production of olives in 1985 was reported to be 827 300 t (FAO, 1986), of which approximately 97% was produced in countries bordering on the Mediterranean Sea, the remaining 3% in North and Central America (mainly California, Argentina, Mexico, Peru) and western Asia (mainly Jordan, Iraq and Iran). Leading producer countries were Italy (31%), Spain (22%) and Greece (17%).

Olive serves as host to a fairly long list of plant parasitic nematodes many of which are recognized pathogens of other crops, and several of them are sedentary forms. The topics of distribution, pathogenicity and control of nematodes associated with olive have been reviewed by Hashim (1982), to which the reader is referred for additional details.

Olive is an extremely vigorous plant which thrives in hilly, relatively dry areas where most groves are situated. Under such conditions nematodes generally occur in small numbers and are apparently of limited economic importance. In irrigated groves, however, and especially in nurseries, the impact of nematodes could be more marked. Two species of *Meloidogyne, M. incognita* and *M. javanica*, although occurring only patchily in existing groves (Hashim, 1982), have been shown to reduce seedling growth drastically in inoculation trials (Diab & El-Eraki, 1968; Lamberti & Baines, 1969*a*), and have been identified as a factor to reckon with in olive nurseries. Several species of *Helicotylenchus*, particularly *H. dihystera, H. digonicus, H. erythrinae* and *H. oleae*, have been observed to cause root necrosis (Inserra *et al.*, 1979), and are considered by some workers to be capable of affecting olive tree growth (Graniti, 1955; Diab & El-Eraki, 1968). *Pratylenchus vulnus* has been implicated by Lamberti (1969) as a factor in olive decline in Italy, and has been demonstrated in inoculation trials, as a potential pathogen of olive (Lamberti & Baines, 1969). Species of *Xiphinema* also commonly occur around olive roots, and at least one of them, *X. elongatum*, has been shown to affect olive plant growth (Diab & El-Eraki, 1968).

A number of rather specialized sedentary plant nematodes attack olive. A biotype of the citrus nematode, *Tylenchulus semipenetrans*, infects olive in California and Italy, and although population levels on olive are usually lower than on citrus (Inserra & Vovlas, 1978), unusually high levels of *T. semipenetrans* have been shown to inhibit olive growth (Lamberti *et al.*, 1976). *Trophotylenchulus saltensis* was described from olive roots in Jordan (Hashim, 1983) and a very specialized cyst nematode, *Heterodera mediterranea*, known so far only from Italy, was shown to feed and multiply on olive roots, in which it forms syncytia and causes disorder of the stelar structure (Vovlas & Inserra, 1983). Two sedentary ectoparasitic nematode species, *Gracilacus peratica* and *Ogma*

rhombosquamatum, have been observed to feed on olive roots and their feeding behaviour has been described in detail (Inserra & Vovlas, 1977; Vovlas & Inserra 1981); however, there is no evidence of a pathogenic effect. Similarly, three species of *Rotylenchulus* have been studied in detail on olive, namely, *R. macrodoratus* (Inserra & Vovlas, 1980), *R. macrosomus* (Cohn & Mor, 1988) and *R. reniformis* (Hirschmann *et al.*, 1966), but evidence of actual plant damage is lacking.

Measures for practical nematode control in olive have been limited so far to nurseries, where preplant fumigation with available nematicides has been recommended for controlling diverse nematode species (Hashim, 1982). Suggestions for bare root dips of seedlings in suspensions of nematicidal chemicals (such as phenamiphos), prior to transfer into groves, have also been offered for reducing root-knot nematode infestation (Lamberti & Di Vito, 1972).

Papaya

The papaya (*Carica papaya* L.) is a native of tropical America and is widely distributed today throughout tropical areas of the world, where it is produced largely for fresh fruit, but is also marketed as a preserve and for juice. Another product of papaya culture is the enzyme papain, which is used as a tenderizer in the food and other industries (Knight, 1980). Total world production of papaya in 1985 was 2 330 000 t (FAO, 1986), of which 51% was produced in Central and South America (largest producers – Brazil, Mexico, Peru, Cuba), 38% in Asia (mainly India, Indonesia, Philippines and China), about 10% in Africa (mainly Zaire, Mozambique and South Africa) and less than 1% in Oceania.

Of the several nematodes reported to be associated with papaya, only two genera appear to be economically significant in papaya cultivation. These are the root-knot nematode (*Meloidogyne* spp.) and the reniform nematode (*Rotylenchulus* spp.), both of which enjoy a worldwide distribution in papaya plantations.

Heavy root-knot infections of papaya, primarily by *M. incognita* and *M. javanica*, have been reported from many countries from all continents (McSorley, 1981). Root galling is often severe – galls can be as large as golf balls (Milne, 1982*a*)! Root-knot nematode causes severe damage in the field (Wolfe & Lynch, 1950), producing root rot, reducing the life expectancy of the plant and drastically decreasing yield levels (Milne, 1982*a*) (Plate 8C). Seedling growth was greatly retarded in pot trials with root-knot nematodes (Lamberti *et al.*, 1980; Darekar & Mhase, 1986). Infected seedlings exhibit severe chlorotic leaf symptoms, tap root suppression and proliferation of lateral roots (Plate 8D). Recommended control measures call for preplant soil fumigation or sterilization especially in seedbeds and selection of non-infested planting sites. Postplant treatment has evidently also been successful; postplant fumigation with DBCP has in some cases led to a doubling in yield of fruit (Milne, 1982*a*), while application of systemic nematicides (particularly aldicarb) effectively reduced root gall formation (Ahmad & Sultana, 1981). No success has so far been attained in finding sources of resistance, and closely-related species such as *Carica quercifolia* Solms and *C. candamarcensis* Hook are also root-knot susceptible (McSorley, 1981). Babatola (1985) screened eight cultivars of *C. papaya* for resistance and found all of them to be highly susceptible.

Reniform nematode infection of papaya, by *R. reniformis*, has also been reported from all continents. *R. parvus* has been identified from Kenya, and unidentified species of *Rotylenchulus* have reportedly been associated with this crop in Thailand and Florida (McSorley, 1981). *R. reniformis* has been implicated in severe plant damage and yield reduction in Puerto Rico (Ayala *et al.*, 1971) and in Trinidad it has been associated with tree death and toppling (Singh & Farrell, 1972). In Fiji, severe damage by the nematode has been reported in nursery seedlings and young plants (Heinlein, 1982; Vilsoni & Heinlein, 1982) and in Brunei, plants have reportedly been killed by a combination of *R. reniformis* and *Phytophthora nicotianae* var. *parasitica* (Brunei Dept. Agric., 1972). Preplant soil fumigation in Hawaii with various chemicals – including DD, DBCP and Methyl Bromide – have effectively controlled the nematode and maintained low populations over periods of up to 6 months, with resultant yield increases in 15-month old plants (Lange, 1960); however, foliar appli-

cations of the systemic nematicides phenamiphos and oxamyl in Puerto Rico, were not only ineffective in reducing nematode numbers but also showed some phytotoxicity (Ayala *et al.*, 1971).

Persimmon

Persimmon belongs to the genus *Diospyros*, of which nearly 190 species are known. Almost all commercial persimmon fruit belongs to the species *D. kaki* L. (hence the common name, Kaki fruit), although *D. lotus* L. and *D. virginiana* L. are often used as rootstocks. *D. kaki*, known also as the Japanese persimmon, is probably native to China and was introduced early to Japan (Itoo, 1980). It is grown commercially today – largely for fresh, but also dried fruit – mainly in Japan, and also in China, USA, Brazil, Italy and Israel. World production figures are not readily available, but Japan, the largest supplier, produced an annual average of about 300 000 t in the late 1970s, while the USA produced a little under 2000 t annually during the same period (Knight, 1980). In more recent years, the annual production in Italy is estimated at somewhat over 200 000 t, in Israel about 15 000 t and Brazil about 10 000 t.

Little is known about economic nematode damage to persimmon. Although root-knot nematode (*Meloidogyne* spp.,) and burrowing nematode, *Radopholus similis*, have been reported to parasitize both *D. kaki* and *D. virginiana* (McSorley, 1981), no reports of actual plant damage by these nematodes appear to exist. The only nematode species associated with damage to the crop appears to be the citrus nematode, *Tylenchulus semipenetrans*, for which persimmon has been reported to be a very susceptible host. Extremely large soil and root populations of *T. semipenetrans* are commonly encountered in unthrifty persimmon orchards in Israel on *D. virginiana* rootstock (Cohn & Minz, 1961) and have also been observed in California on *D. lotus* rootstock (Nesbitt, 1956). More recently, a similar observation on *D. lotus* roots has been reported in Italy (Di Maio, 1979), where a resultant 20–30% loss in yield was estimated. Although no direct control measures appear to have been tested, it would seem probable that pre and postplant chemical applications, as recommended in citrus cultivation, could effectively reduce *T. semipenetrans* populations on persimmon, if such treatments would be considered economically feasible. Other cultural control measures against the nematode in citrus groves could also be relevant to persimmon. No information is as yet available on the level of resistance to the nematode of the various persimmon rootstocks or other *Diospyros* species.

NUT CROPS

Cashew

The cashew nut (*Anacardium occidentale* L.) is a native of Brazil, where more than a quarter of the world crop is produced today. World production in 1985 totalled 437 034 t, 41% of which was produced in South East Asia (largely in India – 36%), 32% in tropical Africa (mainly Guinea Bissau and Kenya), and 27% in Central and South America (FAO, 1986). Limited information on nematodes attacking cashew exists: high populations of *Criconemoides, Xiphinema* and *Scutellonema* have been found around unthrifty trees in Brazil (Lima *et al.*, 1975), and da Ponte (1986) recognizes "xifinematose" – caused by *Xiphinema index* – as one of the more common diseases of cashew in Northeast Brazil, although data on its economic impact are lacking. Recently, *Rotylenchulus reniformis* – apparently in its migratory form – was reported from around cashew trees in Costa Rica (Lopez & Azofeifa, 1985), but again, evidence of damage is not clear. It is important to emphasize that cashew has been shown clearly to be immune, or at least highly resistant to different populations of the root-knot nematode in West Africa (Netscher, 1981) and in Brazil (da Ponte & Maria, 1973).

Macadamia

Macadamia nuts (*Macadamia integrifolia* Maiden & Betche and *M. tetraphylla* L. Johnson) originate from Queensland, Australia where 15% of the world crop is still produced. They are also grown commercially in Hawaii which produces about 70% of the world crop today, central America and in East and South Africa. Total world production was reported in 1985 as 6460 t and is estimated to reach 15 000 t by 1990 (Anon., 1985). Despite the increasing importance of macadamias in world trade, virtually no information on nematode damage to this crop is available.

Pistachio

The pistachio tree (*Pistacia vera* L.) is native to western Asia and Asia Minor, where 86% of the world crop is still produced. Total world production in 1985 was 127 274 t, of which Iran alone produced 55%, Turkey about 20% and Syria just under 10%. Other eastern Mediterranean countries produced some 5% of the world crop. Since the 1960s pistachio acreage in California increased rapidly, and by 1985, the USA accounted for just under 10% of the world production (FAO, 1986). Pistachio growers often use species of *Pistacia* other than *P. vera* as rootstocks. Some of these, particularly *P. atlantica* Desf. and *P. terebinthus* L., have increased resistance to *Meloidogyne javanica* (Australia, 1975) and possibly to other root-knot species (McKenry & Kretsch, 1984), although root galling does occur. McKenry and Kretsch (1984) surveyed pistachio orchards in California for plant parasitic nematodes, and found the common occurrence of *Paratylenchus hamatus, Pratylenchus neglectus* and *Xiphinema americanum; Meloidogyne* spp. were recovered in a minority of the orchards. They concluded that plant parasitic nematodes did not present a serious problem to pistachio production in California. Two species of *Pistacia, P. lentiscus* and *P. vera*, are natural hosts of *Heterodera mediterranea* in Italy (Vovlas & Inserra, 1983), and *P. vera* roots were reported to be infected and heavily galled by the sedentary nematode *Rotylenchulus macrodoratus* (Vovlas, 1983).

VINE CROPS

Passion fruit, kiwifruit and grape are widely cultivated, fruit-bearing vine crops. Because they are not included in many other nematological reviews the first two crops are treated here. An excellent review of nematodes attacking grape has been written by Raski and Krusberg (1984).

Kiwi

Actinidia deliciosa (A. Chevalier) C. F. Liang *et* A. R. Ferguson, native to China, was known primarily as Chinese gooseberry until 1962 when New Zealand growers began to market the fruit as kiwifruit. Ichang gooseberry, monkey peach and sheep peach are other common names. The fruits are mostly consumed fresh, with smaller markets for the juice, and as flavouring. The plant is a vigorous, woody vine that is long-lived, in some cases more than 50 years. It grows and produces fruit best in northern tropical areas. Production in New Zealand, which grows 99% of the world supply, grew from 300 t in 1937 to 40 000 t in 1983. Other production areas include California (2000 ha) and Italy (2000 ha), followed by small plantings in Southeast Asia, France, Spain, Chile and the South Pacific (Morton, 1987).

The only significant nematode damage reported on kiwifruit is caused by *Meloidogyne* spp. In France and Italy, *Meloidogyne hapla* and *M. arenaria* induce small, discreet root galls whose histopathology is similar to that on other crops. In both countries, root-knot infestations were associated with unthrifty plants. The possibility of interactions with major soilborne pathogens of kiwifruit such as *Agrobacterium tumefaciens* and *Phytophthora cinnamomi* have been suggested (Scotto La Massèse, 1973; Talame, 1976; Mancini & Moretti, 1978). No reports of resistant rootstocks

or results of nematode management trials in the field have been published. Chemical bare-root dips with ethoprop and phenamiphos gave good control of root-knot infestations in nursery stock (Dale, 1972; Grandison, 1983).

Passionfruit

Two varieties of *Passiflora edulis* Sims are known as passionfruits – purple passionfruit, *P. edulis* and yellow passionfruit, *P. edulis* f. *flavicarpa*. Other common names for both forms include grenadilla, parcha, parchita, lilikoi, maracuja, peroba, grenadille and couzou. A woody, shallow-rooted vine, the plant is native to a region from southern Brazil to northern Argentina. In this area, the yellow form is processed for juice and the purple form is consumed fresh. Although purple passionfruit was often preferred initially in other areas of the world, it is more susceptible to some nematodes and to Fusarium wilt, and yields substantially less fruit than the yellow form, so that acceptable selections of both types have been developed. Passionfruit is grown widely in South and North America, the Caribbean, South Africa, Israel, India, Sri Lanka, Australia, New Zealand, Fiji and Hawaii. It is found to a lesser extent throughout Southeast Asia, the Pacific Islands, Taiwan, Ivory Coast, Zimbabwe and Kenya. Yellow passionfruit is tropical or near-tropical and purple passionfruit is subtropical. Plantation life ranges from 3 to 8 years and is strongly affected by management of soilborne diseases (Morton, 1987).

Although a number of plant parasitic nematodes are reported associated with passionfruit (Boesewinkel, 1977; Loof & Sharma, 1979: Milne, 1982*a*), only reniform and root-knot nematodes are reported to cause economic damage. Both nematodes can severely limit fruit production and plant longevity. *Rotylenchulus reniformis* was detected in 84% of sites sampled in Fiji (Kirby, 1978) with numbers as high as 36 000 nematodes/200 cm^3 soil. Yellow passionfruit seedlings growing in naturally infested soil were smaller, had chlorotic leaves and darker roots than plants growing in steamed soil in pot studies. However, no effort was made in this experiment to control the *Phytophthora* species which causes collar rot, the most severe disease of passionfruit. In Brunei, *R. reniformis* is reported to enhance collar rot, and plant life is doubled when infested soil is treated with nemacur granules prior to planting. High populations of the nematode were consistently detected in surveys of experimental field plots (Peregrine & Yunton, 1980).

Meloidogyne incognita (Reddy *et al.*, 1980) *M. javanica* and *Meloidogyne* sp. (de Villiers & Milne, 1973) appear to vary in pathogenicity to passionfruit. In Kenya it has been suggested that root-knot nematodes are not an economic problem on the crop (Ondieki, 1975), and in Fiji, *M. incognita, M. arenaria* and *M. javanica* did not reproduce on yellow passionfruit or affect plant growth in pot studies (Kirby, 1978). Therefore, passionfruit is recommended as a suitable rotation crop in Fiji against root-knot nematodes. Significant resistance based on root galling studies was also reported for both yellow and purple passionfruit in Brazil (Klein *et al.*, 1984). In South Africa, however, *Meloidogyne javanica* and possibly other species are considered as serious pests on yellow and especially purple passionfruit (Milne, 1982*a*). It is unclear whether damage is due primarily to initial penetration of seedling and young plant roots by the nematode or to long-term parasitism. Methyl bromide fumigation of seedbeds is reported to increase plant growth, and preplant treatment of planting sites resulted in marked yield increase (de Villiers & Milne, 1973). It is suggested that soils be leached after methyl bromide fumigation to avoid phytotoxicity. Use of rootstocks such as *P. caerulea*, which are tolerant to root-knot nematodes, has also been suggested (Milne, 1982*a*; Terblanche *et al.*, 1986). Since the vine is relatively short-lived and seedling establishment is of great importance, crop rotations should also be useful for nematode control (Milne, 1982*a*).

Passionfruit has also been suggested as a good rotation crop in South Africa against *Radopholus similis* which does not infect either *P. edulis* or *P. edulis* f. *flavicarpa* (Milne & Keetch, 1976).

MISCELLANEOUS FRUIT TREES

Acerola

The acerola, or West Indian Cherry (*Malpighia glabra* L. and *Malpighia* spp.) is known in cultivation mainly in the West Indies and tropical Central America, from where it originates, and has more recently been introduced to Hawaii, India and Africa (Knight, 1980). It is still very limited in production, but is enjoying increasing interest as a commercial product. Puerto Rico is currently the leading producer, and much of our knowledge on nematodes attacking acerola comes from that country. Ayala (1969) has reported that the plant can be almost destroyed as a result of root-knot nematode (*Meloidogyne incognita*) infection. Ayala and Ramirez (1964) list *Malpighia* species as hosts of the reniform nematode, *Rotylenchulus reniformis*. Root-knot nematodes are also recognized as economic pests of acerola in Hawaii (Holtzmann, 1968) and especially in Florida, where preplant soil fumigation was recommended, and a tolerant rootstock, *M. suberosa* L., has been assayed, but found inadequately productive (Ledin, 1963). Phenamiphos treatment was found ineffective in controlling nematodes (McSorley & Parrado, 1982).

Breadfruit

Breadfruit and the closely related jackfruit, belong to the plant genus *Artocarpus* and are fruit trees of largely local significance throughout the tropics – in Africa, Asia and South America. Little is known about nematode problems on these plants, but two very important nematodes – the root-knot nematode *Meloidogyne* spp. and the reniform nematode, *Rotylenchulus reniformis* – have been reported to attack them (Caveness, 1967; Sharma & Sher, 1973; Razak, 1978; McSorley, 1981). Several species of *Helicotylenchus* have also built up to extremely large populations around breadfruit roots (Caveness, 1967).

Loquat

The loquat, *Eriobotrya japonica* L., is believed to have originated in China, but has been cultivated in Japan since antiquity. In addition to Japan, which during the 1970s produced between 15 000 to 20 000 t annually, loquats are today produced commercially in many warm-climate countries throughout Asia, the Mediterranean region, southern Africa, Australia and North and South America (Knight, 1980). Despite its considerable – and obviously growing – economic importance, the nematode problems affecting loquat cultivation have not been studied. Perhaps the only potentially pathogenic nematode known to attack loquat is *Rotylenchulus macrodoratus*, which was found to reproduce and induce histological changes in loquat roots (Inserra & Vovlas, 1980).

Mangosteen

A native of Malaysia, the mangosteen (*Garcinia mangostana* L.) is still grown predominantly in southeast Asia, and has also been introduced into Central America. Although not much is known about nematode problems affecting this fruit tree, it is noteworthy that mangosteen has recently been reported from India as a host of the citrus nematode, *Tylenchulus semipenetrans* (Chawla *et al.*, 1980).

Pomegranate

The pomegranate (*Punica granatum* L.) originates from Persia, and is cultivated in western and Central Asia and in the Mediterranean region; it is also grown commercially in California. The

predominant parasitic nematodes affecting pomegranate are the root-knot nematodes, *Meloidogyne incognita, M. incognita acrita* and *M. javanica* (McSorley, 1981). In Israel, heavy root-galling and visible damage to pomegranate trees in young orchards under irrigation is frequently encountered. In Libya, investigations revealed that out of 12 genera of plant parasitic nematodes commonly present in pomegranate nurseries, *M. incognita* and *M. javanica* were the most widespread; phenamiphos application gave good control of the root-knot nematodes, provided protection to roots for 60 days against nematode invasion and improved fruit yields (Siddiqui & Khan, 1986). Among 23 nematode species found in the rhizosphere of pomegranate in Jordan, Hashim (1983*a*) reported particularly large populations of *Helicotylenchus pseudorobustus, Tylenchorhynchus clarus* and *Longidorus* sp. associated with trees showing severe decline symptoms. However, application of carbofuran did not improve tree performance.

Sapodilla

The sapodilla (*Manilkara zapota* (L.) Royen) is native to Mexico and central America, and is today grown largely in tropical America, India and the east Asian tropics. Mexico, the leading producer, supplied an annual crop of 11 217 t in the mid 1970s (Knight, 1980), but its consumption is still limited mainly to the regions where it is cultivated. Some nematode problems of sapodilla were investigated by Saeed (1974), who demonstrated pathogenicity of *Hemicriconemoides mangiferae* to sapodilla at a population density of 6 nematodes/cm^3 of soil, and suppressed populations with DBCP treatment for a 10-month period. He also reported population build-up of *Helicotylenchus indicus* and *Pratylenchus* spp. around sapodilla roots.

Soursop

The soursop, or custard apple (*Annona muricata* L. and other *Annona* species) originated in tropical America and is now distributed in most tropical countries throughout the world. However, international trade in this fruit is very limited. Caveness (1967) found it to be a suitable host for several *Helicotylenchus* species, including *H. cavenessi*.

Tamarind

The tamarind (*Tamarindus indica* L.), known particularly for its use as a condiment and as an ingredient of chutneys, probably has an East African origin, but was early introduced to India where annual production in the early 1960s is said to have averaged 230 000 t (Knight, 1980). It is grown today in most tropical regions throughout the world, and particularly in the Far East. Of the several nematode species associated with the crop, only *Hemicriconemoides mangiferae* has been considered as pathogenic at a population density of 6 nematodes/cm^3 of soil (Saeed, 1974). The tamarind has also been reported as a host of *Radopholus similis* (McSorley, 1981).

References

Abivardi,C. (1973). A stylet nematode, *Tylenchorhynchus cylindricus* Cobb 1913, infesting the common guava, *Psidium guajava* L. in Iran. *Nematologia mediterranea*, 1:139–140.

Ahmad, M. M. & Sultana, K. (1981). Studies on chemical control of root-knot nematodes. In: *Proceedings 3rd Research Planning Conference on root-knot nematodes, Meloidogyne* spp., Region VI, 20–24 July 1981 Jakarta, Indonesia. Raleigh, NC, USA; North Carolina State University: 130–121.

Ahmed, E. M. & Barmore, C. R. (1980). Avocado. In: Nagy, S. & Shaw, P. E. [Eds.]. *Tropical and Subtropical Fruits. Composition, Properties and Uses*. AVI Publishing, Inc., Westport, Connecticut: 121–156.

Anon. (1985). Dried Fruit and Nuts. *International Fruit World*, 43(2):320–353.

Anorga Morales, J. & Rodriguez Fuentes, M. E. (1978). Importancia de los niveles de infestacion de *Meloidogyne*

sp., en el cultivo de la guayaba. *Centro Agricola. Revista Cientifica de la Facultad de Ciencias Agricolas*, 5:47–53.

Australia. (1975). CSIRO Division of Horticultural Research. Report 1973–75. Adelaide, Australia, 137 p.

Ayala, A. (1969). Nematode problems in Puerto Rican agriculture. In: Abad-Ramos, J. [Ed.] *Proceedings of the Symposium on Tropical Nematology*. Agric. Exp. Sta., Univ. of P. Rico, Rio Piedras: 135–145.

Ayala, A., Acosta, N. & Adsuar, J. A. (1971). A preliminary report on the response of *Carica papaya* to foliar applications of two systemic nematicides. *Nematropica*, 1:10.

Ayala, A., & Ramirez, C. T. (1964). Host range, distribution and bibliography of the reniform nematode, *Rotylenchulus reniformis*, with special reference to Puerto Rico. *Journal of Agriculture of the University of Puerto Rico*, 48:140–161.

Babatola, J. O. (1985). Effects of the root-knot nematode, *Meloidogyne incognita* on *Carica papaya* seedlings. *Pakistan Journal of Nematology*, 3:87–90.

Badra, T. & Khattab, M. M. (1982). Chemically-induced resistance to *Rotylenchulus reniformis* by ethephon growth regulant and relevant pathometabolites in mango seedlings. *Nematologia mediterranea*, 10:49–56.

Bello-Perez, A. & Jimenez-Millan, F. (1963). *Heterodera fici* Kirjanova, 1954 (Nematoda), nueva especie para la fauna española. *Boletin de la Real Sociedad Española de Historia Natural. Sección Biológica*

Boesewinkel, H. J. (1977). New plant disease records in New Zealand: records in the period 1969–76. *New Zealand Journal of Agricultural Research*, 20:583–589.

Bolin, H. R. & King, Jr., A. D. (1980). Figs. In: Nagy, S. & Shaw, P. E. (Eds). *Tropical and Sub-tropical Fruits. Composition, Properties and Uses*. AVI Publishing, Inc., Westport, Connecticut: 492–505.

Brancalion, A. M., Zanon, J. I. & Zem, A. C. (1981). Ocorrencia do nematoide *Heterodera fici* no Rio Grande do Sul. *Revista de Agricultura, Piracicaba*, 56:4.

Brunei Department of Agriculture. (1972). *Annual report of the plant pathologist 1972*. Brunei Dept. of Agric. Bandar Seri Begawan, Brunei, 24 p.

Cavaletto, C. G. (1980). Lychee. In: Nagy, S. & Shaw, P. E. Eds. *Tropical and Sub-tropical Fruits Composition, Properties and Uses*. AVI Publishing, Inc., Westport, Connecticut: 469–478.

Caveness, F. E. (1967). Shadehouse host ranges of some Nigerian nematodes. *Plant Disease Reporter*, 51:33–37.

Chawla, M. L., Samathanam, G. J. & Sharma, S. B. (1980). Occurrence of citrus nematode (*Tylenchulus semipenetrans* Cobb. 1913) on roots of mangosteen (*Garcinia mangostana*). *Indian Journal of Nematology*, 10:240–242.

Cohn, E. (1968). *Nematodes as possible vectors of virus diseases of citrus and other fruit crops*. Second annual Rep. to USDA, Project No. A10-CR–72, Bet Dagan, Israel, 28 p.

Cohn, E. & Minz, G. (1961). Citrus nematode on American persimmon in Israel. *Plant Disease Reporter*, 45:505.

Cohn, E. & Mor, M. (1988). Morphology and parasitism of the mature female of *Rotylenchulus macrosomus*. *Revue de Nématologie*, 11:385–389.

Coiro, M. I. & Lamberti, F. (1978). Reproduction of *Xiphinema index* under different environmental conditions. [Proc. 6th Conf. on virus and virus diseases of the grapevine]. *Monografias INIA (Instituto Nacional de Investigaciones Agrarias)*, 18:255–257.

Cuadra, R. & Quincosa, A. (1982). Comportamiento de differentes especies de *Psidium* como patrones para guayabos resistentes a *Meloidogyne* (Nematoda: Heteroderidae). *Ciencias de la Agricultura*, 13:19–26.

Dale, P. S. & van der Mespel, G. J. (1972). Control of root-knot nematodes on Chinese gooseberry (kiwi fruit), *Actinidia chinensis*, by chemical bare-root dip. *Plant Disease Reporter*, 56:850–851.

Darekar, K. S. & Mhase, N. L. (1986). Effect of initial inoculum levels of *Meloidogyne incognita* on growth parameters of papaya seedlings. *International Nematology Network Newsletter*, 3(3):4–5.

De Villiers, E. A. & Milne, D. L. (1973). The control of nematodes on passionfruit. *Citrus and Sub-Tropical Fruit Journal* No. 480:7, 9, 11, 13.

Diab, K. A. & El-Eraki, S. (1968). Plant parasitic nematodes associated with olive decline in the United Arab Republic. *Plant Disease Reporter*, 52:150–154.

Di Maio, F. (1979). Il nematode *Tylenchulus semipenetrans* Cobb, su radici di loto. *Informatore Fitopatologico*, 29:13–14.

Di Vito, M. (1976). *Heterodera fici* su *Ficus carica* in Basilicata. *Nematologia mediterranea*, 4:107–108.

Di Vito, M. & Inserra, R. N. (1982). Effects of *Heterodera fici* on the growth of commercial fig seedlings in pots. *Journal of Nematology*, 14:416–418.

Ducharme, E. P. & Suit, R. F. (1953). Nematodes associated with avocado roots in citrus spreading decline areas. *Plant Disease Reporter*, 37:427–428.

FAO Production Yearbook (1986). Food & Agriculture Organization of the United Nations. Vol. 39, 330 p.

Fernandez Diaz-Silveira, M. (1975). El *Psidium friedrichsthalianum* como patron para guayabo, resistente a los nematodos del genero *Meloidogyne*. *Revista de Agricultura, Cuba*, 3:80–85.

Ferraz, L. C. C. B., Pereira, F. M. & Valente, J. (1982). Considerações sobre o uso de nematicidas em viveiro visando a recuperação demudas de *Ficus carica* cv. roxo de valinhos infestadas por *Meloidogyne incognita*. In: Lordello, L. G. E. (Ed). *Trabalhos apresentados a VI reunias Brasileira de nematologia, 8–12 feveiro de 1982, Fortaleza. Publicação No. 6*. Piracicaba, SP, Brazil; Sociedade Brasileira de Nematologia: 13–20.

Gonzalez, G. & Sourd, F. (1982). Ensayo de tres especies de *Psidium* y su tolerancia a los nematodos. *Ciencia y Tecnica en la Agricultura, Citricos y Otros Frutales*, 5(2):13–25.

Grandison, G. S. (1983). Root-knot nematode control on kiwifruit (*Actinidia chinensis*) by chemical bare-root dip. *Plant Disease*, 67:899–900.

Graniti, A. (1955). Un deperimento dell' Olivo in Sicilia associato a due specie di nematodi. *Olearia*, 9:114–120.

Gur, A. (1955). [The Fig]. *Ministry of Agriculture, Israel, Depts, of Horticulture & Agric. Education, Bulletin No. 57*, 67p. (in Hebrew)

Hashim, Z. (1982). Distribution, pathogenicity and control of nematodes associated with olive. *Revue de Nématologie*, 5:169–181.

Hashim, Z. (1983). Description of *Trophotylenchulus saltensis* n. sp. with a comment on the status of *Trophotylenchulus* Raski, 1957 and a proposal for *Ivotylenchulus* n. gen. (Nematoda: Tylenchida). *Revue de Nématologie*, 6:179–186.

Hashim, Z. (1983a). Plant-parasitic nematodes associated with pomegranate (*Punica granatum* L.) in Jordan and an attempt to chemical control. *Nematologia mediterranea*, 11:199–200.

Heinlein, M. (1982). Treatments for the control of plant parasitic nematodes in nursery potting soils. *Fiji agricultural Journal*, 44:85–88.

Hirschmann, H., Paschalaki-Kourtzi, N. & Triantaphyllou, A. C. (1966). A survey of plant-parasitic nematodes in Greece. *Annales de l'Institut phytopathologique, Benaki*, 7:144–156.

Holtzmann, O. V. (1968). Plant-nematode associations previously unreported from Hawaii. *Plant Disease Reporter*, 52:515–518.

Inserra, R. N. & O'Bannon, J. H. (1974). Systemic activity of phenamiphos for control of *Meloidogyne arenaria* on *Gardenia jasminoides* and *Ficus carica*. *Plant Disease Reporter*, 58:1075–1077.

Inserra, R. N. & Vovlas, N. (1977). Parasitic habits of *Gracilacus peratica* on olive feeder roots. *Nematologia mediterranea*, 5:345–348.

Inserra, R. N. & Vovlas, N. (1978) *Tylenchulus semipenetrans* on olive trees in Northern Italy. In: *3rd International Congress of Plant Pathology, München, GFR, 16–23 Aug., 1978. Abstracts of Papers:* 151.

Inserra, R. N. & Vovlas, N. (1980). The biology of *Rotylenchulus macrodoratus*. *Journal of Nematology*, 12:97–102.

Inserra, R. N., Vovlas, N. & Golden, A. M. (1979). *Helicotylenchus oleae* n. sp. and *H. neopaxilli* n.sp. (Hoplolaimidae), two new spiral nematodes parasitic on olive trees in Italy. *Journal of Nematology*, 11:56–62.

Itoo, Saburo (1980). Persimmon. In: Nagy, S. & Shaw, P. E. (Eds). *Tropical and Subtropical Fruits. Composition, Properties and Uses*. AVI Publishing, Inc., Westport, Connecticut: 442–468.

Kirby, M. F. (1978). Reniform and root-knot nematodes on passionfruit in Fiji. *Nematropica*, 8:21–25.

Klein, A. L., Ferraz, L. C. C. B. & DeOliveira, J. C. (1984). Behaviour of different passionfruit plants in relation to the root-knot nematode. *Pesquisa Agropecuaria Brasileira*, 19:207–209.

Knight, Jr., R. (1980). Origin and World Importance of Tropical and Sub-tropical Fruit Crops. In: Nagy, S. & Shaw, P. E. (Eds). *Tropical and Sub-tropical Fruits. Composition, Properties and Uses*. AVI Publishing, Inc., Westport, Connecticut: 1–120.

Krezdorn, A. H. & Adriance, G. W. (1961). Fig growing in the South. *Agricultural Handbook No. 196*. ARS, USDA, Washington, 26 p.

Krezdorn, A. H. & Glasgow, S. K. (1970). Propagation of *Ficus carica* on tropical species of *Ficus*. *Proceedings of the Tropical Region, American Society for Horticultural Science*, 14:156–164.

Lamberti, F. (1969). Presenza in Italia di un deperimento dell' Olivo causato dal nematode *Pratylenchus vulnus*, All. et Jens. *Phytopathologia mediterranea*, 8:232–234.

Lamberti, F. & Baines, R. C. (1969). Effect of *Pratylenchus vulnus* on the growth of 'Ascolano' and 'Manzanillo' olive trees in a glasshouse. *Plant Disease Reporter*, 53:557–558.

Lamberti, F. & Baines, R. C. (1969*a*). Pathogenicity of four species of *Meloidogyne* on three varieties of olive trees. *Journal of Nematology*, 1:111–115.

Lamberti, F. & Di Vito, M. (1972). Sanitation of root-knot nematode infected olive-stocks. In: *Actas do III Congresso da Uniao Fitopat. Medit., Oerias, 22–28 Outobro, 1972:* 401–411.

Lamberti, F., Rohini, H. M., Ekanayake, V. & Zacheo, F. (1980). Effect of two *Meloidogyne* species on the growth of pawpaw seedlings. *Indian Journal of Nematology*, 10:225–230.

Lamberti, F., Vovlas, N. & Tirro, A. (1976). Infettivita e patogenicita di tre popolazioni italiane di *Tylenchulus semipenetrans* su agrumi ed altri ospiti. *Nematologia mediterranea*, 4:85–91.

Lange, A. H. (1960). The effect of fumigation on the papaya replant problem in two Hawaiian soils. *Proceedings of the American Society of Horticultural Science* 75:305–312.

Ledin, R. B. (1963). The Barbados or West Indian cherry. *University of Florida Agricultural Extension Service Circular* 250, 14 p.

Lima, J. A. A., Menezes, M., Karan, M. de Q. & Martins, O. F. G. (1975). Gêneros de nematoides fitopatogênicos isolados da rizosfera do cajueiro, *Anacardium occidentale* L. *Fitossanidade, Brazil*, 1(2):32–35.

Loof, P. A. A. & Sharma, R. D. (1979). Plant parasitic nematodes from Bahia State, Brazil: the genus *Xiphinema* Cobb, 1913 (Dorylaimoidea). *Nematologica*, 25:111–127.

Lopez, R. & Azofeifa, J. (1985). Nematodos fitoparasitos asociados con frutales en algunos cantones de la provincia de Alajuela. *Agronomia Costarricense*, 9:193–196.

Mahto, Y. & Edward, J. C. (1979). Studies on pathogenicity host parasite relationship and histopathological changes of some important fruit trees due to predominant phytonematode associated with them (Part 1). *Allahabad Farmer*, 50:403.

Mancini, G., Moretti, F. & Catroneo, A. (1978). Histological studies on *Actinidia chinensis* and *Salix alba* infested by *Meloidogyne* spp. *Nematologia mediterranea*, 6:235–238.

Martin, G. C. (1959). Plant species attacked by root-knot nematodes (*Meloidogyne* spp.) in the Federation of Rhodesia and Nyasaland. *Nematologica*, 4:122–125.

McKenry, M. V. & Kretsch, J. O. (1984). Nematodes in pistachio orchards. *California Agriculture*, 38(11/12):21.

McSorley, R. (1981). *Plant parasitic nematodes associated with tropical and sub-tropical fruits*. Agric. Exp. Sta. Inst. of Food & Agric. Sci., University of Florida, Gainesville, Bull. 823, 49 p.

McSorley, R. & Parrado, J. L. (1982). Effect of Nemacur on phytoparasitic nematodes of Barbados cherry. *Fungicide and Nematicide Tests, American Phytopathological Society*, 39:90.

McSorley, R. & Parrado, J. L. (1983). Effect of Nemacur on phytoparasitic nematodes of mango, 1982. *Fungicide and Nematicide Tests,American Phytopathological Society*, 39:92–93.

Milne, D. L. (1982). Nematode pests of litchi. In: Keetch, D. P. & Heyns, J. (Eds). *Nematology in Southern Africa*. Sci. Bull. Dep. Agric. Fish. Repub. S. Afr., Bulletin No. 400:38–41.

Milne, D. L. (1982*a*). Nematode pests of miscellaneous sub-tropical crops. In: Keetch, D. P. & Heyns, J. (Eds). *Nematology in Southern Africa*. Sci. bull. Dep. Agric. fish. Repub. S. Afr., Bulletin No. 400:42–46.

Milne, D. L. & Keetch, D. P. (1976). Some observations on the host plant relationships of *Radopholus similis* in Natal. *Nematropica*, 6:13–17.

Morton, J. F. (1987). In: Curtis, F. D., Jr. (Ed). *Fruits of Warm Climates*. Creative Resource System, Inc. Winterville, NC 505 p.

Narbaev, Z. N. & Sidikov, D. T. (1985). [The possible parasitization of *Heterodera fici* on other crops]. *Uzbekskii Biologicheskii Zhurnal*, 4:57–58.

Nesbitt, R. B. (1956). New host plants of plant parasitic nematodes in California. *Plant Disease Reporter*, 40:276.

Netscher, C. (1981), Arbres resistants au *Meloidogyne* spp.: utilisation comme brise-vent au Sénégal. *L'Agronomie Tropicale Nogent*, 36: 175–177.

Ondieki, J. J. (1975). Diseases and pests of passionfruit in Kenya. *Acta Horticulturae*, 49:291–293.

Peacock, F. C. (1956). The reniform nematode in the Gold Coast. *Nematologica*, 1:307–310.

Peregrine, W. T. H. & Yunton, B. (1980). A preliminary note on nematode pests in Brunei. *Tropical Pest Management*, 26:416–419.

Poehling, H. M., Wyss, U. & Neuhoff, V. (1980). Microanalysis of free amino acids in the aseptic host-parasite system: *Ficus carica – Xiphinema index* (Nematoda). *Physiological Plant Pathology*, 16:49–61.

Ponte, J. J. da (1986). Mapeamento e importancia das doencas do cajueiro no nordeste do Brasil. *Nematologia Brasileira*, 10:59–68.

Ponte, J. J. da & Maria, L. (1973). Imunidade do cajueiro, *Anacardium occidentale* L., a nematoides do genero *Meloidogyne* Goeldi, 1887. *Ciencia Agronomia, Fortaleza*, 3:35–36.

Raski, D. J. & Krusberg, L. R. (1984). Nematode parasites of grapes and other small fruits. In: W. R. Nickle [Ed.] *Plant & Insect Nematodes*. Marcel Dekker Inc. NY: 457–506.

Razak, A. R. (1978). Variation in plant response, gall size and form induced by *Meloidogyne* on some Malaysian crops. *Kasetsart Journal*, 12:43–45.

Reddy, P. P., Singh, D. B. & Ravishankar, H. R. (1980). Host records of the root-knot and retriform nematodes. *Haryana Journal of Horticultural Sciences*, 9: 134–135.

Rodriguez-Fuentes, M. E. & Landa Bolanos, J. (1977). Desinfeccion quimica del suelo para semilleros de guayabo (*Psidium guajava* L.) contra nematodos fitoparasitos. *Centro Agricola. Peirsta Cientifica de la Facultad de Ciencias Agricolas*, 4(3):57–77.

Ruehle, G. D. (1959). Growing guavas in Florida. *Agric. Ext. Serv. Bull.* 170, Gainesville, 20 p.

Saeed, M. (1974). Studies on some stylet-bearing nematodes associated with sapodilla (*Achras zapota* L.) with special reference to *Hemicriconemoides mangiferae* Siddiqi, 1961. *Ph.D. Thesis, Univ. Karachi*, 137 p.

Scotto La Massèse, C. (1973). A new European host of *Meloidogyne hapla* and *Rotylenchus robustus: Actinidia chinensis. Nematologia mediterranea* 1:57–59.

Scotto La Massèse, C., Deportes, L., Mercier, S. & Roger, J. (1984). Les principaux ennemis du figuier: les nematodes et maladies. *Phytoma – Défense des Cultures*, 354:39–41.

Shafiee, M. F. & Osman, A. (1971). The use of nematicides and acaricides for the control of nematodes and mites in established mango orchards. *Phytopathologia mediterranea*, 10:271–273.

Sharma, R. D. (1978). Nematodes associated with avocado (*Persea americana* Mill.) in Cerrado soils. *Societa Brasileira Nematologia Publicaciones* No. 3:65–70.

Sharma, R. D. & Sher, S. A. (1973). Plant nematodes associated with jackfruit (*Artocarpus heterophyllus* Lam.) in Bahia, Brazil. *Nematropica*, 3:20–23.

Sher, S. A. (1955). Nematodes attacking avocado. *California Citrograph*, 40:198.

Sher, S. A., Foote, F. J. & Boswell, S. B. (1959). A root lesion nematode disease of avocados. *Plant Disease Reporter*, 43:797–800.

Sher, S. A. & Raski, D. J. (1956). *Heterodera fici* Kirjanova 1954 in California. *Plant Disease Reporter*, 40:700.

Shesteperov, A. A. (1979). [Pathogenicity of *Meloidogyne* in Cuba]. In: *Gallovye nematody sel'skokhozyaistvennykh Kul'tur i mery bor'by s nimi. (Materialy simpoziuma, Dushanbe, 25–27 sentyabra 1979 g.)*. Dushanbe, USSR, 'Donish' 65–67.

Siddiqui, Z. A. & Khan, M. W. (1986). A survey of nematodes associated with pomegranate in Libya and evaluation of some systemic nematicides for their control. *Pakistan Journal of Nematology*, 4:83–90.

Sikora, R. A. (1988). Presence, distribution and importance of plant parasitic nematodes in irrigated agricultural crops in Niger. *Meddelingen Fakulteit Landbouwetenshappen Rijksuniversiteit Gent*, 53: 821–834.

Singh, N. D. & Farrell, K. M. (1972). Occurrence of *Rotylenchulus reniformis* in Trinidad, West Indies. *Plant Disease Reporter*, 56:551.

Talame, M. (1976). Actinidia attacked by nematodes. *Informatore Agrario*, 32:23281–23282.

Terblanche, J. H., Grech, N., Frean, R., Crabbe, F. & Joubert, A. (1986). Good news for passionfruit industry. *Citrus and Subtropical Fruit Research Institute Information Bulletin* No. 164:1–2, 4–5.

Thorne, G. & Allen, M. W. (1950). *Paratylenchus hamatus* n. sp. and *Xiphinema index* n. sp., two nematodes associated with fig roots with a note on *Paratylenchus anceps* Cobb. *Proceedings of the helminthological Society of Washington*, 17:27–35.

Vilsoni, F. & Heinlein, M. (1982). Influence of initial inoculum levels of the reniform nematode on the growth of mung, pawpaw, pigeonpea and sweet potato. *Fiji Agricultural Journal*, 44:61–66.

Vovlas, N. (1983). Gall formation on *Pistacia vera* by *Rotylenchulus macrodoratus*. *Journal of Nematology*, 15:148–150.

Vovlas, N. & Inserra, R. N. (1981). Parasitic habits of *Ogma rhombosquamatum* and description of the male. *Journal of Nematology*, 13:87–90.

Vovlas, N. & Inserra, R. N. (1983). Biology of *Heterodera mediterranea*. *Journal of Nematology*, 15:571–576.

Willers, P. & Grech, N. M. (1986). Pathogenicity of the spiral nematode *Helicotylenchus dihystera* to guava. *Plant Disease*, 70:352.

Wilson, III, C. W. (1980). Guava. In: Nagy, S. & Shaw, P. E. (Eds). *Tropical and Subtropical Fruits. Composition, Properties and Uses*. AVI Publishing, Inc., Westport, Connecticut: 279–299.

Wolfe, H. S. & Lynch, S. J. (1950). Papaya culture in Florida. *Agricultural Extension Service Bulletin* 113, Gainesville, 32 p.

Wyss, U. (1987). Video Assessment of Root Cell Response to Dorylaimid and Tylenchid Nematodes. In: Veetch, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Society of Nematologists Inc. Hyattsville, Maryland: 211–220.

Wyss, U., Lehmann, H. & Jank-Ladwig, R. (1980). Ultrastructure of modified root-tip cells in *Ficus carica*, induced by the ectoparasitic nematode *Xiphinema index*. *Journal of Cell Science*, 41:193–208.

Young, T. W. & Ruehle, G. D. (1955). The role of burrowing and meadow nematodes in avocado decline. *Plant Disease Reporter*, 39:815–817.

Yuksel, H. S. (1981). *Heterodera fici* Kirjanova 1954 in Aaegean Region. *Journal of Turkish Phytopathology*, 10:45–51.

Chapter 11

Nematode Parasites of Coconut and Other Palms

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The botanical order, Arecales, has but a single family, Arecaceae, also known as Palmae. Palm is the common name for any flowering plant of the family. Although many of the 2600 known species of palms have some particular economic importance to any given local population, only a few are of major economic importance worldwide.

Cocos nucifera L., the coconut palm, which originated in Malaysia, South East Asia, is widely distributed throughout the tropics.

Elaeis guineensis Jacq., the African oil palm, with its origin in Central Africa has now been introduced throughout the tropics.

Phoenix dactylifera L., date palm, is native to the near East where it has been cultivated for its fruit for nearly 8000 years. Over one-third of the dates of the world are grown in Iraq.

Areca catechu L., arecanut occurs mainly in the humid regions of Asia and the Malay Islands.

Metroxylon spp., the sago palms, provide a starchy food material which is stored in their trunks as they develop to the point of flowering. Sago palms of this genus are native to the Indonesia archipelago.

The fruits and seeds of eight genera of the world's palms are oil-bearing and can be commercially exploited for oil. Only *Cocos* is entirely of an old world origin; *Elaeis* has one species (*guineensis*) which is of old world origin and another (*oleifera*) which belongs to tropical America. The other six genera are considered neotropical. There are many palms which are ornamental and are important in horticulture and landscaping.

Coconut

It is generally accepted that coconut palm originated in South East Asia and was transported to the Americas and the West Indies by means of ocean currents as evidence primarily by its presence on shores and the water-resistant pericarp of its fruit or coconut.

Coconut palm is most adapted to temperatures around 27°C with a diurnal range of about 7°C; it does not thrive at temperatures lower than 20°C and is damaged at temperatures below 15°C. Rainfall requirements are about 2500 mm per annum; when less than 1000 mm per annum, irrigation is normally necessary. The absence of rain for more than three months causes a shedding of young fruit and a reduction in fruit size. The palm does best with about 2000 hours of sunlight per year,

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

or an average of six hours daily. Thus, with few exceptions, cultivation is limited by the 20° parallels of latitude and the 500 m contour line.

The largest producers of coconuts are the Philippines, Indonesia, Sri Lanka and India. Significant quantities are produced, however, from most tropical countries of South and East Asia, East and West Africa and the Pacific. Despite some large plantations, coconuts are predominantly a small holder crop with the average holding less than one hectare.

The total world area under coconuts was estimated in 1986 as being close to nine million hectares, with a total production of over 39 million tonnes (FAO, 1987). In all producing countries, coconuts make a significant contribution to the diet in addition to being an important source of export earnings.

Nematodes of Coconut

Many different nematodes have been found associated with coconut (Govindankutty & Koshy, 1978, 1979) but the major nematode disease affecting the crop is red ring disease caused by *Rhadinaphelenchus cocophilus*. The only other nematode known to cause damage to coconut is *Radopholus similis*.

Rhadinaphelenchus cocophilus

The red ring nematode, *Rhadinaphelenchus cocophilus*, was first described by Cobb (1919) as *Aphelenchus cocophilus* from specimens sent from Grenada.

Brief history of red ring disease

The disease was first reported as ocurring in Trinidad by Hart in 1905. The first investigations into its nature was by Stockdale in 1906, who thought that two different diseases were being confused since they both culminated in decay of the bud. One of these was red ring disease, then called root disease, and the other bud rot initiated by *Phytophthora palmivora* Butl. Barrett (1906), however, reported that there were few genuine cases of bud rot among the coconuts in Trinidad and that 95% of the losses were really due to root disease.

Nowell (1919) found that a large number of roots examined from trees in Trinidad contained hundreds of nematodes of the same species. They were also present in the constant red ring found in trees in Grenada and also in the material collected in Trinidad by Rorer (1911). Later, he examined stained sections from many other sources and confirmed Rorer's earlier conclusion that a fungus was not the causal organism, but noted that nematodes of the same species previously observed were constantly present in stems, leaves and roots. The name red ring disease was then used by Nowell (1919) and became the eventual name for the disease.

Distribution of the disease

At present, red ring disease has a restricted distribution and has only been reported from the West Indies (Trinidad, Tobago, Grenada and St. Vincent) and from Latin America (Dominican Republic, Venezuela, Guyana, Surinam, French Guyana, Colombia, Ecuador, Peru, Mexico, Brazil, Panama, Nicaragua, Costa Rica, Honduras, Belize and El Salvador). It is also reported that red ring disease occurs in Guatemala, but does not occur in the northern Caribbean islands, Florida, Cuba or other parts of the world (Dean, 1979).

Symptoms of red ring disease

Young coconut palms easily succumb to red ring disease. There is no record of any tree, once affected, having recovered. The disease occurs more commonly in trees two and a half years old to ten years old, with greatest incidence in those four to seven years old. Occasionally, a palm as young as one and a half years or as old as twenty years or more may be attacked.

The symptoms characteristically described are those for palms of the tall cultivar of coconuts or

Fig. 1. Red ring in cross section of coconut trunk (Photo: D. J. Hooper).

"typica" which grow in the West Indian islands. These symptoms differ somewhat in the dwarf variety "nana" and also some panama talls. Chlorosis first appears at the tips of the oldest leaves and spreads towards their bases but, occasionally, one of the younger leaves may first be affected. The brown lower leaves may break across the petiole or the lower part of the rachis or they may become partly dislodged at the base and hang down (Plate 9A). Nuts are shed prematurely either simultaneously with the development of leaf symptoms or slightly before. The crown often topples over about four to six weeks after symptoms first appear due to associated severe damage caused internally by the larvae of the palm weevil. However, the trunk remains standing in the field for several months until it decays. At the onset of symptoms, the chlorotic yellow appearance of the leaves around the stem is sometimes indistinguishable from those of trees growing under conditions of poor drainage or during intense drought.

The most characteristic symptoms are the internal lesions. In a cross-section of the stem, they appear as an orange to brick-red coloured ring, two to four cm wide, and at a distance of three to five cm in from the periphery (Fig. 1, Plate 9B). In longitudinal section, the reddened tissue may appear as two united bands joined in the bole forming a U-shape (Fig. 2). Lesions at the upper end of the stem in the vicinity of the crown are discrete; appearing first as streaks and then dots. The meristematic tissue in the bud remains white and apparently healthy. There is no putrefaction of the bud associated with red ring disease. In the roots, the normally white soft cortex becomes orange to faint red in colour and dry and flaky in texture when diseased. In the leaves, a solid core of mottled tissue, dull red to brown in colour, extends from the leaf-base for varying distances up to about 75 cm in the petioles.

The disease is not recognizable externally in its very early stages. The roots, stems and leaf petioles are already infested and there is full development of internal symptoms before the first external symptoms become visible. In the dwarf cultivars, the red colour gives way to shades of brown. Thus, instead of a red ring internally, there is a brownish band. The discrete spots are also brownish and the yellow discolouration of the leaves is not often apparent. Generally, the leaves

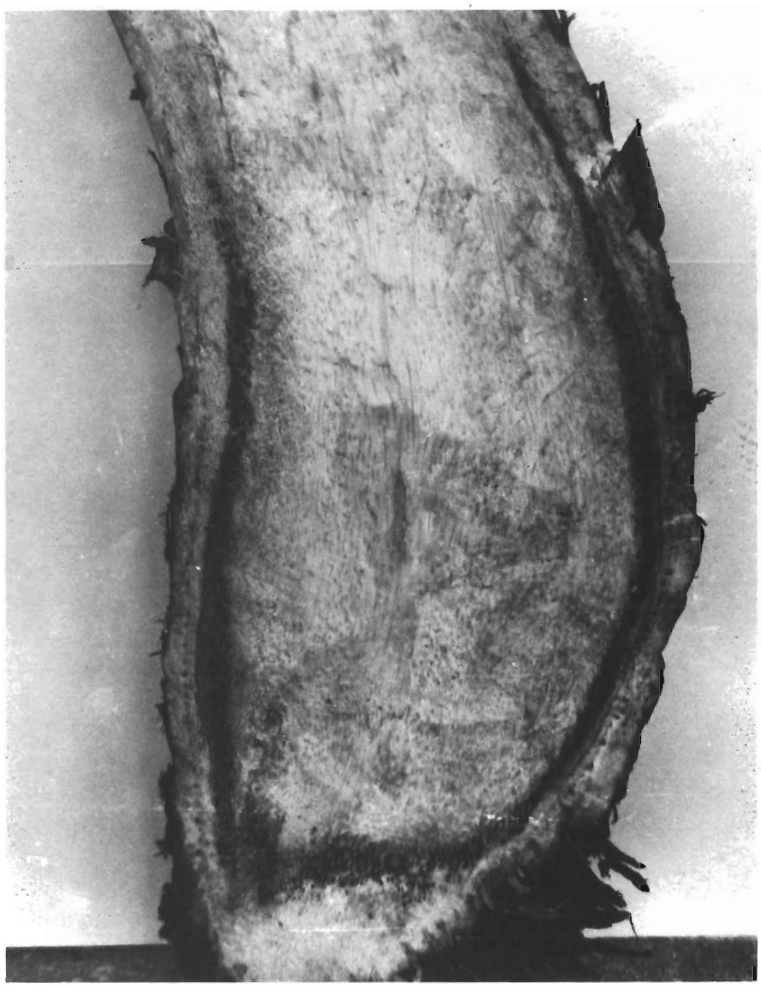

Fig. 2. Longitudinal section of coconut trunk showing 'red ring' tissues forming a U-shape in the bole.

become dried and brown, beginning at the tips of the leaflets and progressing downwards. The yellow dwarf cultivars respond in the same way as the green and the crosses between talls and dwarfs, or between Panama tall and any dwarf. They show a browning instead of a characteristic reddening of the leaves and stem tissue.

Biology of the red ring nematode

The vector of the red ring nematode is an insect, the palm weevil (*Rhynchophorus palmarum* L.), and the biology and life cycle of *R. cocophilus* is intimately associated with the weevil. However, experimentally, it has also been shown that red ring disease can be caused by the nematodes via the root system.

Studies on the biology of the nematode were initiated by both Cobb and Nowell around 1919. Cobb found that 50% of adult palm weevils and their larvae contained the red ring nematode. As

a result, he implicated the palm weevil as being a carrier of the nematode from diseased palms to healthy ones. On the other hand, Nowell's opinion was that the nematode was soil inhabiting.

The general consensus is that *R. cocophilus* does not build up large populations in the soil, as some of the earlier investigators had believed to support their early recommendations of isolated trenches to control the movement of the nematode (Martyn, 1953). It would seem, moreover, that although root infection could be induced artificially, it was not a normal method of initiation of the disease in the field; in the ordinary course of events, the nematodes would not persist in the soil in sufficient numbers to give a reasonable chance of infection. If a persistent source of inoculum was present, eg. buried red ring trunk, (which has been found to remain quite fresh for two weeks after burial), or if a high population of *R. cocophilus* (10^4nematodes/cm^3) is artificially added to the soil, the nematodes could gain entry through damaged or senescent roots and eventually migrate up into the trunk, producing the usual symptoms.

Transmission of red ring nematode

Larvae of the palm weevil feed by burrowing through coconut stems and, when this occurs in trees with red ring disease, they can become infested with the nematode. Adult weevils emerging from diseased trees carry the nematode to new sites. Nematodes enter the haemocoel of weevil larvae via the gut tract; in adult weevils, the nematodes can be found in the gut, body cavity and the region of the ovipositor (Fig. 3).

Vector weevils can become infested with many thousand nematodes, but only a certain percentage of the insect population is so infested. A significant proportion of the insects appear to have a defence mechanism which destroys the nematodes in the haemocoel of the weevil larvae. The mechanism, which is probably one of resistance rather than immunity, is present in those insects which do not carry large numbers of the third stage or infective juveniles. In diseased fields in Trinidad, about 16% of the insects were found to be vectors, not having a defense mechanism and hence contained several thousand red ring nematodes in their bodies. Such vector weevils in Trinidad, are smaller and generally less than 30 cm in length from the tip of the head to the tip of the abdomen (Griffith, 1968).

Survival of the red ring nematode depends on the third-stage juvenile. They are sometimes found in tracheal sacs in the insect from where they move directly to the ovipositor of the female vector palm weevil. The nematodes are injected into the tissues of the coconut tree when the insect deposits its eggs, normally in a leaf axil in the crown of the tree. The palm weevil can be considered the intermediate host, whereas the coconut palm, in which the nematode multiplies, is the definitive host.

Biology of *R. cocophilus* in coconut tissues

The nematodes invade only parenchymatous tissue in roots, stems and leaves and artificially infested nuts. At first, nematodes occur as intercellular parasites in newly invaded tissue but later they can be found both intercellularly and intracellularly. In many cases, lysigenous cavities are formed in which large numbers of nematodes are found. One gram of such tissue can contain as many of 10 000 nematodes. Nematodes have never been found in xylem vessels nor has there been any evidence of direct damage to the tracheal elements. Despite this, however, many of the vessel elements in the discoloured areas become occluded with tyloses. It has been shown that the uptake of water injected into the stems of trees is much slower in diseased trees than in healthy trees. Thus, one feature of the external symptoms coincides with a pathological condition due to water imbalance in the plant.

The cause of the restriction of nematodes to the narrow band or ring of necrotic tissue in stems has never been satisfactorily explained. Nowell (1923) found no anatomical nor physiological factors in trees which might have accounted for it. Martyn (1953) expressed the view that the outer limit of the red zone was determined by the harder tissue at the periphery of the stem and the inner limit was set by aeration and water supply. Nevertheless, occasionally, there is a solid cylinder of discol-

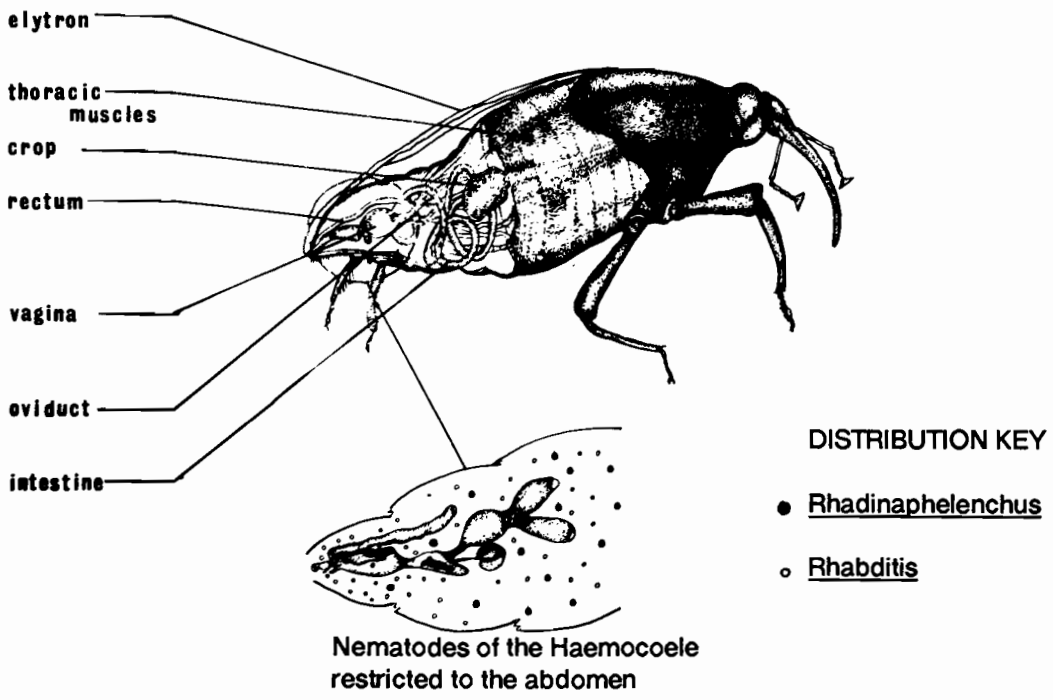

Fig. 3. Location of *Rhadinaphelenchus cocophilus* (and *Rhabditis*) nematodes in body of palm weevil.

oured tissue instead of just a band. Nematodes are often found intercellularly in white, apparently healthy tissue for 1 cm on the outside and 2.5 cm on the inside of the red ring tissue. They are less abundant here than in the body of the ring where they are found both intercellularly and intracellularly. It would, therefore, appear that there are other factors which naturally limit the occurrence and activity of the nematode on the outside and inside of the ring. The most outstanding characteristic of all tissue invaded by *R. cocophilus* is the presence of relatively large intercellular spaces. The inadequacy of intercellular space may, therefore, determine the outer limit.

Nematodes inoculated into the mesocarp of nuts were found to have a life cycle, from egg to egg, of 9–10 days (Blair, 1964). The red ring nematode can persist in the diseased coconut tissue for about three months (Griffith, 1968). Coinciding with the decline in numbers of the persistent *R. cocophilus* juveniles is a rise in number of a *Rhabditis* sp. which are introduced by the palm weevils into the coconut trees (Fig. 4). *Rhabditis* is capable of multiplying in certain of the palm weevils, however, the red ring nematode is not. Ashby (1921) found that juveniles were extremely susceptible to dessication. They died within six hours of drying and fifteen hours when provided with small fragments of tissue. The absence of moisture for half an hour only, followed by exposure to saturated atmosphere for 24 hours, resulted in death of the juveniles in nine cases out of ten.

Environmental factors affecting red ring disease

The larvae of the palm weevil often die when they develop in a tree which is attacked by *Phytophthora palmivora* Butl. (bud rot) or *Micrococcus roseus* Ali-Cohen (cedros wilt disease) subsequent to the contracting of red ring disease. Cannibalism in larvae of the palm weevil resulting from overcrowding often affects the number of emerging weevils. It is known that *M. roseus* produces disease in affected palm weevils. Some ground lizards also feed on the adult insects.

The heaviest losses due to red ring disease occur at the end of the wet season and in the first two or three months of the dry season, i.e. between December and March, in Trinidad (Hagley,

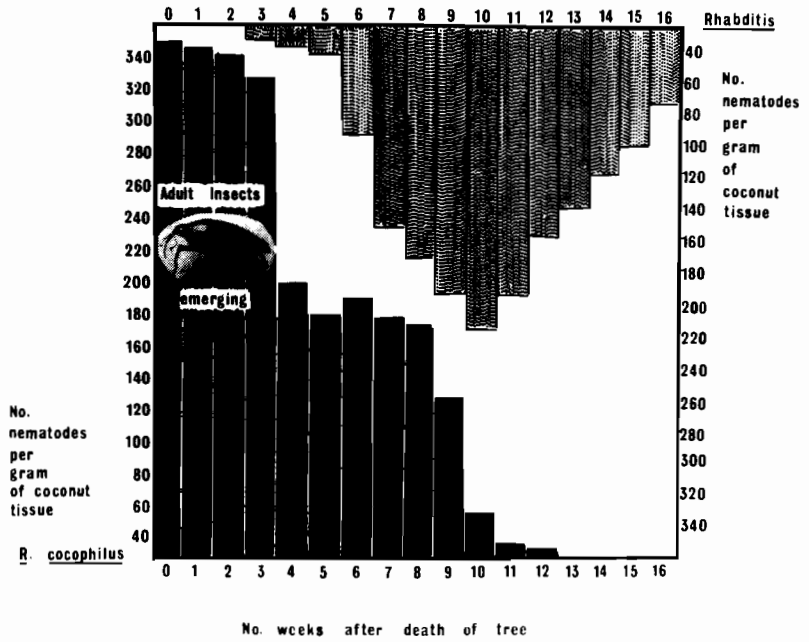

Fig. 4. Longevity of *Rhadinaphelenchus cocophilus* and *Rhabditis* sp. in diseased coconut tissues after death of tree.

1963). The abundance of the disease may be associated with other insects which wound the tree first, inducing fermentation to which the palm weevil is attracted for oviposition. The age of the diseased palm is important since the palm weevil rarely becomes infested with nematodes from old trees. Thus, there is never an epidemic in old groves even if abandoned.

The palm weevil is a pest in its own right and may relate to the environment differently. *R. palmarum* is a pest of the coconut palm, the gru-gru palm and several others. Many of the host palms are wild in the forest and in other uncultivated areas of Latin America, and many represent reservoirs which could become a source of migrant insects.

In many Latin American countries, there exists different levels of attack from red ring disease only and palm weevil attack without red ring disease. In Ecuador, the palm weevil is a major pest and the adult insects attack healthy trees of any age. In other countries, such intense attack without red ring disease is quite rare, but, in Ecuador, the insect is a pest in a habitat consisting of several other kinds of food source like pineapples, papayas and a low population of the red ring nematodes.

The effects of climate on red ring disease incidence is very apparent as one moves from the dry southern Ceara coconut regions to the northerly more humid areas like Bahia in Brazil. In Ceara, where the dry season extends for seven and a half months, the incidence of red ring is less than in Rio Grande del Norte, where the dry season is for five and a half months and less than in Paraiba where the season is for three and a half months. However, in Pernambuco, where the dry season only lasts for two months, the incidence is almost as high as in Bahia Sul where there is little or no dry season.

Other hosts

Though red ring is primarily a disease of the coconut palm, it has been found in many palms (Table 1) including an unidentified species of *Cocos* in the Botanic Gardens, Grenada (Nowell, 1924), and the date palm, *Phoenix dactylifera*, in the Botanic Gardens, Trinidad. Hagley (1963) found one case

of natural infestation of the cabbage palm *Roystonea oleracea*. Disease incidence was reported to be high in the plantation of oil palms, *Elaeis guineensis*, in Venezuela in 1953 (Malaguti, 1953). Nowell (1924) reported successful inoculation of the cabbage and the gru-gru palm, *Acrocomia aculeata*. Latterly, various ornamentals have been artificially inoculated, among them are the Sabal palm, *Sabal palmetto* and the cocorite palm *Mauritia caribea*. The disease has also been found in Brazil on *Attalea cohune*, the Cohune nut.

The palm weevil does not transmit the nematode to any other non-palm host species e.g. sugarcane, papaya and pineapple. On the other hand, countries like the U.S.A., which utilize the *Sabal* sp. for decorative purposes in the presence of *Rhynchophorus cruentatus*, need to ensure proper quarantine measures against both the palm weevil, *R. palmarum*, and the red ring nematode.

TABLE 1 Palms known to be susceptible to *Rhadinaphelenchus cocophilus*.

Acrocomia aculeata (Jacq.) Lodd. ex Mart.	Gru-gru palm
A. intumescens Drude	
Attalea cohune Mart.	Cohune palm
Cocos nucifera L.	Coconut
Cocos sp.	
Elaeis guineensis Jacq.	Oil palm
Mauritia flexuosa L.	Ita palm
M. caribea	Cocorite
M. mexicana	
Maximiliana maripa (Corr. Serr.) Drude	
Oenocarpus distichus Mart.	
Phoenix canariensis Chaub.	
P. dactylifera L.	Date palm
Roystonea oleracea (Jacq.) O. F. Cook	Cabbage palm
R. regia (Kunth) O. F. Cook	Royal palm
Sabal palmetto Lodd. ex Toen & Schult	Sabal palm
Sabal sp.	

Epidemiology and general control

Red ring disease in new groves generally begins by infection of a four to ten-year-old palm by a weevil carrying the nematodes. Effective patterns of control may be employed during several phases of the development of the epidemic.

The rate of spread from the primary infector plant depends upon the development of vector palm weevils within the diseased tree. Parasitization by the nematodes may limit the number of developing vectors and reduce the size, fecundity and longevity of the vector adults. Three months after infection, a new tree can be infected by a vector (female) emerging from the infector plant. If the insect is unmated and infertile, no vector will develop from this infection and red ring can die out when the diseased palm dies. This diseased tree, however, forms a source of inoculum as it becomes chemically attractive to all palm weevils including potential vectors. Phytosanitary measures of control are most effective at this time since disease symptoms are apparent before the progeny of the newly invaded insects emerge after three months.

Invasion and secondary infection begins when other insects are attracted to the original standing diseased tree to mate and oviposit. Their progeny are of the two phenotypes (vectors and non-vectors) with the quantity of progeny depending on size and age of the infected tree (i.e. space, food and intra and interspecific competition) and stage of infection.

Fertile vectors developing from the heterozygous matings and vector by vector mating augment and maintain the increment of disease in the grove. Secondary infective weevils are often limited

by cannibalism between larvae within the diseased tree and the short longevity of the insects in the field. Vector insects live for about ten days whereas the general population survives for about 30 days. Nematodes are unlimited in this phase since diseased trees contain millions of the persistent infective stage of the nematode. As the decomposed trees have no attractive influence to the palm weevils, and nematodes do not survive for more than three months in the diseased tissue nor in the soil for more than 48 hours, the vast majority of the nematode population dies out.

Emerging non-vector and potential vector palm weevils disperse from leaf-axils of diseased trees or wounded trees still emitting attractive compounds. These oviposit in newly diseased palms and cause increased insect population. Control measures relate directly to the abundance of the disease. Since all diseased trees are breeding grounds for insects and red ring nematodes, the killing of diseased trees and reducing their attractiveness is essential to the reduction of the disease and insect population. In older trees, weevils can develop in inflorescences and spathes and some petioles, all of which are of little potential in nematode transmission. Older trees, therefore, can break the link in disease spread.

Specific control measures for red ring disease in coconut

There are no simple means of controlling red ring disease and no effective measures are available for control of the nematode in living palms. Control is based on prevention rather than cure by the destruction of infested palm material, and by the trapping and killing of the weevil vectors before they spread the nematodes.

Many trees show yellowing and browning of leaves which may not be due to red ring disease. To prevent unnecessary destruction of trees, a "core sample" of the trunk should be taken with a 2 cm pipe (see below) to determine the presence of red ring disease and the nematodes before control measures are employed.

Insecticide and herbicide treatments

The leaf axils of all red ring disease trees should be sprayed thoroughly with 0.1% Lannate (Methomyl) insecticide solution (Griffith, 1971). When trees show early symptoms of the disease, the leaf axils should be sprayed with 0.1% Lannate solution to kill off the palm weevils living in these axils. Immediately afterwards the trees should be killed with herbicides (eg. Weedicide "100" or Silvisar "510"). The diseased tree is killed by boring three holes about 10 cm deep with a 2 cm diam. length of pipe around the trunk of the tree. The holes should be made slanting downwards at an angle of about 45° and at a level about 15 cm above the soil. Add 10 ml of herbicide (one tablespoon) in each hole. The tree should be dead in about 14 to 21 days.

When trees are discovered in advanced stages of the disease or when they are seen in a "broken neck" condition, they cannot be poisoned with herbicides. Such trees should be cut down and the pieces and remaining stump sprayed thoroughly with at least 4.5 l of 0.1% Lannate solution. If the tree is adequately sprayed with the insecticide all larvae and pupae of the palm weevil which were developing in the diseased tree will be killed. After 14 days, burn the dried out remains with the aid of kerosene.

Traps or guard baskets

The traps or guard baskets are designed to protect plantations from frequent outbreaks of the disease. They do so by attracting and killing the palm weevils which may enter the plantations from nearby diseased trees. Guard baskets are made of 2 cm mesh wire. They are cylindrical, 1 m high and 0.3 m in diameter. These baskets are filled with chunks of fresh tissue from diseased coconut trees to attract the beetle. If such trees are not available, chunks of palmiste or "gru-gru" trees may be used. The guard baskets are sprayed completely with about 4.5 l of 0.1% Lannate solution and distributed on the ground in the plantations at one basket per acre (2.5 baskets/ha) of young coconut trees. This procedure is especially recommended in the dry season when the weevils are most active in the cool nights. Guard baskets remain for about two weeks, after which the tissue and insecticide

in the basket should be burnt. Fresh tissue should be placed in the basket and treated as previously described. Several variations are used in practice with different types of tissue (pineapples, papaya, etc.).

Biological control measures

At present, possible biological control measures against red ring disease are focussed on the susceptible vector weevil which is parasitized by several nematode species of Rhabditidae or Heterorhabditidae throughout Latin America. Often these nematodes have a biological relationship with the palm weevil in which they may multiply and in some instances pass through the eggs of the vector insects. Since the vector insects can be heavily parasitized, the maintenance of a high population of the nematodes in the environment introduces selective pressure against the vectors. Such measures are being employed in Trinidad with a species of Rhabditidae which is maintained in coconut agroecosystems at a level of at least 10% of the captured insect population. In most Latin American countries where oil palms are grown, researchers are examining the potential of their agroecostyems to restrict the development of the vector insects.

Methods of diagnosis

Recovery of *R. cocophilus* from coconut tissue

The methods used for recovering nematodes from the palm differ principally according to the degree of activity of the nematodes in the tissue and also the density of nematodes per g of infested tissue. In the method originally used by Fenwick (Fenwick & Maharaj, 1963), diseased coconut tissue is chopped into fine pieces about one cm in thickness, placed in a large funnel of water, whose stem is closed at one end with a tube and clip, and whose neck has a light plug of cotton acting as a filter separating the tissue from the 10 to 20 ml of clear water in the stem. This can be modified by actually macerating the diseased tissue in a blender in order to liberate more lethargic nematodes. The following modification was devised by Schuilling & Van Dinther (1981). Fifteen g of chopped tissue, suspended in 250 ml of water, are blended in an electric mixer for 30 sec. The resultant suspension is made up of one litre in a bottle and allowed to stand for 30 min. The contents of the bottle are then sedimented over another container filled with water. After 30 min the contents of the lower bottle are discarded. The contents of the top bottle are sieved four times through a 60 mμ sieve.

The well established methods for obtaining samples of nematodes from living trees are still used. A stainless steel tube, sharpened at one end, is driven at an angle of 45° at the point selected for sampling. The extracted core is placed in a blender with 50 ml of water and processed for 2 mins. The contents of the blender are then poured into a dish and left for 20 min for the nematodes to emerge. The nematodes are then recovered by sieving. Generally, advantage is taken of the level of activity of the nematode during extraction methods. In coconut and the palmiste palms the nematodes are most active in the stem tissue except in the very necrotic regions. The core tissue generally shows a red cylinder of necrotic red ring tissue.

Radopholus similis

The burrowing nematode, *R. similis*, occurs in most tropical and subtropical areas of the world and has been reported from coconut palms in Florida, Jamaica, Sri Lanka and India (Van Weerdt *et al.*, 1959*a*, 1959*b*; Ekanayake, 1964; Latta, 1966; Weischer, 1967; Koshy *et al.*, 1978). Koshy (1986*b*) suggested co-evolution of the nematodes along with black pepper and certain cultivars of banana in the western hills of South India. It occurs deep inside the forests on wild black pepper and is widespread on a number of crops like coconut, arecanut, black pepper, banana, betel vine, ginger, etc., in South India.

Symptoms of damage

The burrowing nematode causes non-specific general decline symptoms such as stunting, yellowing, reduction in number and size of leaves and leaflets, delay in flowering, button shedding and reduced yield. *R. similis* infestation produces small, elongate, orange-coloured lesions on tender creamy-white roots. Consequent to nematode parasitization and multiplication, these lesions enlarge and coalesce to cause extensive rotting of the roots (Plate 9C). Tender roots of coconut seedlings with heavy infestation become spongy in texture. Surface cracks develop on the semi-hard orange-coloured main roots. Lesions and rotting are confined to the tender portions of the root. Lesions are also not conspicuous on the secondary and tertiary roots since these are narrow and rot quickly on infestation.

As many as 4000 nematodes are known to occur in one g (2.5 cm length) of main roots. The nematode also attacks the plumule, leaf bases and haustoria of seedlings. The above-ground symptoms being non-specific, the only definite method to identify an infested palm is to look for characteristic lesions on fresh, creamy-white to orange-coloured tender main roots.

R. similis does not enter or penetrate the coconut roots that have developed a hardened or suberised epidermis but does penetrate the absorbing region behind the root-cap covered by very delicate epidermis by lysis of cells. The cavities that form in the outer cortex are always surrounded by deeply stained and heavily suberised cells of irregular shape, whereas those formed in the inner cortex do not have any such deformed darkly stained border cells. Maximum number of nematodes and cavities are seen in the outer cortex. Nematodes have not been observed in the stelar region or in the closely packed four to six layers of cells outside the endodermis even in heavily infested roots. In the early stage of infection, roots have separate cavities which later merge with each other.

Multiple cavities and their coalescence destroys the cortex to a great extent, but the stelar tube remains intact. Eggs and all stages of nematodes with different orientations are seen in the cavities in longitudinal sections (Fig. 5) (Koshy & Sosamma, 1982*a*, 1987; Koshy, 1986*a*, 1986*b*).

Biology and life cycle

The burrowing nematode is a migratory endoparasite and is capable of spending its entire life within roots. Most juvenile stages and adult females including gravid females infest healthy succulent root tips; fourth stage and adult males do not. The nematode takes 25 days at 25° – 28°C to complete one life cycle (J2 to J2).

The coconut isolate of *R. similis* from Kerala, India is the "banana race" as they do not infest *Citrus* spp. or *Poncirus trifoliata* (Koshy & Sosamma, 1977) and has a haploid number (n=4) of chromosomes (Koshy, 1986*b*). The *R. similis* population from coconut root is easily cultured axenically on carrot discs placed on one per cent water agar (Koshy & Sosamma, 1980). It can also be cultured within the mesocarp of growing tender coconuts without affecting the size or quality of the nuts (Koshy & Sosamma, 1982*b*).

Survival and means of dissemination

The burrowing nematode survives under field conditions for six months in moist soil (27 to 36°C) and one month in dry soil (29 to 39°C); it survives for 15 months in moist soil (25.5 to 28.5°C) and three months in dry soil (27 to 31°C) under glasshouse conditions. The nematode survives in roots of stumps of felled coconut palms for up to six months (Sosamma & Koshy, 1986) and as adult females in coconut roots and soil during summer months causing annual recurrence of infection (Koshy, unpubl.).

Coconut seedlings are raised by sowing seednuts in the interspaces in coconut plantations in Kerala, India. Most of the nurseries in Kerala and Tamil Nadu (South India) are infested by *R. similis*. One year old coconut saplings raised in these infested nurseries harbour large populations of the nematode in roots internal and external to the husk. Such seedlings when distributed for planting help in the dissemination of the nematode over long distances.

Fig. 5. Longitudinal section of coconut root showing *Radopholus similis* in cavities formed in the cortex.

Environmental factors affecting parasitism

Infested coconut roots yield a maximum number of *R. similis* during October to November and minimum during March to July in India. Factors favourable to nematode multiplication are a mean soil temperature below 25°C and a light rainfall coupled with availability of tender fleshy roots. Nematode populations in roots of individual palms were found to vary considerably during low and high peaks depending upon the age, cultivar and conditions of the palms involved (Koshy & Sosamma, 1978*a*). The burrowing nematode multiplies well on coconut in loamy sand followed by riverine alluvium, but least in Kari type soils. However, it causes maximum plant damage in riverine alluvium and the lowest in laterite soil (Sosamma & Koshy, 1985).

Other hosts

The coconut isolate of *R. similis* has a wide host range including several economically important plants, weeds and trees. Of 115 plant species tested, 48 species belonging to 45 genera in seventeen families were recorded as hosts (Koshy & Sosamma, 1975; Sosamma & Koshy, 1977, 1981).

Disease complexes

The fungi *Cylindrocarpon effusum, C. lucidum* and *Cylindrocladium clavatum* have been recorded in association with lesions produced by *R. similis* in coconut roots. In pathogenicity studies, the

fungus *C. effusum* did not cause any appreciable damage to inoculated seedlings. The fungus, when inoculated simultaneously with the nematode, reduced the rate of multiplication of the nematode and damage to coconut seedlings (Sosamma & Koshy, 1978, 1983; Koshy & Sosamma, 1987).

Economic importance and population damage threshold levels

Surveys of different coconut growing tracts of Kerala, Karnataka and Tamil Nadu States of India (964 000 ha) revealed the widespread occurrence of *R. similis*. Twenty-four per cent of the root samples yielded *R. similis*, and, of these, 50% yielded one or more *R. similis*/g of root (Koshy *et al.*, 1978; Sosamma, 1984). Thirty per cent increase in yield was recorded by application of *Hydnocarpus* sp. oil cake at 8 kg/palm/year or phorate and aldicarb at 10 g a.i./palm in June – July and October – November to the burrowing nematode infested coconut palms (Koshy, 1986*b*).

An initial inoculum density of 62 500 nematodes per seedling caused 48, 21, 76 and 79% reduction over control in height, girth, shoot and root weight respectively over a period of five years in sandy loam soil in pots under field conditions. The threshold inoculum density causing significant reduction in various growth parameters was 100 nematodes/seedling or one nematode in 576 cm^3 or 800 g sandy loam soil over a period of five years. At this inoculum level the nematode caused 35, 14, 65 and 65% reduction over control in height, girth, shoot and root weight respectively (Koshy & Sosamma, 1987).

In field tanks in India, the nematode causes yellowing, loss of vigour, stunting and delay in flowering of inoculated plants (Plate 9D). After five years an initial inoculum level of 10 nematodes/ 35 640 cm^3 of soil caused 13, 13 and 24% reduction over controls with regard to height, number of leaves and girth compared to 17, 14, and 35% reduction with an inoculation of 100 nematodes/ 35 640 cm^3 of the soil. The average field population is 26 nematodes per 35 640 cm^3 of soil. At a higher inoculum level of one nematode in 3.5 cm^3 of soil, the percentage reduction over control in height, number of leaves and girth was 44, 30, and 51 respectively (Koshy & Sosamma, 1988).

Control

Control of the burrowing nematode on a perennial palm such as coconut with a massive root system is difficult, especially under the high density multispecies cropping system that exists along the West Coast of South India involving susceptible crops like arecanut, banana, black pepper, betel vine, ginger, turmeric, etc. Unlimited use of nematicides for the control of the burrowing nematode may cause problems of residual toxicity in coconut water and copra (Habeebullah *et al.*, 1983). Apart from this, it may also lead to residual toxicity in the products of the intercrops. Therefore, control of nematodes by field application of nematicides alone is not a practical proposition.

Cultural practices

The cultural practices existing in Kerala and Karnataka (India) such as the application of oil cakes, farm-yard manure and green foliage to the basins, also the growing of intercrops like cacao that enriches the soil with sizeable quantities of shed foliage which helps in the build-up of beneficial organisms, may inhibit nematode multiplication.

Resistance and tolerance

All the coconut cultivars (29 exotic, 15 indigenous and 15 hybrids) screened for resistance to *R. similis* in India were found susceptible in varying intensities. The dwarf cultivars, Kenthali and Klappawangi, recorded the least nematode multiplication and lesion indices. Similar reactions were noticed in hybrids such as Java Giant × Kulasekharam Dwarf Yellow, Kulasekharam Dwarf Yellow × Java Giant, Java Tall × Malayan Yellow Dwarf and San Ramon × Gangabondam (Sosamma *et al.*, 1980, 1986; Sosamma, 1984).

Chemical

Burrowing nematode infestation in coconut nurseries has been detected in India. Increased incidence of *R. similis* can occur when banana is used as a shade crop in coconut nurseries. In these cases, there is a need for treatment of nurseries with nematicides to produce nematode free seedlings to prevent spread of the nematode into the main field and to uninfested areas.

A dip in 1000 ppm DBCP for fifteen min is effective in controlling nematodes in seedlings for *R. similis* infested coconut nurseries (Koshy & Sosamma, 1979). Complete control of *R. similis* can be obtained with soil application of phenamiphos or phorate at 25 kg a.i./ha during September, December and May in infested coconut nurseries (Koshy & Nair, 1979; Koshy & Sosamma, 1979; Koshy *et al.*, 1985).

Summary of control measures

The following measures are suggested towards developing an integrated management schedule for *R. similis* infestation on coconut palms:

1. Application of cow dung, farm yard manure, oil cakes and green manure to the basins. *Crotolaria juncea* may be cultivated in the basins and interspaces and used as a green manure.
2. Application of phorate at 10 g a.i./palm twice yearly.
3. Avoiding use of bananas as a shade crop in coconut nurseries.
4. Use of nematode free planting material of coconut and other intercrops.
5. Use of tolerant or less susceptible cultivars or their hybrids in infested areas.

Methods of diagnosis

Sampling

Soil and root samples for detection of *R. similis* should be collected when maximum populations of the nematode occur (October-November in India). Maximum populations of *R. similis* are found on coconut at a distance of 100 cm from the bole of the palm and at a depth of 50–100 cm. Tender, creamy-white to orange coloured, semi-hard, main roots (about one cm diameter) showing lesions and rotting should be collected to obtain live populations in large numbers.

Extraction

The semi-hard, orange coloured, main root bits are peeled and sliced longitudinally into four to eight pieces of three to five cm length. These sliced root bits are submerged in water contained in Petri dishes or shallow pans at a temperature of 20–25°C, which is ideal for increased extraction from polyphenol rich coconut roots (Koshy *et al.*, 1975; Koshy, 1986*b*). After every 24 hours of incubation, the water needs to be changed; 50% of the population is extracted after 72 hours. Most of the nematodes are recovered within four to seven days.

Determination of populations and crop loss

Nematode populations in the tender portions of the main roots can be estimated by staining and blending. Roots may be cut into two cm long pieces, sliced longitudinally into eight sections and then stained.

Conclusion and future prospects

The burrowing nematode, *Radopholus similis* is second in importance to the red ring nematode, *Rhadinaphelenchus cocophilus* on the basis of its damage potential on coconut. Though the nematode has been reported in association with various coconut diseases (Govindankutty & Koshy, 1979), no detailed investigations seem to have been carried out anywhere else except India. Screening for resistance/tolerance to *R. similis* in coconut cultivars and their hybrids have indicated the availability of possible resistance in some cultivars. Though breeding in coconut is a long-term process, this area could be profitably exploited. Developing an integrated management schedule for the coconut based

on subsistence farming systems involving susceptible perennial crops like arecanut, black pepper, cacao, banana, etc., should be the priority area of research.

Oil Palm

The oil palm, *Elaeis guineensis* Jacq., has a natural distribution in West Africa between latitudes 13°N and 12°S from the coast to the Great Lakes. Ecologically, it is found in the transition regions between the rain forest and the savanna. It has also been extensively cultivated in Malaya and Indonesia. Commercial production of oil palm in Central and South America dates back only to the 1960's, though production is expanding in all tropical South America. In the New World, it is a plantation crop with holdings of several hundred to several thousand hectares per unit. Whereas in Africa or Asia it can be a large plantation or small holders crop as with the coconut.

Nematodes of Oil Palm

Generally, the major diseases of the oil palm are found in its area of origin. Curiously, though there are fungal, bacterial and suspected viral or mycoplasma induced diseases, no records of any economic losses due to nematode damage occur in the old world. However, *Rhadinaphelenchus cocophilus* causes economic loss in oil palm in South America.

Rhadinaphelenchus cocophilus

Red ring disease caused by *R. cocophilus* has been known in the oil palm from Venezuela since before 1953 (Webster & Gonzales, 1959) from a single plantation of 1000 ha where the disease caused severe losses. Malaguti (1953) demonstrated that oil palm, which had recently arrived in Latin America from Africa, was invaded by the red ring nematode.

Symptoms of red ring disease in oil palms and biology

The colouration in the diseased palm is similar to that of the browning associated with the "nana" or dwarf cultivar of coconuts, that is, brownish rather than reddened tissue internally (Plate 9E). Also, the leaves dry out and turn brown instead of the usual yellowing and then browning associated with the tall cultivar of coconuts (Plate 9F). The ultimate symptoms of red ring disease in oil palm are similar to those of the coconut palm, but there are some fundamental differences which can lead to new and distinct measures for treating the disease in the crop.

Pathogenesis is longer than in the coconut. In the coconut, the young three to ten year-old palm is virtually dead within three months after infection. In the case of the oil palm, this process can take three to four years with a palm of the same age group. This is partially because the nematode does not colonize as rapidly in the oil palm tissue as it does in the coconut. Where 5000–10 000 nematodes/g of tissue can be found in the red ring zone of coconut, a similar region in the oil palm yields less than 500 nematodes/g tissue. A further difference is that most nematodes are found outside the necrotic zone, even in areas which show no necrosis such as the distal or basal portion of the stem and occasionally in the rachis of the inflorescence.

As in the case of the coconut, the most persistent form of the nematode is the third stage juvenile which can subsist for a long time in the diseased tissue. In the coconut, this juvenile form readily proceeds to the adult in the healthy tissue not showing symptoms. But, in the oil palm, this interval is prolonged for some reason with the result that colonization of the oil palm is not rapid and pathogenesis is attenuated. A notable feature in accordance with this, is that the band of necrotic tissue is always very narrow. Eggs appear as usual in the brownish spots which are present in the advancing area of the disease. Such necrotic areas indicate evidence of plant reaction to the cellular damage caused by abundance of the nematode. The nematodes often show no evidence of their presence and an abundance of nematodes can occur without the plant reacting visibly.

The canopy in an oil palm plantation is always closed and humid presenting ideal conditions for the vector of the nematodes, the palm weevil, which is crepuscular.

Special disposition of diseased oil palms

In young five to ten-year-old groves there is a tendency for the diseased palms to be clustered in a 50 m radius which gradually expands. In older groves, however, the diseased trees appear to be distributed at random giving the impression that the vectors come from fields which are more susceptible to the simultaneous development of both the nematode and the palm weevil. The major constraint is the poor opportunity for association of the developing weevil larvae in the oil palm with a large number of nematodes. This is a result of the slower rate of colonization of the nematode in the oil palm compared to the coconut palm. Therefore, weevil trapping in oil palm estates is an important form of control for the disease. Moreover, location and elimination of sources of infection, other than oil palm, near the affected grove is important. Phytosanitary measures, however, comprise the most utilized method of control in Latin America.

Other hosts for red ring disease in some oil palm estates in brazil

The wild palm *Oenocarpus distichus* Mart., was found by Schuilling and Van Dinther (1981) to be capable of contracting red ring disease and housing the vector palm weevil. This is a typical palm of primary and secondary forest of the Amazon estuary. Nematodes are often fewer in number, often less than 100 per g of tissue. However, palm weevil larvae found growing in these trees were also internally contaminated.

Economic importance and damage threshold levels

In Latin America, there is an apparent direct correlation between levels of red ring disease in coconuts and those in oil palms. Countries with high levels of red ring disease in coconut groves also have high levels of red ring in oil palm groves. Generally, in oil palms 8–10 years old, the incidence is around 0.1% and in palms over 20 years old the incidence is rare. However, in some zones adjoining old coconut establishments, the incidence of disease in oil palms, 11–18 years old, can be as high as 30%. In one parcel of 62 hectares of the plantation of Palmeras de la Costa in Colombia, the maximum accumulated disease total for 1987 was 8.3% (Villanueva & Gonzales, 1988).

Little leaf disease of oil palms

The oil palm, as most palms, has a tendency towards producing so called "little leaves", the cause of which may be diverse and related to symptoms of other diseases. In Surinam, Van Hoof and Seinhorst (1962) observed that little leaf syndrome was associated with attack by the red ring nematode. Little leaf trees can easily be recognized by their erect, short and often deformed leaves with suberized patches especially on the inner side of the leaf stalks.

Many *R. cocophilus* have been found on discoloured tissue of young (up to 1.75 m long) folded leaves, still protected from the sun. The nematodes apparently live ectoparasitically in the buds of the palms. In one survey, of 50 diseased oil palms cut for investigation, only one did not contain nematodes. *R. cocophilus* was never found on the young leaves of numerous trees that did not suffer from little leaf but were cut for other reasons (Van Hoof & Seinhorst, 1962).

Control

Generally, control of red ring disease in oil palm is similar to that in coconut by a combination of methods. The destruction of diseased trees is paramount as soon as the symptoms are detectable in order to destroy inoculum. In countries such as Columbia, emphasis is placed on weevil trapping measures since symptoms of the disease on the infected palm are often very obscure, more so in some cultivars than others. Various types of traps are utilized ranging from dug-out lengths of palm

trunks resembling canoes to slabs of palm tissue covered by leaves. Sometimes, portions of trunks are left exposed. In all the traps, a solution of 0.1% Lannate is sprayed.

Experiments are being undertaken to kill the nematodes in diseased trees using nematicides. This measure is unsuccessful in coconuts because the nematode colonizes the palm tissue too rapidly but in oil palm, the slow rate of colonization allows for such a possibility to control the nematode directly.

Methods of diagnosis

The methods for extraction of *R. cocophilus* from oil palm are similar to those described for the nematode in coconut, however, in the oil palm, the nematodes seem to thrive more in the petioles than in stems and roots.

Date Palm

The date palm, *Phoenix dactylifera* L., is dioecious and artificial pollination by man has played a significant role in the historical development of the crop. More than one third of all the dates of the world are grown in Iraq. Though the palms will grow throughout the tropics, the number of heat units required from the time of blossoming to ripening should be between 4000 to 5500 for various cultivars. Growth of the palm ceases around 10°C. Suitable climatic conditions occur in the dry parts of California where the palm has been successfully grown on a commerical scale. In this introduced environment the palm has to cope with the new prevailing nematode fauna.

Nematodes of Date Palm

The date palm is affected by numerous pests and diseases wherever it is grown, but nematodes, with the exception of root knot nematodes, *Meloidogyne* spp., have not been well studied. However, nematodes have not been found to be a limiting feature in the countries with date as an ancient culture.

Meloidogyne

Root knot nematodes were found in the Coachella Valley of California on date palms in 1925 where they are now known to be widely distributed in commercial date plantings. Buhrer *et al.* (1933) first reported the occurrence of root knot nematodes on date, and Jensen (1961) found *M. incognita* on roots of date palms in nurseries. Carpenter (1964) reported that root knot nematodes, principally *M. javanica* can severely damage or kill date palm seedlings.

Young seedlings of 50 date cultivars were susceptible to infection by root-knot nematodes; more than 90% of the seedlings were killed prior to emergence when seeds were sown in heavily infested soil. Secondary damage by fungi to roots of field-grown palms infested with the nematodes seemed to be an important factor in the deterioration and death of roots. Minz (1958) reported the occurrence of *M. arenaria*, *M. hapla*, *M. incognita* and *M. javanica* on date palms in Israel. *Meloidogyne* sp. was reported from Sidi Yaia in Algeria (Lamberti *et al.*, 1975), and from the Mauritanian oases of Tayaret and Terjitt (Netscher & Luc, 1974).

Other nematodes

In Algeria, Lamberti *et al.* (1975) reported the occurrence of *Pratylenchus penetrans* on date palm roots in the crescent of oases from Beni Ounif to Biskra. *R. cocophilus* is also known to affect the date palm. A specimen in the Botanic Gardens, Trinidad, came down with red ring disease and produced a brownish ring. However, date palm prefers a hot dry environment which limits the activities of the palm weevil, the vector of the red ring nematode.

Arecanut

Arecanut or betel nut, *Areca catechu* L., occurs in the humid regions of Asia and the Malay Islands. It is a masticatory of great antiquity and betel-chewing is a habit of nearly one-third of the world's population. The ripe fruits are sometimes used as an anthelmintic and astringent in Europe.

Nematodes of Arecanut

A number of nematodes have been reported from the rhizosphere of arecanut (Nair, 1964; Weischer, 1967; Pizarro, 1969; Koshy *et al.*, 1976, 1978; Reddy, 1978; Sundararaju & Koshy, 1982*a*; Sundararaju *et al.*, 1984; Rama, 1987; Dasgupta & Rama, 1987), but only *Radopholus similis* is known to be an important parasite of the palm. A number of other palms have been reported as hosts of *R. similis* (Table 2) and it would not be unexpected if nematode problems with some of these other palms became apparent in the years ahead.

Radopholus similis

The burrowing nematode, *R. similis* was first reported from soil around roots of arecanut palm in Mysore, India by Kumar *et al.* (1971) and later by Koshy *et al.* (1975, 1976).

Symptoms of damage

The most conspicuous symptoms of *R. similis* infestation is the appearance of lesions and rotting on roots. The nematode produces small, elongate, orange-coloured lesions on the young, succulent, creamy-white to light-orange coloured portion of the main and lateral roots. Subsequently, the adjoining lesions coalesce and cause extensive root rotting. The thick primary roots produced from the bole region of the palm exhibit large, oval sunken, brown to black lesions, 2 mm to 2 cm in length.

TABLE 2 List of palms reported as hosts of the burrowing nematode, *Radopholus similis*.

Archontophoenix cunninghamiana Wendl. & Drude	Seaforthia palm
	Picabeen bungalow palm
Areca (*Actinorhytis*) *calapparia*	
Areca catechu L.	Betel-nut palm
A. langlosiana	
A. macrocalyx Becc.	
A. normanbyii	
A. triandra Roxb.	
Arecastrum romanzoffianum (Cham.) Becc.	Queen palm
Chamaedorea cataractarum Mart.	
Cocos nucifera L.	Coconut
Collina elegans (Mart.) Liebm.	Parlour palm
	Neanthebella palm
Elaeis guineensis Jacq.	Oil palm
Phoenix canariensis Chabaud.	Canary Island date palm
P. dactylifera L.	Date palm
Rapis excelsa	Large lady palm
Roystonea regia (H.B.K.) Cook.	Royal palm

Nematodes occur inter- and intracellularly in the cortex, but do not enter the stelar tissues. Large numbers of nematodes and their eggs are seen in the cavities that develop consequent to nematode feeding in the cortex (Sandararaju, 1984).

Biology and life cycle

The burrowing nematode takes 25–30 days to complete one life cycle (J_2-J_2) on arecanut seedlings at a temperature range of 21–31°C under glasshouse conditions. Chromosome studies have recorded the presence of a haploid number of chromosomes (n=4) in many isolates of *R. similis* from arecanut roots (Koshy, 1986*b*). The arecanut isolate of *R. similis* belongs to the banana race (Koshy & Sosamma, 1977) and multiplies well on carrot discs maintained on one per cent water agar (Sundararaju, 1984).

The population densities of *R. similis* in arecanut fluctuate; maximum population occurs in roots during October to November and minimum during March to June in India. Populations are also known to vary between samples, types of roots, palms, groves and soil types during the same period (Koshy & Sosamma, 1978*a*).

Disease complexes

The fungus *Cylindrocarpon obtusisporum* is found associated with lesions caused by *R. similis* in arecanut roots. The fungus when introduced three weeks after nematode inoculation caused more damage to plants compared to inoculations with the nematode alone and it inhibited the rate of multiplication of the nematode (Sundararaju & Koshy, 1984, 1987).

Economic importance and population damage threshold levels

R. similis was recorded from 32% of root samples in the three major arecanut growing States in South India with a maximum population of 440 nematodes/g of root. *R. similis* was found in 55, 45, 44, 30 and 11% root samples from plantations intercropped with banana, black pepper, cardamom, coconut and cacao respectively, compared to 25% from plantations monocropped to arecanut (Sundararaju, 1984).

The population damage threshold level on arecanut seedling is 100 nematodes/seedling or one/800 g of laterite soil. The percentage reduction of growth over uninoculated plants at this inoculum level can be 23, 39, 25, 19 and 38% with respect to shoot length, shoot weight, girth at collar region, root length and root weight under pot conditions in laterite soil.

Control

Resistance/tolerance

None of the 46 accessions of arecanut germplasm in the CPCRI germplasm collection is immune or highly resistant to *R. similis*. The cultivars Mangala (VTL–3) and Fiji (VTL–26) are highly susceptible whereas the cultivars Singapore (VTL–17), Solomon Islands – 2 (VTL–18c) and Saigon (VTL–27) are less susceptible to *R. similis*; cultivars Indonesia 6 (VTL–11) Mahuva 8 and Andaman–5 (VTL–29e) are tolerant to *R. similis* (Koshy *et al.*, 1979; Sundararaju & Koshy, 1982*b*). The cultivar Indonesia–6 (VTL–11) and Singapore (VTL–17) are known to yield 15% more nuts over local South Canara cultivar (Anon., 1974). Thus, these cultivars could profitably be recommended for *R. similis* infested areas. The hybrid VTL–11 × VTL–17 is highly resistant to *R. similis*.

Chemical

As arecanut is chewed directly by many consumers, dosage, frequency and time of application of nematicides on arecanut have to be done carefully to avoid residues in the nut.

A pot culture experiment carried out under field conditions revealed that fensulfothion and aldicarb at 1 g a.i./seedling applied thrice a year for three consecutive years in pots gave control of *R. similis* both in soil and roots. Increase in plant growth with regard to shoot length, shoot weight,

root length, root weight, number of leaves and collar girth with fensulfothion were 46, 168, 33, 173, 25 and 41% respectively over control plants after three years (Sundararaju & Koshy, 1986*a*). In a field experiment in India, treatment with fensulfothion at 50 g a.i./palm and aldicarb at 10 g a.i./palm applied during May/June, September/October and December/January for five years resulted in control of *R. similis* and a substantial increase in both number and weight of nuts compared to untreated palms (Sundararaju & Koshy, 1986*b*). However, the nuts were not analyzed for their residues, if any, and the cost benefit ratio has not been determined.

Summary of control measures

Control of *R. similis* on arecanut is difficult under the high density, multispecies, subsistence farming systems involving perennial crops such as coconut, banana, black pepper, betel vine, cardamom and cacao. Use of nematicides for the control of burrowing nematode on coconut or arecanut may cause problems of residual toxicity. The following control measures are suggested:- 1. use of nematode-free planting material of arecanut and other intercrops; 2. avoiding *R. similis* susceptible intercrops such as black pepper and banana in infested areas; 3. use of resistant/tolerant cultivars of arecanut, when available, and other crops in farming systems; and 4. minimum use of nematicides.

Methods of diagnosis

Soil and root samples for detection of *R. similis* should be collected at a distance of 25–75 cm from the bole of the palm at a depth of 25–75 cm when high population densities are present, such as during October/November in India.

The method suggested for extraction of *R. similis* from coconut root can also be adopted for arecanut.

General Conclusions on Nematodes of Palms

The foregoing has shown that fatal diseases in palms due to nematodes are unknown except for those palms which are naturally attacked by *Rhadinaphelenchus cocophilus* and its insect vector *Rhynchophorus palmarum*. The fact that red ring disease is at present confined to the new world restricts its economic importance to those palms that occur in the area, but others, such as the areca palm, are likely to be naturally susceptible even in their areas of origin. Nematodes which have been recorded as pathogenic to palms in their areas of origin are only those which exist in the rhizosphere such as *Radopholus similis* of arecanut and coconut. This problem has not yet been recognized in the new world but it is very possible that this and other nematode root problems on palms will become apparent in the years ahead.

The major concern of nematologists, plant pathologists and quarantine personnel, therefore, is to ensure against the possibility of red ring disease becoming universal since the likelihood that other species of the palm weevil could be vectors to *R. cocophilus* is quite strong. The palms of horticultural value are also susceptible and could in fact increase the likelihood of the disease eventually moving out of Latin America in a palm where symptoms are not so distinct and in which pathogenesis is prolonged. Indeed, there is every probability that symptomless carriers might exist as palms which are slowly colonized by the nematode. Another feature is the well known problems associated with the confusion in symptomatology in diseases of palms which can hide the problem of a nematode until it is too late.

The International Bureau of Plant Genetic Resources has been helping in a number of coconut and other palm germplasm collection programmes and some methods have been suggested for examination of palm material at the ports of export and entry for introduction of coconut germplasm for research purposes.

Generally, as crop plants for small farmers, cordon sanitaires are always necessary for vector-borne pathogens which can have fatal and cumulative effects on the agroecosystems. Thus, control measures for palm diseases have always got to be cheap, effective and readily applicable in all

economic circumstances. Essentially, of course, biological control measures and resistant cultivars should always be sought. The stability of the coconut agroecosystem favours management procedures with limited pesticide usage.

References

Anonymous (1974). Annual Report 1973. Central Plantation Crops Research Institute, Kasaragod, Kerala, India. 80p.

Ashby, S. P. (1921). Some recent observations on red ring disease. *Agricultural News (Bridgetown)*, 20:350–351.

Barrett, O. W. (1906). Notes upon miscellaneous crops. *Proceedings of Agricultural Society of Trinidad*, 7:303.

Bhaskara Rao, E. V. V. & Koshy, P. K. (1982). *Coconut germplasm collection in Pacific Ocean Islands*. Deputation Report, Central Plantation Crops Research Institute, Kasaragod, Kerala, India, 47p.

Bhaskara Rao, E. V. V. & Koshy, P. K. (1984). Quarantine aspects in bulk import of coconut germplasm for gene banks and seed gardens. *FAO Plant Protection Bulletin*, 36:53–56.

Blair, G. P. (1964). Red ring disease of the coconut palm. *Journal of Agricultural Society of Trinidad and Tobago*, 64:31–49.

Buhrer, E. M., Cooper, C. & Steiner, G. (1933). A list of plants attacked by the root knot nematode (*Heterodera marioni*). *Plant Disease Reporter*, 17:64–96.

Carpenter, J. B. (1964). Root knot nematode damage to date palm seedlings in relation to germination and stage of development. *Date Growers Institute Report*, 41:10–14.

Chitwood, B. G. (1935). Nomenclatorial notes 1. *Proceedings of the Helminthological Society Washington*, 2:51–54.

Chuo, S. K., s'Jacob, J. J. & Wouts, W. M. (1977). Royal palm, *Roystonea regia* (H.B.K.) Cook, a new host of the burrowing nematode *Radopholus similis* (Cobb, 1893) Thorne, 1949. *Singapore Journal of Primary Industries*, 5:91–95.

Cobb, N. A. (1919). A newly discovered nematode *Aphelenchus cocophilus* n.sp. connected with a serious disease of the coconut palm. *West Indian Bulletin*, 17:203–210.

Corbett, M. K. (1959). Disease of the coconut palm. *Principes*, 3:83–96.

Dasgupta, N. K. & Rama, K. (1987). Plant parasitic nematode associated with plantation crops. *Review of Tropical Plant Pathology*, 4:289–304.

Dean, C. G. (1979). *Red ring disease of* Cocos nucifera *L. caused by* Rhadinaphelenchus cocophilus (*Cobb, 1919) Goodey, 1960. An annotated bibliography and review*. Technical Communication No. 47, Commonwealth Institute of Helminthology, St. Albans, U.K., 70p.

Ekanayake, U. B. M. (1964). Annual report of the crop protection officer, Coconut Research Institute for 1963. *Ceylon Coconut Quarterly*, 15:50–57.

FAO (1987). *1986 Production Yearbook*. Food and agriculture organization of the United Nations, Rome, Vol. 40, 306p.

Fenwick, D. W. (1967*a*). Coconut Research in Trinidad and Tobago. *Oleagineaux*, 22:87–88.

Fenwick, D. W. (1967*b*). The effect of weevil control in the incidence of red ring disease. *Journal of Agricultural Society of Trinidad and Tobago*, 67:231–244.

Fenwick, D. W. & Maharaj, S. (1963). Recovery of *Rhadinaphelenchus cocophilus* (Cobb, 1919) Goodey, 1960 from coconut tissues. *Journal of Helminthology*, 37:11–14.

Goodey, J. B. (1960). *Rhadinaphelenchus cocophilus* (Cobb, 1919). The nematode associated with red ring disease of coconuts. *Nematologica*, 5:98–102.

Govindankutty, M. P. & Koshy, P. K. (1978). Nematodes associated with coconut palm (*Cocos nucifera* L.) *11th session, Plant Protection Committee, South East Asia and Pacific Region, 22–29 September, 1978. Kathmandu*, Nepal, 31p.

Govindankutty, M. P. & Koshy, P. K. (1979). Nematodes associated with the coconut palm (*Cocos nucifera* L.) In: *Technical Bulletin 2 – Nematodes, fungi insects and mites associated with the coconut palm.* Central Plantation Crops Research Institute, Kasaragod, India: 1–50.

Griffith, R. (1968). The relationship between the red ring nematode and the palm weevil. *Journal of Agricultural Society of Trinidad and Tobago*, 68:342–356.

Griffith, R. (1971). Red ring disease: the mechanism of spread and recommendations for control. *Nematropica*, 1:2.

Habeebullah, A., Reghupathy, A., Rethinam, P. & Koshy, P. K. (1983). Residues of aldicarb in coconut. *Seminar on pesticides and environment, 4–5 August, 1983*. Coimbatore, Tamil Nadu, India: 21 [Abstr.]

Hagley, E. (1963). The role of the palm weevil *Rhynchophorus palmarum* L. as vector of red ring disease in coconut. 1. Result of preliminary observations. *Journal of Economic Entomology*, 56:375–380.

Hart, J. H. (1905). Coconut disease. *Bulletin of Miscellaneous Information, Royal Botanic Gardens, Trinidad*, 6:241–243.

Holdeman, Q. L. (1986). The burrowing nematode, *Radopholus similis*, sensu lato. *Division of Plant Industry. California Department of Food and Agriculture and the Agriculture Commissioners of California*, 52p.

Jensen, H. J. (1961). The nematode menace. *American Nursery-man*, 114:7–8, 105–113.

Johnston, R. (1910). The serious coconut palm diseases of Trinidad. *Bulletin of Department of Agriculture, Trinidad*, 9:25–29.

Koshy, P. K. (1986*a*). *Research on plant parasitic nematodes at the Central Plantation Crops Research Institute, October 1972 to June 1986*. Central Plantation Crops Research Institute, Regional Station, Kayangulam, Kerala, India, 45p.

Koshy, P. K. (1986*b*). The burrowing nematode *Radopholus similis* (Cobb, 1893) Thorne, 1949. In: Swarup, G. Dasgupta, D. R. (Eds) *Plant parasitic nematodes of India – Problems and Progress*, IARI, New Delhi, India. 223–248.

Koshy, P. K. & Nair, C. P. R. (1979). Control of *Radopholus similis* (Cobb 1893) Thorne, 1949 in coconut nursery. *Indian Journal of Nematology*, 9:15–19.

Koshy, P. K. & Sosamma, V. K. (1975). Host range of the burrowing nematode, *Radopholus similis* (Cobb, 1893) Thorne, 1949. *Indian Journal of Nematology*, 5:255–257.

Koshy, P. K. & Sosamma, V. K. (1977). Identification of the physiological race of *Radopholus similis* populations infesting coconut, arecanut and bababa in Kerala, South India. *Indian Phytopathology*, 30:415–416.

Koshy, P. K. & Sosamma, V. K. (1978*a*). Studies on the population fluctuations of *Radopholus similis* in coconut and areca roots. *Indian Phytopathology*, 31:180–183.

Koshy, P. K. & Sosamma, V. K. (1978*b*). Susceptibility of coconut plumule to *Radopholus similis* (Cobb, 1893) Thorne, 1949. *Indian Journal of Nematology*, 8:77–78.

Koshy, P. K. & Sosamma, V. K. (1979). Control of the burrowing nematode *Radopholus similis* on coconut seedlings with DBCP. *Indian Journal of Nematology*, 7:32–33.

Koshy, P. K. & Sosamma, V. K. (1980). Culturing of burrowing nematode, *Radopholus similis* on carrot discs. *Indian Journal of Nematology*, 10:247–249.

Koshy, P. K. & Sosamma, V. K. (1982*a*). A simple method for inoculation and production of symptoms by *Radopholus similis* on coconut. *Indian Journal of Nematology*, 12:200–203.

Koshy, P. K. & Sosamma, V. K. (1982*b*). Culturing of *Radopholus similis* within mesocarp of coconut. *Plant Disease*, 66:811.

Koshy, P. K. & Sosamma, V. K. (1983). Pathogenicity of *Radopholus similis* on *Areca catechu*. *Indian Phytopathology*, 36: 469–472.

Koshy, P. K. & Sosamma, V. K. (1987). Pathogenicity of *Radopholus similis* on coconut (*Cocos nucifera* L.) seedlings under green house and field conditions. *Indian Journal of Nematology*, 17:108–118.

Koshy, P. K. & Sosamma, V. K. (1988). Studies on *Radopholus similis* on coconut. *Annual Report for 1987. Central Plantation Crops Research Institute*, Kasaragod, Kerala, India, 79p.

Koshy, P. K., Sosamma, V. K. & Nair, C. P. R. (1975). Preliminary studies on *Radopholus similis* (Cobb, 1893) Thorne, 1949) infesting coconut and arecanut palms in South India. *Indian Journal of Nematology*, 5:26–35.

Koshy, P. K., Sosamma, V. K. & Sundararaju, P. (1976). Yellow leaf disease: Nematological studies. *Arecanut and Spices Bulletin*, 8:37–41.

Koshy, P. K., Sosamma, V. K. & Sundararaju, P. (1979). Reactions of thirty one Areca germplasm collections to the burrowing nematode *Radopholus similis*. *Plant Disease Reporter*, 63:433–435.

Koshy, P. K., Sundararaju, P. & Sosamma, V. K. (1978). Occurrence and distribution of *Radopholus similis* (Cobb, 1893) Thorne, 1949 in South India. *Indian Journal of Nematology*, 8:49–58.

Koshy, P. K., Sundararaju, P., Sosamma, V. K. & Ravikumar, K. (1985). Efficacy of four systemic nematicides against *Radopholus similis* in coconut nursery. *Indian Journal of Nematology*, 15:148–151.

Kumar, A. C., Viswanathan, P. R. K. & D'Souza, G. I. (1971). A study of plant parasitic nematodes of certain commercial crops in coffee tracts of South India. *Indian Coffee*, 35:222–224.

Lamberti, F., Greco, N. & Zaouchi, H. (1975). A nematological survey of date palms and other major crops in Algeria. *FAO Plant Protection Bulletin*, 23:156–160.

Latta, R. (1966). Attempts to relate nematodes to lethal yellowing disease of coconut palms in Jamaica. *Tropical Agriculture Trinidad*, 43:59–68.

Lordello, L. G. E. & Zamith, A. P. L. (1954). Constatação da moléstia do "anel vermelho" do coqueiro no Estado do Rio de Janeiro. Redescrição do agente causador – *Aphelenchus cocophilus* (Cobb, 1919) Goodey, 1933, (Nematoda, Aphelenchidae). *Anais da Escola Superior de Agricultura "Luiz de Queiroz"*, 34:125–132.

Malaguti,G. (1953). "Pudricion de Cogollo" de la palmera do aceite Africana (*Elaeis guineensis* Jacq.) en Venezuela. *Agronomia Tropical*, 3:13–21.

Martyn, E. B. (1953). Red ring disease of coconuts in Trinidad and Tobago. *Tropical Agriculture*, 32:45–53.

Minz, G. (1958). Two *Diplodia* species in date palms. *Ktavim*, 8:213–216.

Nair, R. B. (1964). Nematodes from arecanut soils. *Arecanut Journal*, 15:87–88.

Netscher, C. & Luc, M. (1974). Nématodes associés aux cultures maraîchéres en Mauritanie. *L'Agronomie tropicale, Nogent*, 29:697–701.

Nowell, W. (1918). Root disease of coconut palms in Grenada. *Agriculture News (Bridgetown)*, 17:398–399.

Nowell, W. (1919). Red ring or root disease of coconut palms. *West Indian Bulletin*, 17:189–192.

Nowell, W. (1923). *Disease of crop plants of the Lesser Antilles*, The West Indian Committee, London, 383p.

Nowell, W. (1924). Red ring disease of coconuts. *Proceedings 9th West Indies Conference, Jamaica*, 167–172.

Pizarro, A. C. (1969). Nematodes associated with roots of coconut and other palms. *Philippine Journal of Plant Industry*, 34:155–158.

Poucher, C., Ford, H. W., Suit, R. F. & Ducharme, E. P. (1967). *Burrowing nematode in citrus*. Bulletin No. 7. Division of Plant Industry, Florida Department of Agriculture, 63p.

Rama, K. (1987). *Ecology of plant parasitic nematodes affecting some major perennial crops in West Bengal*. Ph.D. Thesis, Visva Bharati, 276p.

Reddy, D. B. (1978). Insect pests, diseases and nematodes of *Areca catechu* and betel vine (*Piper betle*) recorded in Asia and the Pacific. *Technical Document No. 114. Plant Protection Committee for the South East Asia, Asia and Pacific region, FAO, Bangkok*, 6p.

Rorer, J. B. (1911). Diseases of the coconut palm. *Circular 4. Board of Agriculture, Trinidad*: 27–33.

Schuilling, M. & Van Dinther, J. B. M. (1981). 'Red ring disease' in the Paricatuba oil palm estate, Para, Brazil. A case study. *Zeitschrift für Angewandte Entomologie*, 91:154–169.

Sosamma, V. K. (1984). *Studies on the burrowing nematode of coconut*. Ph.D. Thesis. Kerala University, Trivandrum, Kerala, India, 166p.

Sosamma, V. K. & Koshy, P. K. (1977). Additional hosts of the burrowing nematode *Radopholus similis* infesting coconut palm in South India. *Plant Disease Reporter*, 61:760–761.

Sosamma, V. K. & Koshy, P. K. (1978). A note on the association of *Cylindrocarpon effusum* and *C. lucidum* with *Radopholus similis* in coconut. *Indian Phytopathology*, 31:381–382.

Sosamma, V. K. & Koshy, P. K. (1981). Other host records of *Radopholus similis*. *Indian Journal of Nematology*, 11:73–74.

Sosamma, V. K. & Koshy, P. K. (1983). A note on the occurrence of *Cylindrocladium clavatum* Hodges & May in lesions caused by *Radopholus similis* on coconut roots. *Current Science*, 52:438.

Sosamma, V. K. & Koshy, P. K. (1985). Effects of different types of soils on multiplication of *Radopholus similis* and growth of coconut seedlings. *Indian Journal of Nematology*, 15:217–222.

Sosamma, V. K. & Koshy, P. K. (1986) Survival of *Radopholus similis*. *National Conference – Plant Parasitic Nematodes of India – Problems and Progress, 17–20 December, 1986, IARI, New Delhi, India*: 107.

Sosamma, V. K., Koshy, P. K. & Bhaskara Rao, E. V. V. (1980). Susceptibility of coconut cultivars and hybrids to *Radopholus similis* in field. *Indian Journal of Nematology*, 10:250–252.

Sosamma, V. K., Koshy, P. K. & Bhaskara Rao, E. V. V. (1988). Response of coconut cultivars to the burrowing nematode, *Radopholus similis*. *Indian Journal of Nematology*, 18:136–137.

Stockdale, F. A. (1906). *Journal of Agricultural Society of Trinidad and Tobago*, 7:9–31.

Sundararaju, P. (1984). *Studies on the burrowing nematode of arecanut*. Ph.D. Thesis, Kerala University, Trivandum, Kerala, India, 133p.

Sundararaju, P. & Koshy, P. K. (1982*a*). Distribution of phytoparasitic nematodes on arecanut in South India. *Proceedings of the Silver Jubilee Symposium on Arecanut Research and Development, 12–14 December, 1982. Vittal, South Kanara, Karnataka, India*: 143–146.

Sundararaju, P. & Koshy, P. K. (1982*b*). Response of *Areca* collections against *Radopholus similis*. *Indian Journal of Nematology*, 12:404–405.

Sundararaju, P. & Koshy, P. K. (1984). A note on the association of *Cylindrocarpon obtusisporum* on lesions caused by *Radopholus similis* on arecanut (*Areca catechu* L.) roots. *Indian Phytopathology*, 37:578.

Sundararaju, P. & Koshy, P. K. (1986*a*). Control of *Radopholus similis* on arecanut seedlings with aldicarb, aldicarb sulfone, carbofuran and fensulfothion. *Indian Journal of Nematology*, 16:4–7.

Sundararaju, P. & Koshy, P. K. (1986*b*). Effect of different nematicides and neem oil cake in the control of *Radopholus similis* in yellow leaf disease affected arecanut palms. *Indian Journal of Nematology*, 16:44–47.

Sundararaju, P. & Koshy, P. K. (1987). Separate and combined effects of *Radopholus similis* and *Cylindrocarpon obtusisporum* on arecanut seedlings. *Indian Journal of Nematology*, 17:302–305.

Sundararaju, P. & Sosamma, V. K. & Koshy, P. K. (1984). Additional host records of root knot nematode, *Meloidogyne incognita*. *Indian Journal of Nematology*, 14:183–184.

Van Hoof, H. A. & Seinhorst, W. (1962). *Rhadinaphelenchus cocophilus* associated with little leaf of coconut and oil palm. *Netherland Plant Pathology*, 68:251–256.

Van Weerdt, L. G., Birchfield, W. R., Esser, R. P. (1959*a*). Observations on some subtropical plant parasitic nematodes in Florida. *Proceedings of the Soil Crop Science Society of Florida*, 19:443–451.

Van Weerdt, L. G., Martinez, A. P. & Esser, R. P. (1959*b*). Results of a survey designed to determine the etiology of lethal yellowing of *Cocos nucifera*. *Proceedings of the Florida State Horticultural Society*, 72:421–430.

Villanueva, A. & Gonzalez, A. (1988). Importancia ecónomica del Anillo Rojo en Palmerasde la Costa S.A. y medidas de control practicadas. *Palmeras de la Costa*, 41p. (mimeo).

Webster, B. N. & Gonzalez, J. (1959). Investigaciones sobre la enfermedad 'anillo rojo' en cocas y palma de aceite. *9th Convencion de la Asociacion Venezolana el Avance de la Ciencia, Servicio Shell para el Agricultor, Estado Arajua, Venezuela.*

Weischer, B. (1967). Report to the Government of India on Plant Parasitic nematodes. *PL 24/52 Report No TA 2332, FAO, Rome*, 15p.

Chapter 12

Nematode Parasites of Coffee, Cocoa and Tea

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COFFEE

Coffee is a perennial dicotyledonous shrub or small tree with woody stem, persistent leaves and hermaphrodite flowers which belongs to the genus *Coffea* in the family Rubiaceae. Chevalier (1947), grouped several species of *Coffea* in different sections. The section Eucoffea is the most cultivated species. This section is divided into subsections: the subsection Erythrocoffea includes the species *Coffea arabica, C. canephora, C. congensis;* Pachycoffea, *Coffea liberica* and *C. excelsa;* Mozambicoffea, *Coffea racemosa* and *C. salvatrix;* Melanocoffea, *Coffea stenophylla;* and Nanocoffea, *Coffea montana,* etc.

A few species of the section Mascarocoffea such as *Coffea resinosa* and *C. macrocarpa* have no caffeine alkaloid in the seeds. It is possible that in the future decaffeineted species can be developed from these species.

Seeds of coffee germinate in 3 to 4 weeks at a temperature of 31–32°C, at 17°C it takes 3 months. The formation of leaves occurs during the whole year but the ratio of shoot and leaf growth varies with the climatic conditions. Flower formation is induced by photoperiod changes; but differentiation requires short days (<13–14 h of light). Very high temperature or prolonged drought during the bud dormancy provokes the formation of abnormal or aborted flowers (Anon., 1985).

Coffee plants produce fruits containing seeds which after hulling and washing are dried, roasted and ground; the powder is used to make the coffee drink. The crop is grown mainly between the tropics of Cancer and Capricorn. Coffee has been of great relevance to the economy of many tropical countries. Its importance to the total export has decreased in percentage but the value of coffee exports has increased. Brazil is the major world producer, representing in 1986, 19.5% of the world production and South America 39.5% (FAO, 1986).

Coffea arabica accounts for 75% of the world coffee exports, and is produced in 60 countries, mostly in South and Central America, while *Coffea canephora* accounts for approximately 25% (Anon., 1985), mostly concentrated in Africa and Asia. Other species of minor relevance to world coffee production are *Coffea racemosa* in Mozambique, *Coffea stenophylla* in Sierra Leone and Ivory

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds) © CAB International 1990

Coast, *Coffea excelsa* in the Central African Republic and Vietnam, *Coffea liberica* in Guayana, Surinam, Malaysia, Philippines, São Tome and Liberia (Krug, 1969).

Arabica coffee, *Coffea arabica* originated from the mountain region in southwest of Ethiopia and Robusta coffee, *Coffea canephora* from Western Africa. *Coffea arabica* is an upland species growing best at altitudes of 900–2000 m on the Equator with temperatures of 17°C–25°C and rainfall of 1200–2000 mm. Humid cloudy conditions are preferable. *Coffea canephora* is not so specific in its requirements, growing from sea level to 1700 m at temperatures of 20°C–32°C and is better suited to lower altitudes such as 400 m in Brazil.

Cultivation techniques

Most commercial coffee is planted from seed, and seedlings are raised in nurseries either in beds or bags of plastic or other material. Germination takes 5–10 weeks and seedlings are transplanted to the field when 6–10 months old. Vegetative propagation by cuttings is possible with coffee but is not the usual practice. Spacing varies between areas, usually 2–4 m between rows of 1 m between plant when one seedling is kept per low basin or "cova", or 2 m apart when 2 plants per low basin or "cova". Shading is not necessary for *C. arabica* but is practised in some areas, it is used less for *C. canephora*. Other trees or crops e.g. banana, are used for shading coffee. Mulching is beneficial in nonfrosted areas. Pruning is variable and not always done. The most common methods involve cutting the main stem at 0.40 m or 1.80 m from the soil or the plagiotropic branches at 0.20 m from the main stem. Trees start bearing after 2.5–3.5 years.

Nematode Parasites of Coffee

Many genera and species of nematodes have been associated with coffee in many countries of the world including very damaging nematodes causing great losses to the coffee farmers and the local economy of developing countries.

Meloidogyne

Root-knot nematodes of the genus *Meloidogyne* are more widely distributed throughout the world in coffee plantations than any other major group of parasitic nematodes (Table 1). Furthermore, when their importance is considered on a worldwide basis, they rank high on the list of pathogens affecting the production of coffee.

Root-knot nematode species of coffee can be separated into two categories: (I) the most common, damaging and well known species on coffee: *M. exigua, M. incognita* and *M. coffeicola;* (II) the less widespread species: *M. africana, M. decalineata, M. megadora, M. hapla, M. kikuyensis, M. inornata, M. javanica, M. oteifae, M. arenaria* and *M. thamesi.*

I. Meloidogyne exigua, M. incognita and *M. coffeicola*

Distribution

Meloidogyne exigua is known to occur, in all major coffee growing countries of South and Central America but is not found outside the American continent (Table 1) although a species identified as *M. exigua* was reported from Java in 1931 (Bally & Reydon, 1931). It was the first nematode species found in coffee, when Jobert was invited to study a severe disease of coffee in Rio de Janeiro, Brazil which he showed to be caused by a nematode (Jobert, 1878): the species was described a few years later by Göldi (1889, 1892). In 1929, *M. exigua* was found in São Paulo State (Brazil) (Rahm, 1929). Since then it has been found in all major coffee producing States in Brazil (Campos *et al.*, 1985; Campos & Melles, 1987), sometimes mixed with other species of *Meloidogyne*. In the 1960's *M. exigua* was found in coffee plantations in Costa Rica, the Dominican Republic and Venezuela (Salas & Echandi, 1961; Shrieber & Grullon, 1969; Flores & Yépez, 1969). In the 1970's this species was also reported from Guatemala, Peru, El Salvador and Puerto Rico (Shieber, 1971; Sabrego, 1971;

Lordello, 1972; Ayala, 1976). More recently *M. exigua* has been found in Colombia, Nicaragua and Bolivia (Gomez, 1980; Vega, 1982; Bridge *et al.*, 1982).

TABLE 1. Species of root-knot nematodes found on coffee and their distribution.

Meloidogyne species	Country
M. incognita	Brazil, Tanzania, Jamaica, Venezuela, Guatemala, Ivory Coast, India
M. exigua	Brazil, Guatemala, Dominican Republic, Nicaragua, Costa Rica, Puerto Rico, Colombia, Peru, El Salvador, Venezuela, Bolivia
M. coffeicola	Brazil
M. javanica	Brazil, Tanzania, Zaire, El Salvador, India
M. hapla	Brazil, Tanzania, Zaire, India
M. africana	Kenya, Zaire
M. decalineata	Tanzania, São Tomé
M. kikuyensis	Tanzania
M. arenaria	Jamaica
M. megadora	Angola, Uganda
M. inornata	Guatemala
M. oteifae	Zaire
M. thamesi	India

M. coffeicola was described by Lordello and Zamith (1960) from the coffee plantation of Terra Boa, Parana State, Brazil. It has not been found outside Brazil. Lordello (1967) found this species attacking coffee in São Paulo State and in 1983 it was also found in Minas Gerais State, Brazil (Guerra Neto *et al.*, 1983).

Meloidogyne incognita, was first found attacking coffee in 1960 in Guatemala (Chitwood & Berger, 1960), where its effects were said to be less severe than those of *M. exigua* (Whitehead, 1969*b*). In 1960 it was reported from the Ivory Coast (Luc & de Guiran, 1960), and then in Tanzania (Whitehead, 1969*a*) and Venezuela (Flores & Yépez, 1969). More recently it has been reported from Jamaica (Hutton *et al.*, 1982) and India (Kumar, 1984).

Although *M. incognita* occurs in many coffee growing areas around the world (Table 1), it was in Brazil where its effects on coffee plantations became catastrophic. *M. incognita* was first found in 1970 attacking coffee in Pindorama, São Paulo State (Brazil) (Lordello & Mello Filho, 1970). However, this nematode may have been present in coffee in Brazil for sometime, since as Lordello (1984) pointed out in many instances the agressive races of *M. exigua* reported from many locations may actually have been different populations or races of *M. incognita*. In 1971, *M. incognita* was found in Espirito Santo State (Lordello & Hashizume, 1971), in 1972 in Paraná (Lordello & Lordello, 1972), in 1975 in Ceará (Ponte & Castro, 1975) and in 1984 in Minas Gerais State (Guerro Neto & D'Antonio, 1984).

In coffee plantations of São Paulo and Paraná, Brazil, *M. exigua, M. coffeicola* or *M. incognita* have occurred for many years in separate or mixed populations with fluctuations in the predominance of each species over the other. In Paraná State, from 1967 to 1970, *M. coffeicola* was found in 16 counties whereas *M. exigua* in only two (Vernalha *et al.*, 1970). Since then surveys have shown a substantial increase in distribution of *M. incognita* and decrease of *M. coffeicola* (Lordello *et al.*, 1974; Carneiro & Carnerio, 1982). It is believed that *M. coffeicola* had been eradicated from many plantations during the renewal of damaged coffee after the 1975 great frost. After this period coffee may have been cultivated in new lands without the nematodes. In São Paulo State in 1968, *Meloidogyne exigua*, was found in 50 counties and *M. incognita* in only four (Lordello *et al.*, 1968). In 1969 *M. coffeicola* was found in 11 counties (Curi *et al.*, 1969). Since 1970, *M. coffeicola* seems to have disappeared from the coffee plantations of São Paulo according to Lordello (1984) whereas *M. incognita* has become widespread in this State.

The two States, Paraná and São Paulo, in addition to Minas Gerais State accounted in 1983 for approximately 80% of coffee produced in Brazil. *M. exigua* was found to be widespread in the coffee growing regions of Minas Gerais (Campos *et al.*, 1985; Campos & Lima, 1986). It was the only species of *Meloidogyne* found in this State until 1983 when *M. coffeicola* was recorded in Machado (Guerro Neto *et al.*, 1983), and later *M. incognita* was found in Nova Resende and São Thomas Aquino towns (Guerra Neto & D'Antonio, 1984). However *M. coffeicola* and *M. incognita* have been restricted to the original sites without any great economic impact on the overall coffee production in Minas Gerais (Campos *et al.*, 1985).

Symptoms of damage

Meloidogyne exigua causes typical rounded galls (Plate 10G) mostly on new roots formed after the first rains in spring and continues to produce them into the summer. The galls are initially white to yellowish brown and turn dark brown as the root becomes older. Egg masses are produced in the cortex under the root epidermis. On the Mundo Novo cultivar of *Coffea arabica* there is no necrosis around the giant cells and there is a tendency for lateral root formation at the region of the gall (Mendes, 1977). Necrotic areas are also to be seen on the galled roots, which may be aggravated by secondary infections, and the section of the root dies. Although many authors have reported that *M. exigua* may not often form galls but instead forms cracks on infected roots (Lordello, 1972), this may be due to a misidentification of the *Meloidogyne* species involved.

Infested seedlings planted in the field show reduced growth and defoliation, and some do not survive the dry season. The management of an infested crop in the field through the seedling stage is very difficult. Depending on the soil type, *M. exigua* can cause a serious defoliation of the adult coffee plant leading to death. In Rio de Janeiro State during the last century, *M. exigua* caused the destruction of whole coffee plantations (Göldi, 1887). Young coffee plants in the field seem to suffer more from attack by *M. exigua* than at any other stage.

In Brazil, *Meloidogyne incognita* causes peeling and cracking of cortical parts of the root tissue in field plants. The cortical cracking results from the hypertrophy of tissues adjacent to the female (Moraes *et al.*, 1973). Darker dots along the root are observed where the females are located. Sometimes localized swelling on the roots resembling galls are seen on lateral roots. Females feeding in roots kill the surrounding tissues leading to the death of sections of the root (Plate 10D) and thus greatly reducing the root system. Young seedlings of coffee grown under the foliage of the infested plants have typical root galls.

The above ground parts of infested plants in Brazil show foliar chlorosis, leaf fall, general decline, (Fig. 1) reduced growth and sometimes plants are killed. In São Paulo State, big coffee plantations have been decimated by this nematode with 5-year-old coffee plantations dying out (Fig. 2). Lordello (1984), has said that *M. incognita* in some areas of São Paulo State is a "Disaster pathogen" becoming the worst enemy of coffee.

In Jamaica, *M. incognita* causes galls on coffee plants, growth and yield reduction (Hutton *et al.*, 1982).

Meloidogyne coffeicola causes peeling and cracking of roots but does not produce galls (Plate 10F). The female is easily found in older tissue especially on the tap root. Attempts at artificial inoculation of *M. coffeicola* on coffee seedlings have failed. The females lay their eggs outside roots, through cracks that they have induced in the root tissue. The numerous dark spots on infected roots are egg masses of the nematodes. Very few females lay eggs inside the roots. The above ground part of the infested coffee plant shows yellowing, leaf fall, and there is a general decline of the plant leading to death.

Biology and life cycle

The life cycle of *M. exigua* is very similar to the four most common species of the genus *Meloidogyne*. The length of time is longer, taking 32–42 days at 25–30°C to complete the cycle (Lima, 1984). Unlike *M. incognita* and *M. coffeicola*, the egg masses of *M. exigua* are mostly located under the

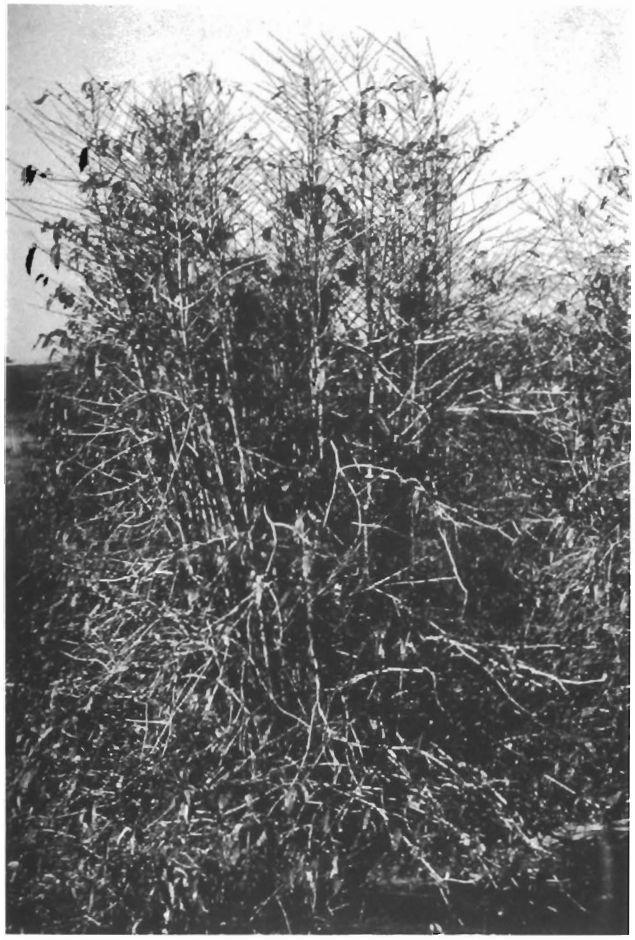

Fig. 1. Leaf drop and chlorosis, general decline of late infested coffee plant caused by *M. incognita* (São Paulo State, Brazil).

epidermis of coffee roots. *M. exigua* and *M. incognita* have saccate bodies but *M. coffeicola* is more sausage shaped with a long neck, and as much as 1300 μm in length (Lordello & Zamith, 1960). The perineal patterns are distinctly different in all these species. Morais and Lordello (1977), showed that *M. incognita* is more pathogenic to coffee than *M. exigua*.

Pathotypes, races or biotypes

Most population variations in the pathogenicity of *M. exigua* in coffee reported by many authors in São Paulo State, Brazil, may be related to misidentification of the pathogen (Lordello, 1984).

In Brazil, three races of *M. incognita* are known to occur (Medina Filho *et al.*, 1981). They have been differentiated by the North Carolina differential host test as proposed in Taylor and Sasser, (1978). There is no evidence of variations in pathogenicity within *M. coffeicola* populations in the field.

Coffea arabica cvs Catuaí, Mundo Novo, Bourbon Amarelo; *C. canephora* cvs Robusta, Guariní and Laurentii, and *C. excelsa* are susceptible to *M. incognita* (Morais *et al.*, 1973).

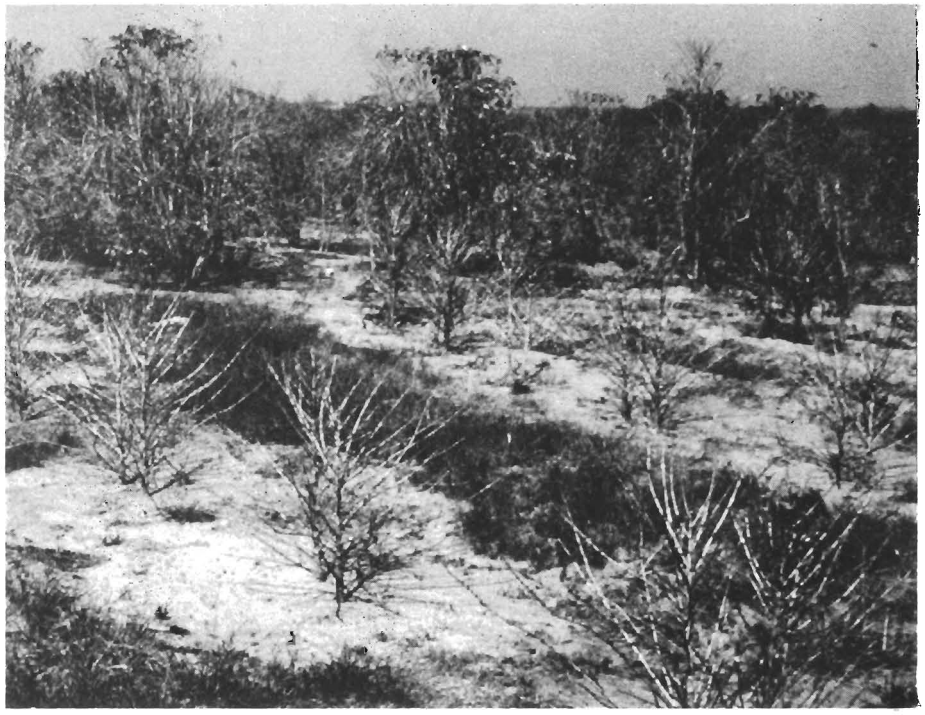

Fig. 2. Dying out of 5-year-old coffee plantation infested by *M. incognita* (São Paulo State, Brazil).

Survival and means of dissemination

M. exigua, six months after eradication of infested plants, is not found in the soil (Morais & Lordello, 1977) and does not survive in soil, in the absence of the host, for more than 6 months (Alvarenga,1973). However *M. incognita* causes high infestation on coffee even when infested soil is kept without host plants for 6 months (Jaehn & Rebel, 1984). *M. coffeicola* seems to have a low capacity to infest coffee seedlings and young trees.

The method of cultivating coffee in the field by using transplanted seedlings produced in nurseries, provides a very efficient dissemination of *Meloidogyne* species on seedling roots, once the nursery is infested. There are many small holder coffee producers throughout the world, including Brazil, who cannot afford to apply chemicals of any other soil treatment, thus increasing the chance for efficient dissemination of nematodes.

Environmental factors affecting parasitism

In spite of Whitehead's (1969) statement that coffee is very resistant to *M. incognita*, the rapid distribution and highly destructive nature of this pathogen in Brazil are due to changes of the pathogen into more agressive pathotypes, adaptation to local environments and to the cultivar grown. Sandy soil seems to enhance the damage caused by *M. incognita* in Brazil (Jaehn, 1984). Poor management of the coffee crop has increased the damage caused by *M. exigua* .

Other hosts

In Brazil, watermelon, onion (Morais *et al.*, 1972, 1973), pepper (Lordello. 1964) and the following weeds found in coffee fields have been reported as hosts of *M. exigua: Solanum nigrum* (Curi, 1973), *Ipomoea acuminata, I. aristolochiaefolia, Stachys arvensis, Leonorus sibiricus, Amaranthus deflexus,*

Galinsoga parviflora, Euphorbia heterophylla and *Taracaxum officinale* (Lima *et al.*, 1985), *Citrullus vulgaris* (Ponte, 1978). In *Ipomoea acuminate, Stachys arvensis* and *Leonorus sibiricus* the reproduction of *M. exigua* was higher than in *Coffea arabica* var. Mundo Novo (Lima *et al.*, 1985). In Colombia, *Commelina diffusa, Hydrocotyle* sp., *Solanum nigrum, Inga* sp., *Cyperus rotundus* are hosts of *M. exigua* (Aragon *et al.*, 1978). Cocoa is a host of *M. exigua* in Bolivia (Bridge *et al.*, 1982).

M. incognita has a wide host range, infecting many vegetable, grain, and fruit crops, weeds and ornamental plants (Ponte, 1978; Nickle, 1984). However, *M. coffeicola* has been found only in *Eupatorium pauciflorum* and *Psychotria nitidula*(Jaehn *et al.*, 1980), hence Lordello and Zamith (1960) have hypothesized that this species became a pathogen of coffee after the clearing of forests where it was a native species.

Disease complexes

The fungus *Rhizoctonia solani* inoculated around plants of *Coffea arabica* or *C. canephora*, after *M. exigua* infestation, caused more root necrosis and defoliation than when both pathogens were inoclulated either simultaneously or separately in the greenhouse (Souza, 1977). Isolations from galled roots and histopathological studies 85 and 115 days after inoculations of nematode-infected plants with *R. solani*, revealed extensive fungal colonization within the coffee root systems.

Economic importance

Most information on the economic importance of root-knot nematodes comes from Brazil where for over a hundred years the areas of cultivation with coffee have migrated across the country due to the pressure of nematode damage. In many instances these nematodes have been the sole cause for convincing the farmer to cease growing coffee. The economic impact of changing to a new crop after nematode infestation are considerable in terms of financial and socio-economic implications. Investments made on drying machines, air drying fruit yard paved with concrete, or devices for peeling the coffee berries etc, are mostly of little use to another crop.

The impact of the incidence of the major species of root-knot on coffee has shifted throughout the years in Brazil. Göldi (1892) reported on the case of the catastrophic disease on coffee in Rio de Janeiro. Since then the Brazilian farmers have learned to deal with *M. exigua*, but coffee in Rio de Janeiro was replaced by sugar cane and that State is no longer an important coffee producer.

In Colombia, *Meloidogyne exigua* and *M. javanica* have caused an estimated loss of US$ 800 million per year on coffee (Barriga, 1976).

A traditional coffee location such as the Alta Paulista region of São Paulo State (Brazil) has been changing to other crops including pasture due to the widespread incidence of *M. incognita* (Curi *et al.*, 1977).

The outbreak of *M. coffeicola* in Paraná State, Brazil in 1960 which killed many coffee trees (Lordello & Zamith, 1960) had a great economic impact. However in the last fifteen years *M. incognita* has spread widely over the best coffee plantations in Brazil in north of Paraná and west of São Paulo States, causing the destruction of whole plantations and changing the farmers' crops. The rapid death of the root systems and the inefficient control with nematicides, forced agricultural scientists to seek a better means of control to avoid the total decimation of the crop in those States.

A very important source of loss due to root-knot nematode is the total destruction of the coffee seedling enforced by law when root-knot is found in nurseries. In Sâo Paulo State (Brazil) 3 231 952 seedlings were destroyed from 1976 to 1977 (Gonçalves *et al.*, 1978).

The different types of losses caused by root-knot nematodes can be summarized: 1. yield decreases; 2. destruction of seedlings in nursery; 3. unemployment in traditional coffee producing areas; 4. decrease of the farmer's income by cultivation of a less profitable crop; 5. losses of investment on equipment or machines specific for this crop; 6. increases in the cost of coffee production due to nematicide application. From the research standpoint, yield loss has tended to preoccupy scientists, to exclusion of the other causes of loss.

Control measures

Control of nematodes in a perennial crop is more difficult than in annual or herbaceous crops. The long-term nature of perennial crops makes rotation schemes, which are succesfully used with annual crops, impractical. With perennial crops, nematodes that survive from the control practices used have time to recover and build up to destructive levels. Old plants left in the yield, weed hosts, or surviving roots of excised plants provide a source of nutrient for nematodes and in part negate the effect of control practices.

The control of coffee root-knot nematodes that are used today by many farmers may be considered under four subgroups:

1) exclusion, including the measures used to keep the parasite from entering the soil in which the host is growing.

2) application of nematicides, for the elimination or reduction of the parasite level after it has become established in the soil where the host is growing.

3) grafting on resistant or tolerant cultivars.

4) other measures under research: breeding coffee for resistance, rotations in areas where old coffee plants have been eradicated.

Exclusion

In Brazil, the impediment to the movement of infested seedlings into new growing areas was more effective in the past than today. Initially the government financed new coffee plantations by subsidies and imposed the use of new technology and prohibited the planting of coffee: (i) in the area previously planted to coffee or even close to the area; (ii) from seedlings infested with nematodes, and (iii) in regions not recommended for growing this crop. In the last 10 years this subsidized money was withdrawn and the government lost their control over planting new coffee plantations. Now the grower has to look independently for information on new technologies from the extension service network, universities, government research companies or other sources. But the inspection of coffee nurseries in Brazil is still maintained and the law for destruction of the infested seedlings is always enforced.

The production of seedlings without root-knot has relied on using soil in nurseries gathered from areas never previously grown with coffee, especially where pasture is currently grown. This soil can be sterilized with methyl bromide at the rate of 150 cm^3 per m^2 of soil (Morais *et al.*, 1977), placed under a plastic cover for 3–4 days and then aerated for 10 days before seeding. Other methods of sterilizing soil includes the uses of steam and exposure of nursery soil to sun for many weeks during the dry season period (Bridge, 1984). The water source has to be carefully selected avoiding dams in which run-off water comes from hillsides cultivated with infested coffee plants. Infected seedlings with root-knot nematodes should be burned and under no circumstances should they be planted into an area free of damaging nematodes.

The place to establish a new coffee crop has to be very carefully selected avoiding the recently eradicated old coffee plants, as well as the proximity of an infested field or on a site at a level below it, where the risk of contamination from run-off water is high. Sometimes a furrow has to be dug to prevent run-off water getting into the infested area. Care has to be taken to wash machines or farm implements used, or that have travelled through infested fields.

Nematicides

Chemicals used today to control nematodes on coffee as on other crops have been mostly restricted to contact or systemic granular products. From the group of fumigants widely used for controlling nematodes in the past (Anon., 1968) only methyl bromide is still widely used to disinfest nursery soil, as mentioned in the exclusion section.

The systemic insecticides, the organophosphate and organocarbamate chemicals, that have potential for nematode control are rarely phytotoxic at concentrations used for field control. The major disadvantages are that they are water dispersed. Nematicidal activity is usually confined to a shallow

root zone or rhizosphere, and is often a result of narcotization and nematode behavior modification rather than killing. Disruption of nematode infection, development and reproduction can temporarily slow or halt increases in nematode numbers. These chemicals give little or no control of fungal or bacterial disease but do provide insecticidal activity depending upon the chemical involved (Van Gundy & Mckenry, 1977).

In general the effective rates of aldicarb, carbofuran and phenamiphos will be in the range of 1.6 to 6.0 grams of active ingredient per plant, in one or two applications during the year. The first application should be in the beginning of the rainy season followed by the second 3 months later. In any case the soil should be wet for the application. A furrow is dug along the both sides of the plant row close to the tree where the product is applied and incorporated into the soil, by machine of by hand.

Application of systemic or contact granular nematicides on severely damaged coffee plants especially infested by *M. incognita* has not been effective due to the rapid killing of greater parts of the root system by the nematode (Curi *et al.*, 1977). Poor control also occurs on seedlings infested by *M. incognita* (Jaehn *et al.*, 1984).

However most of granular nematicides are effective in decreasing nematode populations a few months after application (Huang *et al.*, 1983; Campos *et al.*,1988). After this time the populations may increase on treated plants, but the plants have good foliage which seems to be induced by some other action besides controlling the nematodes (Campos & Lima, 1986).

Granular nematicides when applied in coffee have to be incorporated into the soil under the edge of the foliage toward the stem. Different machines have been developed to do this work. Another aspect on the application is the timing; since the granular products require water to liberate the active ingredient, application at the beginning of the rainy (November, in Brazil) season has been indicated (Campos *et al.*, 1985).

Grafting

The widespread distribution and the agressive parasitism of *M. incognita* in west of São Paulo forced the researcher in Brazil to seek for an efficient control measure other than chemicals. An introduction of *Coffea canephora* C. 2258, from Turrialba, Costa Rica, showed high resistance to *M. exigua* and resistant and/or tolerance to several populations of *M. incognita* (Fazuoli, 1986). The rate of resistance was initially 70%, but through selections in the field highly infested with *M. incognita* , this rate has increased significantly. The line obtained by selections from C 2258 has been named LC 2258. On LC 2258 the *C. arabica* var. Mundo Novo or Catuaí Vermelho was grafted and then planted in infested fields. The growth and production were very good, but, in many locations, the non-grafted plants of *C. arabica* did not survive (Fig. 3). Even though the compatibility between scion and stocks still has to be studied (Fazuoli, 1986), the cooperatives of coffee growers have produced many thousands of grafted seedlings and given them to the farmers to show the possibility of this means of controlling *M. incognita* in coffee. It is a promising means of control in regions infested with *M. incognita*.

Other measures under research

Many researchers are still seeking for resistance to *M. incognita* in germplasm of *Coffea* , notwithstanding the occurrence of three races of the species on coffee plantations in Brazil (Moraes *et al.*, 1973*b*; Medina Filho *et al.*, 1981; Fazuoli, 1986). Work also has been done on resistance to *M. exigua* (Curi *et al.*, 1970).

Moraes *et al.*, (1977*b*), studied rotation with cotton, soybean and corn in *M. exigua* infested areas and concluded that, after one year's rotation with these crops, the grower can return to coffee cultivation. But Carneiro and Carneiro (1982), who screened 29 crops for rotation in *M. incognita* infested coffee fields, found that only *Arachis hypogaea* and *Ricinus communis* were immune. *Styzolobium deeringianum* and *Crotalaria spectabilis* showed resistance to this nematode.

Several lines of *Coffea canephora, C. congensis* showed resistance to race 3 of *Meloidogyne*

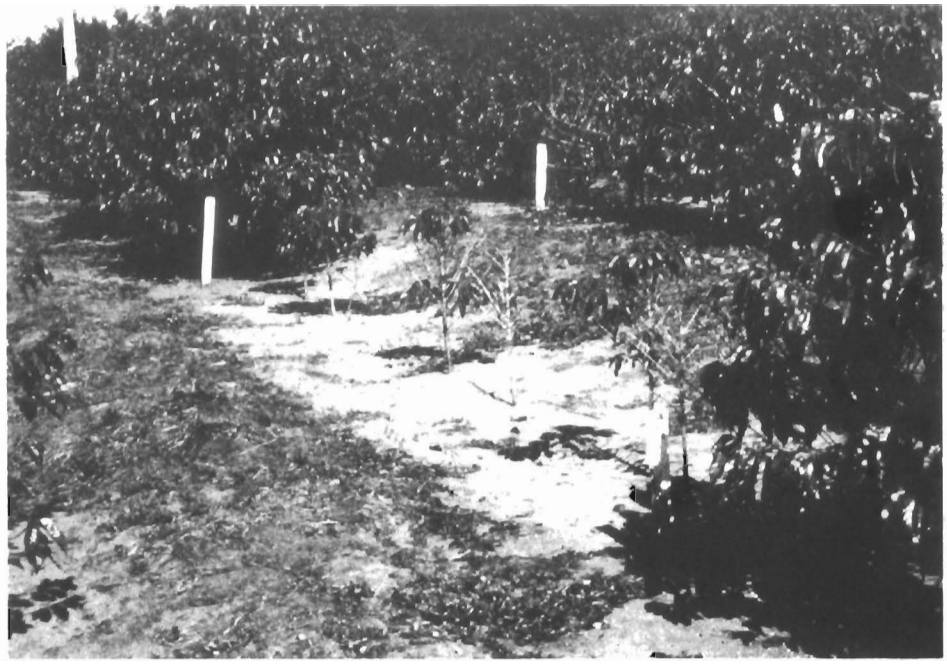

Fig. 3. Four-years-old grafted *Coffee arabica* on *Coffea canephora* LC 2258 planted in natural infested field with *Meloidogyne incognita* (São Paulo, Brazil). Dead *Coffea arabica* plants between the stakes were not grafted (Photo: L. C. Faznoli).

incognita , and some progenies of *Coffea canephora*, Sarchimor (derived from crossing Vila Sarchi × Timor Hybrid), Icatu (advanced line derived from crossing *C. arabica* × *C. canephora*) have shown moderate resistance. However, all germplasm of *C. arabica* tested is susceptible to race 3 of *M. incognita* (Gonçalves & Ferraz, 1987).

Among the root knot nematodes of coffee in Brazil, *M. incognita* causes the greatest losses, becoming a limiting factor to growing coffee in certain areas due to (i) its great capacity to destroy the root systems, (ii) it being easily disseminated, (iii) it having a high persistence in soil, (iv) the inefficiency of chemical control measures, and (v) it having different races.

Methods of diagnosis

Diagnosis of the occurrence of *M. exigua* in field is not difficult because this nematode induces typical round galls on roots of infested coffee plants unlike damage by *M. incognita* and *M. coffeicola*. With these latter species, laboratory diagnosis is required to search for *M. incognita* or *M. coffeicola* in non galled sections of the root system. *M. coffeicola* is mostly found in older sections of the root especially the principal root. But, in all cases, the current sampling extraction procedures can be used to recover the second stage juveniles in soil which helps to identify the disease in combination with the symptomatology on the plant.

II. Meloidogyne africana, M. decalineata, M. megadora, M. hapla, M. arenaria, M. kikuyensis, M. inornata, M. javanica, M. oteifae and *M. thamesi*

Distribution

Even though relatively few surveys have been done in Africa to produce a good picture of the distribution of nematodes in different countries where coffee is grown, the data available suggest that *Meloidogyne africana, M. decalineata, M. kikuyensis,* and *M. megadora* seems to be restricted to relatively few Africa countries. In Tanzania and Zaire, where more data is available, many species of *Meloidogyne* occur in coffee (Table 1) but the other species of this group seem to have restricted ecological requirements limiting their occurrence. *M. decalineata* was the predominant species in Kilimanjaro, and the Usambra mountains of northern Tanzania (Swai, 1981). *M. kikuyensis* was also reported from coffee in the region of Kilimanjaro (Swai, 1981). *Meloidogyne africana* is widespread in Kenya and Zaire (Whitehead, 1959; Lordello, 1972). Bridge (1984) reported the occurrence of *M. decalineata* and other species of *Meloidogyne* in different areas of Tanzania. *M. megadora* is found in Angola and Uganda(Whitehead, 1968*a*; Whitehead, 1969*a*).

Meloidogyne infections on coffee have also been found in Zimbabwe (Way, 1981). *M. hapla* and *M. javanica* are rarely found on coffee in Tanzania suggesting that there is also some resistance in coffee to these species (Whitehead, 1969*a*,*b*; Bridge , 1984). *M. arenaria* has been found on coffee in Jamaica (Anon., 1963, in Whitehead, 1969*b*). *M. oteifae* occurs in Zaire (Elmiligy, 1968) and *M. inornata* in Guatemala (Shieber & Sosa, 1960 in Lordello, 1972). *M. thamesi* has been found in coffee soil in India (Kumar, 1984).

Symptoms of damage

M. oteifae forms galls of moderate size on roots of *Coffea robusta* (Elmiligy, 1968). *M. africana* and *M. decalineata* usually cause small galls from 1 to 5 mm in diameter (Plate 10E, Fig. 4). Affected seedlings are generally stunted with numerous rootlets behind the affected root-tip (Whitehead, 1959). Heavy infestations in mature trees were associated with general unthriftiness but the nematodes may not have been wholly responsible for this (Whitehead, 1969*a*,*b*). *M. africana* attacks *Coffea arabica* in Kenya, causing poor growth of coffee seedlings in farms and nurseries (Anon., 1977; Whitehead, 1959), and *Coffea robusta* in Zaire (Whitehead, 1969*b*). *M. decalineata* causes root galls in *Coffea canephora* and *C. arabica* in nurseries as well as yellowing of coffee leaves and reduction of plant growth in field (Lordello & Fazuoli, 1980).

M. hapla causes a slight root-galling and swellings in coffee different from other species which occur in Tanzania (Bridge, 1984) (Table 1). In Brazil it causes typical galls with different diameters close to *M. exigua*. Necrosis and induction of lateral roots are also observed close to the nematode (Lordello, 1982).

Other hosts

M. arenaria, M. javanica and *M. hapla* are found infecting a great number of crops and weeds in many countries of the world (Ponte, 1978; Nickle, 1984). In Africa, *M. africana* is found infecting corn, cowpea, clove, potato, pyrethrum; *M. megadora* in many coffee species and *M. kikuyensis* in cowpea (Whitehead, 1969*a*). In Brazil *M. thamesi* is found infecting cocoa, *Turnera ulmifolia* L., *Spondias lutea, Rivina humilis, Petiveria hexaglochin* Fisch & Mey and *Leonorus sibiricus* (Ponte, 1978; Lordello, 1984) and *M. inornata* infecting soybean (Ponte, 1978).

Economic importance

Although there is no information available in Tanzania on the actual yield losses caused by nematodes it is estimated that yield losses of trees severley infested with the African coffee root-knot nematodes will be in the region of 20% in optimum conditions, extending to the point of non-productivity (Bridge, 1984). The stress to which trees are subjected to because of nematode damage will also cause premature fruit drop, twig dieback and defoliation, nutrient deficiency symptoms and stunted growth.

Fig. 4. Root galls caused by *M. decalineata* (Tanzania) (Photo: J. Bridge).

Control measures

The control measures described for *M. exigua, M. incognita* and *M. coffeicola* are likely to be effective for the control of African root-knot nematodes, but application of these measures on a practical basis in African countries is uncertain. However a test of different *Coffea* species, crosses and selections against root-knot nematode in Tanzania has been done by Bridge (1984) which indicated that some resistance may occur. Reports from the Kenya Coffee Research Station cited by Whitehead (1968*b*), suggests resistance to *Meloidogyne* sp. in *Coffea corrisoi, C. conuga* and some lines of *C. congensis* in Angola. Whitehead (1969*b*) said that coffee is very resistant to *M. javanica* and *M. kikuyensis*.

Pratylenchus

The lesion nematodes, *Pratylenchus* spp. known to occur on coffee are *Pratylenchus coffeae, P. brachyurus, P. goodeyi, P. pratensis* and *P. loosi*.

Distribution

For a long time *P. brachyurus* was the only *Pratylenchus* species known to infect coffee in South America (Lordello, 1972). Later *P. coffeae* was found in Dominican Republic (Schieber & Grullon 1969), El Salvador (Whitehead, 1969*b*; Gutierrez & Jimenez, 1970), Guatemala (Schieber, 1971), Puerto Rico (Ayala, 1976), Costa Rica (Figueroa & Perlaza, 1982), and Brazil (Monteiro & Lordello,

1974). *P. coffeae* also occurs on coffee in India (Palanichamy, 1973), Southeast Asia, Barbados, Martinique, and Tanzania (Whitehead, 1969; Bridge, 1984) Madagascar and Indochina (Whitehead, 1968). In Java it became a very damaging and major pest of coffee (Whitehead, 1968) as well as in India (Palanichamy, 1973). In El Salvador it was a predominant species.

P. brachyurus has been found in many regions in Brazil (Lordello & Mello Filho, 1969; Gonçalves *et al.*, 1978; D'Antonio *et al.*, 1980; Campos & Lima, 1986), in West Africa and Peru (Whitehead, 1968b). In São Paulo State, Brazil, *P. brachyurus* was more widespread than *P. coffeae* (Gonçalves *et al.*, 1978). In Minas Gerais State, Brazil, *P. brachyurus* was found in 20% of the counties samples (D'Antonio *et al.*, 1980).

P. pratensis has been reported from one locality in South India by Somasekhar cited by Whitehead (1968*b*) and *P. loosi* from Ceylon by Hutchinson cited by Whitehead (1968). *P. goodeyi* occurs on coffee in Tanzania (Bridge, 1984).

Symptoms of damage

Roots of coffee infected by *P. coffeae* turn yellow, then brown and most lateral roots are rotten. Infected plants look stunted and have few small chlorotic leaves. The earliest symptoms of infection in the newly transplanted trees are yellowing of leaves, loss of young primary branches and stunting of the shoot. A gradual wilt sets in, followed by death of the whole tree (Whitehead, 1969*b*).

Severely infected plants may die prematurely. In the field the symptoms may occur in patches with reduced yield according to the disease severity. Lesions occur on roots with consequent destruction of the whole root system (Monteriro & Lordello, 1974). *P. coffeae* is the most destructive nematode of *Coffea arabica* in South India (Palanichamy, 1973).

P. brachyurus causes reduced plant and root growth, shedding of leaves and nutritional deficiency (Lordello, 1984), The influence of infestations of *P. goodeyi, P. loosi* and *P. pratensis* on coffee growth is not known.

Races

Cross inoculation studies with populations of *P. coffeae* from *Coffea arabica* in seven different hosts revealed differences in reproduction and pathogenticity suggesting a physiological specialization in this species (Kumar & Viswanathan, 1972).

Other hosts

P. brachyurus is found infecting a great number of crops in many countries of the world (Lordello & Mello Filho, 1969; Nickle, 1984). Grasses which commonly occur within coffee plantations in South America such as *Melinis minutiflora* and *Hyparrhenia rufa* are good hosts for this species (Lordello, 1972). *P. coffeae* has a wide host range (Nickle, 1984).

Control measures

Abrego (1974) showed the efficacy of oxamyl, phenamiphos and aldicarb for controlling *P.coffeae* in coffee nurseries in El Salvador.

Increased yields of coffee were obtained in the second year in treated plots with carbofuran (Abrego, 1974). Good control of *P. coffeae* was also obtained with Nemacur and it remained effective under field conditions for 90 days after application (Kumar, 1982). In India it was found that *Coffea robusta* is more tolerant to *P. coffeae* than *C. arabica* or *C. excelsa* (Anon., 1974), hence the use of *Coffea robusta* as rootstocks is the most promising means of control (Palanichamy, 1973). In fact, Schieber and Grullon (1969) suggested also the use of *Coffea canephora* var. *robusta* as a source of resistance for rootstocks in grafted plants.

To prevent serious infestation with these nematodes the coffee growers should, where possible, disinfest nursery soil and plant seedlings in non-infested field soil. Methyl bromide at rates of 150 cm^3/m^3 of soil is the most effective means of sterilizing soil but other methods are available (see control of root-knot nematodes above).

Other Nematode Parasites of Coffee

Among other species of nematodes parasitic to coffee, *Rotylenchulus reniformis* has caused greatest damage to this crop. In the Philippines, *R. reniformis* attacked *Coffea arabica, C. robusta* and *C. excelsa* with equal severity (Valdez, 1968). In India it is an important parasite of *C. arabica* (Anon., 1966). *R. reniformis* is reported also from coffee seedlings in a commercial nursery in Brazil (Lordello, 1980) and is also recorded on *Coffea* spp in New Guinea, Fiji, Tonga and Western Samoa (Bridge, 1988).

D'Souza and Screenivasan (1965), pointed out that coffee does not grow well in infested fields with an inoculum density of *R. reniformis* greater than ten nematodes per 50 cm^3 of soil. Screening genotypes for resistance has been done. Macedo (1974) found resistance in *Coffea canephora* cv Guraini whereas on cultivar Mundo Novo and Catuaí of *C. arabica* a few mature females deposited eggs. No further information on the importance of this nematode and control measures are available.

Whitehead (1968*b*), commented on the great importance of *Radopholus similis* to coffee in Java reported by Zimmermann. This nematode was considered the most harmful nematode to that country and second only in importance to *Pratylenchus coffeae.*

Vovlas (1987) reported on the widespread occurrence of *Trophotylenchulus obscurus* as a pest of coffee in São Tomé, West Africa. At feeding, *T. obscurus* introduces the anterior body portion into the peripheral layers of the cortex and the nematode feeds from a single nurse cell which undergoes senescence, and, as a consequence, causes considerable damage to the cortical cells. Dark brown capsules containing eggs, juveniles and males can be observed on the root surface.

Many other parasitic nematode species belonging to the genera *Caloosia, Criconemella, Discocriconemella, Helicotylenchus, Hemicriconemoides, Hoplolaimus, Longidorus, Ogma, Paratrichodorus, Pratylenchus,Peltamigratus, Rotylenchus, Scutellonema, Trichodorus, Tylenchorhynchus and Xiphinema* have been found associated with coffee plants (Luc & de Guiran, 1960; Whitehead, 1968; Whitehead, 1969; Lordello, 1972; Sharma & Sher, 1973; Van Doorsselaere & Samsoen, 1981; Bridge *et al.*, 1982; Bridge, 1984; Bridge & Page, 1983; Campos *et al.*, 1987; Vovlas, 1987). However, information on their pathogenicity, damage, yield loss and possible control measures is lacking.

Conclusions and Future Prospects

Growers must be made aware of the nematode threat to the coffee crop. Certain nematode species, especially those belonging to *Meloidogyne* , which are not considered important today may become a constraint for coffee production in certain regions in the future. In addition, specific regional coffee ecosystems, poor management and changes in host-parasite relationships may favour the outbreak of a nematode disease in a coffee region. *Meloidogyne* diseases of coffee have been important causes for the movement of coffee producing areas in Brazil. Complex disease situations caused by mixtures of many species of *Meloidogyne* do occur in coffee plantations around the world.

Agricultural scientists need to examine whether coffee nematodes are a problem in their own countries and follow the progress of any nematode disease particularly to avoid the dissemination of the nematode causing, in consequence, losses which can harm the country's economy.

A better future for this crop as far as the nematode diseases are concerned can be reached by the introduction of regulations restricting the planting of infested coffee seedlings and planting in the areas of old infested coffee plantations. Equally important is the practical mechanism to enforce these regulations.

The use of seedlings for field planting and the perennial nature of the crop increases the risk of severe nematode infestation.

Grafting commercial cultivars on resistant or tolerant rootstocks to damaging nematodes, could be a useful control strategy in regions with widespread distribution of very destructive nematodes.

Biological control especially with *Pasteuria* sp could be a promising strategy in the future to control root-knot or other nematodes.

COCOA

Cocoa and chocolate are derived from the seeds of *Theobroma cacao*, a small tree indigenous to the forests of Central and South America which belongs to the family Sterculiaceae. The centre of origin is the upper Amazon in South America.

The fruit, which is botanically a berry, usually contains from twenty to forty seeds, each surrounded by a pulp which is developed from the outer integument of the ovule. The action of yeasts removes the mucilage around the seeds, which facilitates subsequent handling and drying of the beans (Urquhart, 1955).

Cocoa is grown in many countries of South and Central America, Africa, Asia and Oceania, located mostly between 10° North and South of the Equator. The three major world producers are Ivory Coast (25% of the world production), Brazil (23%), Ghana (12%) (FAO, 1986).

Cocoa is a lowland crop growing best from sea level to altitudes of 1 400 m on the equator with temperatures of 16°C–34°C and rainfall of 1500 mm. It reacts unfavorably to sudden changes of temperatures or humidity. The main factor limiting the growth of cocoa at the higher altitudes is temperature. The daily variation of temperature should not exceed 9°C (Urquhart, 1955; Braudeau, 1970).

Cultivation techniques

Seed propagation is cheapest. Seed can be planted directly in soil (West Africa), in nursery seedbeds, in baskets or plastic bags. Germination takes 1 or 2 weeks and seedling are transplanted to the fields when 2–6 months old. Propagation is also possible by cuttings, buddings, grafts and marcots. Spacing varies between areas. Closer spacing is used in Africa such as 2.4 m × 2.4 m; 3 m × 3 m; 3 m × 2 – 2.5 m and 4.5 m × 4.5 m. In America and Asia spacing is predominately 4 m × 4 m; 3.6 m × 3.6 m and 3 m × 3 m. Shading is commonly used. Thinned natural forest for shading predominates mostly in Africa, while in America, Asia and Oceania the shade trees planted are mostly: *Erythrina* spp, *Gliricidia* spp. *Albizzia* spp. *Pithecolobium* spp. and *Leucaena* spp. Managing the shade conditions during the development of the crop is done in some producing countries. Pruning is done to shape or form the young tree, to maintain the subsequent shape or form and to renovate or rehabilitate the tree.

Nematodes of Cocoa

Nematodes such as *Dolichodorus* and *Meloidogyne* species especially *M. incognita* and *M. javanica* have caused losses in cocoa areas around the world including yield decrease, sudden death of trees and growth retardation of seedlings in nursery. In addition many other genera and species of root feeding nematodes have been found in association with cocoa (Table 2) although the pathogenic relationship, for most of them, has not been proved.

Meloidogyne

Meloidogyne spp. are the most important nematodes of cocoa due to their pathogenicity and wide distribution in cocoa producing regions.

Distribution

Root-knot nematodes have been found in cocoa since 1900 (Ritzema Bos in Sosamma *et al.*, 1980 *a*), and they have been reported from Zaire. São Tomé, Java (Ghesquière, 1921; Cotterel 1930; Fluitter & Mulholland, 1941), Ghana, Malawi, Ivory Coast (Edwards, 1955; Luc & de Guiran, 1960

TABLE 2. List of endoparasitic and ectoparasitic nematodes associated with cocoa roots.

Criconemella spp.	*Peltamigratus holdemani*
Dolichodorus minor	*Pratylenchus brachyurus*
Helicotylenchus spp.	*P. coffeae*
Hemicriconemoides cocophillus	*Radopholus similis*
Hemicycliophora spp.	*Rotylenchulus reniformis*
Heterodera sp.	*Rotylenchus microstriatus*
Hoplolaimus spp.	*Scutellonema brachyurus*
Longidorus sp.	*S. clathricaudatum*
Meloidogyne arenaria	*Trichodorus monohystera*
M. exigua	*Trophurus imperialis*
M. incognita	*Tylenchorhynchus martini*
M. javanica	*Xiphinema spp.*
M. thamesi	

Bridge et al., 1982; Sharma, 1982; Sharma & Loof, 1974; Sharma & Sher, 1973, 1974; Sosamma *et al.*, 1980*a,b*; Thorold, 1975; Whitehead, 1969.

Martin, 1961), Nigeria (Caveness, 1967), Venezuela (Torrealba, 1969), Brazil (Lordello, 1968) and India (Sosamma *et al.*, 1980*b*).

Meloidogyne incognita seems to be the most frequently found in cocoa (Luc & de Guiran, 1960; Sharma & Sher, 1974). It is a common pest in West Africa (Whitehead, 1969), India (Sosamma *et al.*, 1980*b*) and is widespread in cocoa regions of Brazil (Sharma & Sher, 1974; Sharma, 1982). In the cocoa region of Espirito Santo State, Brazil, it is the most frequent nematode in sampled sites (Sharma & Sher, 1974).

However other species of *Meloidogyne* have also been found on cocoa: *M. exigua* in Bolivia (Bridge *et al.*, 1982), *M. javanica* in Malawi (Corbett, 1961) and in Central Africa (Martin, 1961), *M. arenaria* and *M. thamesi* in Brazil (Sharma, 1979).

Symptoms of damage

In artificially infested seedlings, *M. incognita* causes dieback, stunting, wilting, yellowing of leaves and small leaves. On roots tiny galls and females with egg masses can be observed (Afolami, 1981). Sharma and Maia (1976) found in the cultivar Catongo that *M. incognita* caused small, rounded and elongated galls with conspicuous egg masses. Stunting was also observed. The leaf tips and margins first turn brown and become dried, this spreads to the entire leaves which are eventually shed. The infested plants looked unthrifty, with decreased height, shoot and dry root weights.

In the field, *M. incognita* produces galls with exposed egg masses on roots, dieback and sudden death of the infested plants. According to Sharma and Sher (1973) when the dieback conditions occurs, the trees die down to their roots, which remain alive and send up shoots in the following growing season and also when the dead terminals are pruned off. The syndrome of the sudden death disease is permanent wilting, the green leaves suddenly turn yellow and brown, and then dry up to remain hanging. Jimenez-Saenz (1971) and Sharma and Sher (1973) associated the occurrence of sudden death with root knot nematodes.

M. javanica also forms galls on cocoa roots (Martin, 1961). In Malawi young cocoa trees grew slowly in patches of soil heavily infested with *M. javanica* (Corbett, 1961). Damage symptoms were also observed on cocoa roots infested by *M. exigua* in Bolivia (Bridge *et al.*, 1982).

Nematodes in the nursery can retard the growth of seedlings or may even kill them. The transplantation of nematode infested seedlings carries nematodes to the plantations where the transplants may die.

Races, means of dissemination, other hosts and economic importance

Among the root-knot nematode species found in cocoa *Meloidogyne incognita* and *M. arenaria* have host races. Although *M. incognita* has four biological races, no attempt has been made to determine the variation within *M. incognita* populations of infested cocoa fields, similarly, *M. arenaria*, which is known to have two races in other crops, has not yet been examined for races differentiation in cocoa.

M. javanica, M. incognita and *M. arenaria* have wide host ranges (Ponte, 1977; Nickle, 1984) and in many instances the commonly used shade plants, such as banana, may become a source of inoculum in the cocoa plantation (Sosamma *et al.*, 1980 *a*). Corbett (1961) recommended the replacement of banana as a shade to cocoa to reduce the nematode infestation in Malawi.

Nursery soil infested with the nematodes will allow the production of infested seedlings which will disseminate nematodes into plantations. Run off water may also disseminate nematodes.

Although data on cocoa yield losses caused by nematodes, are not yet available, evidence suggests their importance to this crop. Sudden death of cocoa plants in the field has been associated with root-knot nematodes (Jimenez-Saenz, 1971; Sharma & Sher, 1973). The widespread distribution of these nematodes in many areas of cocoa production could limit productivity and have an economic impact on infested regions.

Other Nematode Parasites of Cocoa

The lesion nematode, *Pratylenchus brachyurus* has been widely found in cocoa in Bahia, Brazil (Sharma & Sher, 1973), and occurs also in Western Africa (Luc & Guiran, 1960). In Java, *P. coffeae* infects roots of cocoa (Fluitter & Mulholland, 1941). But many other root feeding-nematodes have been identified in cocoa (Table 2).

Sharma (1971) associated dieback and death of the nursery plants with the presence of *Dolichodorus* sp. (now *D. minor*). The entire root system was reduced, blackened, and showed disintegrated cortex and beadlike gall formation. The galled portion was reddish-brown and hard.

Control

In perennial crops such as cocoa, nematodes that survive the control practices have time to recover and build up again to destructive levels. Hence the most efficient control strategies are: 1) to produce seedlings free of major pathogenic nematodes and 2) to cultivate in soils or areas from which the nematodes are absent.

Soil to be used in the nursery should be sterilized by treating with methyl bromide at a rate of 196 cm^3 per m^3 of soil (Ferraz, 1979), or collected from areas that are not infested by root-knot species and *Pratylenchus* sp. Another method is hot air treatment using a hot air sterilizer which raises the temperature to 100°C for an hour (Sharma, 1975).

The land for cultivating cocoa must be surveyed for important nematodes before transplanting clean seedlings. In the case of established plantations already infested, especially by root-knot nematodes, the grower should use nematicides to manage the population level and avoid economic damage.

For agricultural field applications most fumigant nematicides are no longer used. The emphasis has been on the production and uses of contact or systemic nematicides for controlling plant parasitic nematodes.

Application of granular nematicides such as Nemacur 10G, Temik 10G at the rate of 50 mg of commercial product/plant and Terracur 5% at 100 mg/plant in plants infested by *M. incognita* in the glasshouse reduced the nematode density and increased the numbers of leaves per plant (Sharma & Ferraz, 1977).

Tarjan *et al.* (1973) reported on the increased yield of 11 to 96% after field application of Mocap or Terracur at the rate of 34kg of the commercial product/ha and Nemacur at 22 kg/ha. The products were applied within a cleared area of 1.0 or 1.5 m around each trunk and then incorporated into

the upper 2.5 cm of soil. Sosamma *et al* (1980*a*)have reported an increase in the number of pods by the application of Dasanit and Nemacur and an increase of yield by the application of Nemacur, Terracur and Mocap.

Care must be taken with the selection of shade plants, avoiding trees susceptible to root-knot or lesion nematodes, for example *Leucaena glauca* and banana (Corbett, 1961; Sosamma *et al.*, 1980*a*).

Methods of diagnosis

Root galling in most cases will be helpful to diagnose the presence of *Meloidogyne* species on cocoa plants. However the extraction of juveniles of those nematodes from soil can help to confirm their presence and identification. Other nematodes will be found by sampling soil or roots.

Conclusions and Future Prospects

Besides the sudden death of cocoa trees in Bahia State, Brazil, and also some localized occurrence of some damaging nematodes on cocoa plantations in other countries, there is no known wide distribution of nematodes in any specific cocoa region causing economic impact. However the potential pathogenicity of some nematodes especially *Meloidogyne incognita*, has already been proved in glasshouse research and the growers must be aware of this potential threat to their crop.

Emphasis in future research work should be on estimation of yield losses and the distribution of damaging nematodes in specific cocoa regions to obtain a better picture of the economic importance and distribution of these organisms.

The perennial characteristics of the cocoa crop means that great care should be taken in the preparation of uninfested seedlings, and also on the choice of land to be planted. The exclusion approach, preventing damage, is cheaper, safer, and more efficient.

Many countries have the potential to increase cocoa production but a profitabe crop will require good management of all different agricultural aspects including nematode diseases. Larger markets and a greater competition on a worldwide basis require greater efficiency of production at lower prices, minimizing costs and risks involved. Nematode infestation is a potential constraint by increasing the cost of cocoa production and decreasing yields.

TEA

Tea is a beverage crop with two extreme varieties, including the small-leaved China type and the large-leaved Indian or Assam type, both of which belong to the same species, *Camellia sinensis*. Commerical tea populations are polymorphic in origin, derived from *Camellia sinensis* (L) O. Ktze., *C. assamica* var, *assamica* (Masters) Wight, and C.*assamica* var. *lasiocalyx* (Planch.) Wight, or the hybrids of these different varieties.

Tea is presently grown at latitudes from 27°S (Corrientes, Argentina) to 43°N (Georgia, USSR), as well as from mean sea level up to an altitude of 2300 m. The tea crop requires well drained acid soils with a pH range of 4.5 to 5.5 and reasonably well distributed rainfall, totalling not less than 1000 mm per annum.

Cultivation techniques

The population of tea bushes in old tea fields is about 7000 per hectare and in many fields the plant population is far below this number due to extensive casualties. The plant population density in the newly planted areas is around 13 000, usually planted along the contour.

When allowed to grow freely, the tea plant could grow to a large tree attaining a height of around 12 m or more. For purposes of commerical exploitation, the plant is kept pruned regularly to be maintained in the form of a bush at a height of around 90 cm.

The unit that is harvested is the tender flush, comprised usually of two leaves and a bud and these units are generally harvested at weekly intervals depending on growth rates.

The average yield of tea could range from as low as 350 kg per ha to as high as 5000 kg per ha of made tea, per annum (which corresponds to about 1500 to 22 400 kg green leaf per hectare, per annum). Though broadly similar, the agricultural and manufacuturing practices could vary in the different tea growing areas of the world.

Nematode species encountered in tea

Due to the wide variability in soil types and climatic conditions under which tea is being cultivated on a commerical scale, the complex of nematode populations that attack the tea plant vary very widely and the intensity of attack of the respective species and the degree of the induced pathogenicity could also vary correspondingly. Furthermore, investigations in respect of damage caused by nematodes to the tea crop is limited to only a few countries, whilst the majority of the countries that grow this crop on a commerical scale, have not carried out any investigations nor surveys on the incidence of these pests.

Several species of plant parasitic nematodes have been encountered in tea soils in the different tea growing areas of the world. However, no positive evidence of pathogenicity have been established in respect of the majority of these nematodes. The species that are either known or suspected to be pathogenic to tea (Table 3) includes the following: *Pratylenchus* spp., *Radopholus similis, Meloidogyne* spp., *Hemicriconemoides kanayaensis, Rotylenchulus reniformis, Helicotylenchus* spp., *Paratylenchus curvitatus, Hoplolaimus* sp., *Rotylenchus* sp. and *Xiphinema* sp.

Pratylenchus

Species of *Pratylenchus* are known to attack tea growing in almost all parts of the world. Amongst these, *Pratylenchus loosi* is the most serious pest in Sri Lanka (Gadd, 1939; Gadd & Loos, 1946; Loos, 1953*a*; Sivapalan, 1972). This species of nematode is also recorded as a serious pest of tea in Japan (Kaneko & Ichinohe, 1963; Takaji, 1969).

In Sri Lanka, this species is widely distributed amongst tea fields at all altitudes. However, damage to tea is mostly confined to elevations of 900 to 1800 m, where severe damage and crop loss occurs in mature tea, newly planted young fields, as well as in nurseries (Hutchinson & Vythilingam 1963*a*). As a consequence of its distribution and pathogenicity to high elevation tea areas, it is commonly referred to as the "up-country species of nematode".

In contrast, in Japan, where tea is cultivated at altitudes of 0 to 300 m, damage to tea by this species occurs at all locations in view of the fact that this country is located in the cooler temperate zone (Takagi, 1969).

P. loosi is also known to cause damage to tea in China, but to-date a proper survey has not been carried out and as such the distribution and extent of damage is not well known (Chen, pers, comm. 1988).

In Darjeeling, India, *P. loosi* was reported for the first time in 1982, but no pathogenicity trials have been carried out (Mukherjea & Dasgupta, 1982).

In Bangladesh, this species of nematode has been observed to cause symptoms of damage to tea only in nurseries. Nursery soils are, therefore, regularly checked for this species (Rashid & Millin, pers. comm. 1988). Despite such observations, no attempt has yet been made to assess the distribution and possible damage in mature tea.

Symptoms of damage

Typical symptoms of injury caused by *P. loosi* in both young and mature tea in the field include: patches of unthrifty tea (Plate 10A), with the affected plants showing spindly growth with sparse foliage. The leaves are dull and yellowish in colour. These symptoms are brought about by an altered rate of uptake of essential nutrients by the damaged root system (Fig. 5). The heavily infested plants

TABLE 3. Distribution of nematodes known/suspected to be pathogenic to tea

Nematode Species	Argentina	Australia	E. Africa	S. Africa	Malawi	Zimbabwe	Kenya	Bangladesh	China	Indonesia	N.E. India	S. India	Japan	Malaysia	Pakistan	Sri Lanka	Taiwan
Pratylenchus loosi								+	+		+		+			+	
Pratylenchus brachyurus		+			+						+						
Radopholus similis				+		+			+	+						+	
Meloidogyne javanica		+	+		+	+			+	+	+	+				+	
Meloidogyne incognita	+	+			+	+	+	+	+	+	+		+			+	
Meloidogyne arenaria					+	+			+							+	
Meloidogyne hapla						+					+						
Meloidogyne brevicauda											+	+				+	
Meloidogyne thamesi									+								
Hemicriconemoides kanayaensis									+				+				+
Rotylenchulus reniformis					+	+					+					+	
Rotylenchus sp.			+	+		+					+						
Helicotylenchus sp.			+		+	+		+			+	+			+	+	
Helicotylenchus erythrinae									+		+		+			+	+
Helicotylenchus dihystera		+									+		+			+	
Hoplolaimus sp.			+		+						+				+	+	
Paratylenchus curvitatus											+		+			+	
Xiphinema sp.			+	+	+	+		+			+		+	+	+		

Fig. 5. Stunted tea plant with feeder roots damaged by *Pratylenchus loosi* (left) and uninfested healthy plant (right).

also have a tendency to enter into the reproductive phase by flowering and setting fruit prematurely (Gadd, 1939; Visser, 1959; Sivapalan, 1967*a*, 1972). Examination of the roots of such infested plants show a marked reduction in the growth of feeder roots. The remaining roots appear brown and dried up when compared to the normal healthy roots that are succulent and whitish in colour. On peeling the bark the larger storage roots display dark brown necrotic patches or lesions of varying size (Plate 10B). The heavily infested plants either recover very poorly from pruning, remain as unthrifty "passengers", or fail to recover at all and die.

Pathotypes (Biological Races)

No positive evidence has yet been established for the existence of different pathotypes of *P. loosi* in tea.

Survival and means of dissemination

P. loosi is known to survive in host-free soils in the lesions of the larger old storage roots of tea that are left uncleared, following uprooting of old tea fields, for as long as three years.

One of the most important means of spread of *P. loosi* amongst tea areas, is by the dissemination of infested plants to fields from contaminated nurseries. Spread of nematodes could also occurs

through: 1) movement of infested soil and water – poor soil conservation measures adopted in infested areas, including the use of weeding implements, tend to loosen the soil that leads to erosion and washing down of contaminated soil into areas hitherto uninfested; 2) uprooting of old tea fields are sometimes carried out from the bottom to the slope upwards, thus exposing the newly planted young tea at the bottom to reinfestation from infested old tea still remaining above; 3) use of contaminated irrigation water in nurseries.

Environmental factors affecting pathogenicity

The severity of damage to tea is dependent on the interaction of various factors such as 1) prevailing climatic conditions; 2) type of soil in which the tea is growing; 3) cultural practices (Gnanapragasam, 1988).

Climatic factors

The distribution of *P. loosi* seems to be governed by soil temperature and soil moisture. The highest population is encountered at altitudes with soil temperatures of 18° to 24° C. Obvious pathogenicity symptoms are also observed in this temperature regime (Sivapalan & Gnanapragasam, 1975). At temperatures above and below this range, the rate of population build-up is less and consequently, damage to tea is also reduced (Sivapalan, 1972).

The results of detailed surveys have revealed that the largest population of this species of nematode is encountered in areas with high and well distributed rainfall and this determines the severity of damage within the same altitude (Hutchinson & Vythilingam, 1963a).

A marked periodic fluctuation in population levels is also observed during the year and this variation is correlated to the rainfall pattern as well as soil temperature (Sivapalan, 1972) (Fig. 6).

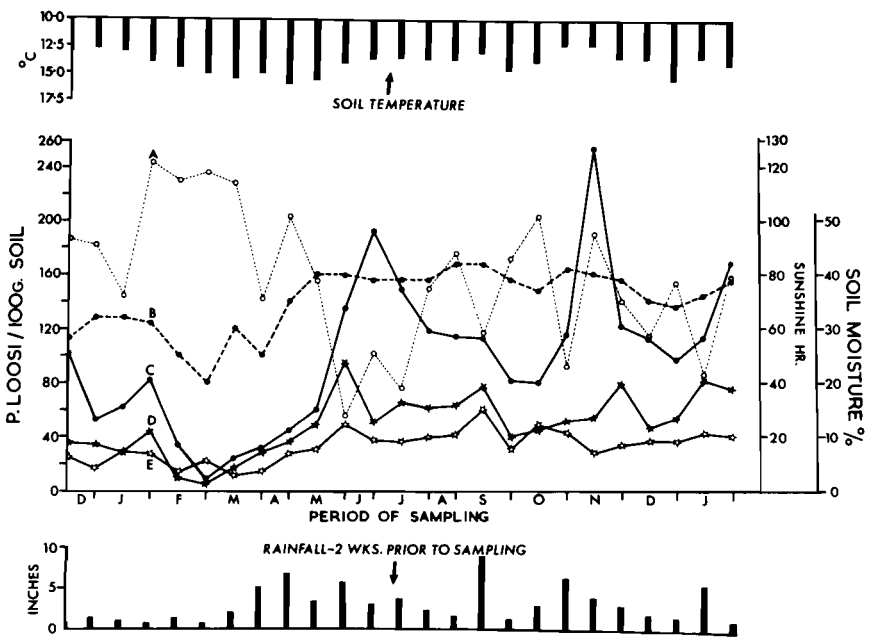

Fig. 6. Soil population (fluctuation of *Pratylenchus loosi* at varying depths (C = 15cm, D = 30cm, E = 45cm) during different times of the year, as determined by soil temperature, rainfall pattern, sunshine (A) and soil moisture (B).

Type of soil

Nematode damage is known to vary with the type of soil (soil texture) as well as the physical condition of the soil. Damage caused by *P. loosi* was observed to be most severe in clayey ill-drained soils (Sivapalan, 1971).

Under poor soil conditions, the rate of replenishment of root damaged by nematodes is highly limited and consequently, the root system deteriorates rapidly and the uptake of nutrients is restricted and the plants soon turn out to be more "passengers". Increasing soil acidity has also been observed to aggravate the above condition (Gnanapragasam, 1987*a*).

Influence of cultural practices

Due to the large genetic variability in seedling tea fields, the pattern of distribution of nematode infestation in such fields is highly clustered. When such old fields are replanted to the genetically uniform high-yielding varieties, the spread of infestation could become more uniform, depending on the susceptibility ratings of specific cultivars.

The presence of shade trees and green manure crops amongst tea fields, which form part of the normal cropping pattern, also influence the distribution pattern and the intensity of build-up of this species of nematode (Sivapalan, 1972).

Other hosts

The presence of other hosts in the vicinity of tea fields also regulate the population levels of this species of nematode. The presence of crops, such as, *Tephrosia vogelii, Sesbania* spp., and *Acacia* spp., as well as certain weeds, increase the incidence of this nematode species in tea fields (Visser, 1959; Sivapalan, 1972; Gnanapragasam, 1985). On the other hand, grasses like Guatemala (*Tripsacum laxum*), Manna (*Cymbopogon confertiflorus*), and *Eragrostis curvula* as well as specific plants like *Tagetes* spp. help to bring down the population (Visser & Vythilingam, 1959; Hutchinson, 1962; Kerr, 1963*a*; Sivapalan, 1972; Gnanapragasam, 1981). *P. loosi* has also been encountered in the roots of *Sorghum vulgare* in Senegal (Baujard, 1986).

Disease complexes

Very limited work has been done on disease complexes involving nematodes parasitizing tea. The only report available is the occurrence of a soft root-rot disease on mature tea roots, leading to death of affected plants during dry weather. The condition of soft root-rot was reported to have been brought about by many factors, the primary one being a predisposition to infestation with *P. loosi* (Arulpragasam & Adaikkan, 1983).

Economic importance and population damage threshold levels

Detailed assessments on crop losses in tea caused by plant parasitic nematodes have been carried out almost entirely in Sri Lanka. Although *P. loosi* has been recovered from several locations, significant damage to tea has been observed mostly at elevations of 900 to 1800 m. The decline in yield in such areas has been estimated to be around 225 to 350 kg made tea/ha/annum (Gadd, 1939; Visser, 1959). Of about 80 000 ha of high elevation tea areas in Sri Lanka, approximately 30% is known to suffer obvious damage by this species of nematode. Economic losses caused could be experienced in the remaining high elevation tea areas as well, but such losses have yet not been ascertained as being chiefly due to nematodes.

It is difficult to estimate with any precision the population damage threshold of any species of nematode causing an economic loss to a given crop, as this is compounded by an interaction with other enviromental factors. In general, a tea plant that is already under stress due to other causes, readily succumbs to infestation by even a low population. However, in experiments carried out under controlled conditions in the greenhouse, the damage threshold of *P. loosi* was estimated to be 40 nematodes per 100 g soil, at 24°C., which is the mean temperature of areas between the elevation range of 900 to 1800 m (Gnanapragasam & Manuelpillai, 1984).

Pratylenchus brachyurus

Unlike *P. loosi, P. brachyurus* causes damage to only young tea (one to three year old plants). In North-East India this species has been detected in the plains of the Assam. In Queensland, Australia, where tea was planted relatively recently, this species has been found to attack tea seedlings up to the age of 12 months. Thereafter, there is no evidence of pathogenicity (O'Brian, pers.comm., 1988). A similar observation has also been made in Malawi (Corbett, 1967) and in N.E.India (Basu, 1968). The damaged plants are stunted and unthrifty and show characteristic nutrient deficiency symptoms. This nematode attacks mainly the feeder roots and occasionally the tap root as well. During its feeding activity, it moves deeply into the root tissue causing the formation of dark red lesions on the epidermal layer (Basu, 1968).

No information is available on *P. brachyurus* with regard to its interaction with enviromental factors and the various cultural practices on the degree of its pathogenicity to tea. However, it is reported that it is prevalent in sandy-loam soils and that it fails to survive in heavy clayey soils (Basu, 1968).

Meloidogyne

Meloidogyne species are the most commonly encountered nematodes in tea in the different tea growing areas of the world. Most of these species attack only the young nursery plants, whilst the mature tea becomes totally immune, with the plants developing resistance at 12 to 14 months in age. The only exception is *M. brevicauda*, which is known to attack mature tea very seriously.

Distribution

The first report of root-knot nematode infestation in young tea was from S. India, where they were found to infest large numbers of tea seedlings (Barber, 1901). In Sri Lanka, large scale failures in tea nurseries was ascribed to infestations caused by root-knot nematodes by Stuart Light in 1928. Since that time, tea has been propagated by vegetative means, rather than from seeds, and infestation of nursery plants by this species of nematode is seldom encountered. The species that are commonly encountered in seedling nurseries in Sri Lanka include, *M. incognita, M. javanica* and *M. arenaria. M. hapla* was rarely found to infest tea (Gnanapragasm, 1985).

In N. E. India, the species of *Meloidogyne* that were found to cause stunting of young seedling tea include *M. javanica, M. incognita* and *M. hapla* (Banerjee, 1967). A survey carried out in Darjeeling in 1975 showed that root-knot nematode damage was more abundant at high altitudes than at lower elevations (Basu & Roy, 1976*a*).

A survey carried out in Malawi in 1960 revealed that almost all the estate samples were infested with root-knot nematodes. As has been reported from other countries, such infested samples were all from tea nurseries, with the species including *M. incognita, M. javanica* and *M. arenaria* (Martin, 1962). In Zimbabwe, the species encountered included *M. incognita, M. arenaria* and *M. hapla* (Keetch & Buckle, 1984).

In China, the incidence of root-knot nematode damage was found to be about 90% in tea seedlings and the death rate was estimated at 40% in the seriously affected nurseries. In Yunnan Province, three species of *Meloidogyne* have been reported, *M. incognita, M. javanica* and *M. arenaria* (Yu Sheng-fu & Xia Bing, 1987). In Zhejian Province, *M. thamesi* has also been found in addition to the other three species (Huan Jin, 1984). In both these provinces, *M. incognita* was found to be more abundant than the other species.

Although *Meloidogyne* species have been encountered occasionally in tea nurseries in Bangladesh, no attempts have been made to estimate the degree of pathogenicity (Millian & Rashid, pers. comm.). *M. incognita* was the only species of root-knot nematode that has been identified from tea roots in nursery beds in Queensland, Australia. Although this species was found to affect plant growth, no specific studies have been made (O'Brian pers. comm.). In Kenya, *Meloidogyne* species have been isolated from only one farm amongst the various tea growing districts so far. However,

no attempts have been made to carry out a proper survery (Othieno, pers. comm.). *Meloidogyne* spp. have also been reported to damage young tea in Argentina (Kricun, pers. comm.).

Symptoms of damage

The species of root-knot nematodes that are known to attack only young tea plants form galls on both the tap root as well as the feeder roots. Some root-knot nematode larvae enter the roots of mature tea bushes but fail to cause giant cells and are apparently unable to complete the moult between the second and third juveniles (Gadd & Loos, 1946). Seedling plants, in which both the tap root as well as the lateral roots are severely attacked, suffer greater damage than the majority of vegetatively propagated clonal tea plants of similar age, probably because seedling plants possess less than half the root bulk of clonal plants (Kerr, 1963*a*).

Although root-knot nematodes are root feeders, the collar regions of tea seedlings have been reported to be infested occasionally with *M. incognita* in Assam, India. The females recovered from such infested locations were found to be poorly developed, although they were found to have led to the development of the characteristic galls on such affected stems (Basu, 1976).

Environmental factors affecting pathogenicity

Since species of *Meloidogyne* have been encountered in almost all tea growing regions, they seem to be well adapted to different climatic and soil conditions. Nevertheless, no detailed studies have been undertaken to correlate the influence of different environmental factors to pathogenicity, In China, the optimum soil temperature for pest incidence has been reported to be 20° to 30°C and in soils with 20% moisture (Rong *et al.*, 1984).

Other hosts

Species of *Meloidogyne* have the largest number of alternate hosts. However, since they attack only young nursery plants, the presence of alternate hosts in mature tea fields have little influence, other than when soils from such areas are used for nursery plant propagation.

Meloidogyne brevicauda

This species of root-knot nematode is the only one that attacks mature tea and has been so far recorded only in Sri Lanka, N. E. India and South India. In Sri Lanka this species has been recorded in only three plantations, all bordering the same jungle at an altitude of 1500 to 2000 m (Hutchinson & Vythilingam, 1963). In South India, it has been recorded in one estate (Venkata Ram, 1963) and in N. E. India this has been recorded only in Darjeeling (Mukherjea & Dasgupta, 1982).

Symptoms of damage

The above-ground symptoms of attack by this species of nematode resemble those brought about by the root-lesion nematode of tea. The infested bushes are stunted as a consequence of poor recovery from successive prunes, the leaves are smaller, yellowish and dull in appearance. The roots show the characteristic presence of large galls (Fig. 7), many of which display pinhole pits. It is often difficult to isolate living mature females and when found they contain only a few eggs (Loos, 1953*b*).

Biology

The average size of a mature female is about five or six times that of a mature female of *M. incognita* (Fig. 8). Despite this massive size, the females are often observed to be empty, with only a few eggs. The mean hatch per egg mass is around 10, whilst in the other common species this is in the order of 200 to 600 juveniles per egg mass (Gnanapragasam & Manuelpillai, 1981). The rest of the life history is very similar to the other species of *Meloidogyne* .

Fig. 7. Typical galling of mature tea roots caused by *Meloidogyne brevicauda*.

Environmental factors affecting parasitism

In studies carried out in controlled soil temperatures, succesful parasitism of tea plants was observed only at 12°C, whilst no parasitism was found to occur at higher temperatures (Gnanapragasam, 1988).

Other hosts

Despite an intensive survey having being carried out for several years for the possible extistence of other hosts to this species of nematode, to-date none have been found. Even the weeds checked amongst infested fields have been found to be free of this species.

Economic importance and population damage threshold

No information is yet available on damage threshold. Nevertheless, the intensity of damage and associated crop loss seems to be very much similar to that caused by *P. loosi* .

Radopholus similis

This species was first reported as a pest of tea in Indonesia, Java (Zimmerman, 1899). Steiner and Buhrer (1933) have also reported tea to be a good host to this species of nematode. The presence of this nematode in tea in Sri Lanka was first reported in 1968, when infestations were observed in young tea fields at an elevation range of 500 to 1000 m (Sivapalan, 1968).

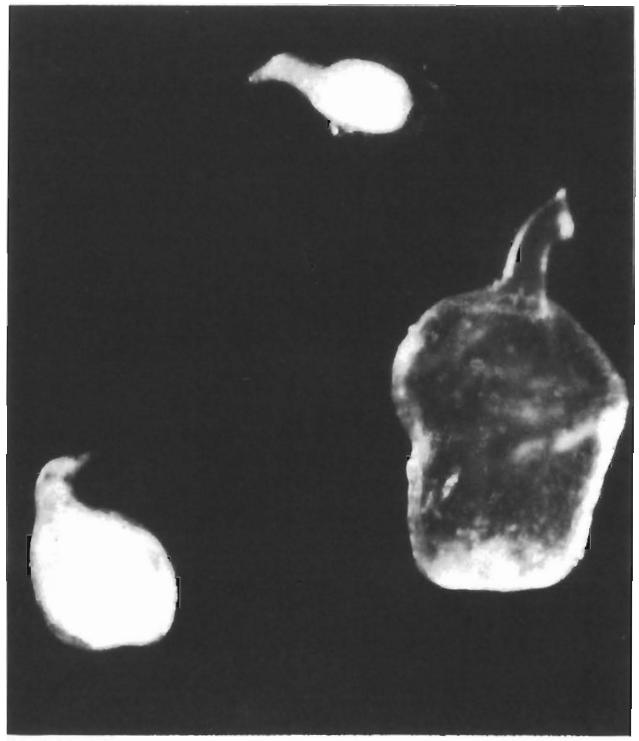

Fig. 8. Comparative size of mature females of *Meloidogyne brevicauda* (right) with females of *M. incognita* (left and above).

Recently, *R. similis* has spread to lower elevations and is known to cause damage to tea even at elevations of 200 m. Even though this species has been reported from tea in China (Chen, pers. comm.), Zimbabwe and S. Africa (Keetch & Buckle, 1984) no detailed work has yet been carried out in the latter three countries.

Symptoms of damage

Damage symptoms on tea are very similar to those brought about by *P. loosi*. Parasitised plants are stunted, with pale leaves (Plate 10c) and they go into premature flowering and fruiting, symptoms which are very characteristic of nematode damage to tea (Sivapalan, 1968).

Environmental factors

R. similis seems to be quite sensitive to cold temperatures and has a poor survival rate in tea at elevations above 1000 m. When both *P. loosi* and *R. similis* are inoculated together on to tea at high elevations, the former takes over rapidly by competitive displacement, with no trace of the latter species within a short period. However, at lower elevations, *R similis* has been observed in the rhizosphere along with *P. loosi*. *R. similis* in tea also seems to favour areas receiving high and uniform rainfall.

Means of dissemination and survival

The method of dissemination of *R. similis* in tea is very much similar to that of *P. loosi*. However, the survival rate in host-free soil is much shorter for *R. similis*.

Other hosts

Several weeds and other plants intercropped with tea were found to be suitable hosts to *R. similis*. Amongst these hosts, the most favoured ones are banana and pepper (*Piper nigrum*). The latter is commonly intercropped along with tea in the mid-elevation tea areas in Sri Lanka.

Guatemala grass (*Tripsacum laxum*), which is often used to recondition old tea fields prior to replanting, was also found to be a host to *R. similis*, contrary to the situation with *P. loosi*. *Eragrostis curvula*, marigold (*Tagetes* spp.) and *Vetiveria conyzoides*, appear to suppress soil populations of *R. similis* (Gnanapragasam, 1986).

Econonomic importance and population damage threshold

In the mid and low elevation tea areas of Sri Lanka, *R. similis* is becoming as economically important as *P. loosi* is in the high elevation tea areas. Decline amongst several newly planted young tea fields in the mid and some low elevation tea areas has been associated with moderate to heavy populations of *R. similis* .

Hemicriconemoides kanayaensis

H. kanayaensis is one of the important nematode pests of tea in Japan. It was originally detected from the roots of tea seedlings in Kanaya, Shizuoka Prefecture and described by Nakasono & Ichinohe (1961). This species has now been detected in several other tea planting districts in Japan (Takaji, 1969).

Symptoms of damage

This species of ectoparasitic nematode feeds only on the feeder roots of tea. Continuous feeding by this nematode results in the sloughing off of the root cortex, revealing a brownish discoloured stele (Takaji, 1969). Maximum populations are encountered at a depth of 30 cm (Kaneko & Ichinohe, 1963).

Biology

A single female contains 14 to 15 eggs. Oviposition studies carried out in the laboratory has shown that this takes place over a period of 15 to 20 days, during the months June/July. The ratio of juveniles to adults was found to reach a peak in July (Takaji, 1969)

Other hosts

Tea is the only reported host of this species of nematode (Takaji, 1969).

Economic importance

Large numbers of this nematode have been found to result in crop failure in tea (Takaji, 1969).

Rotylenchulus reniformis

The reniform nematode, *R. reniformis*, was first observed in tea in Indonesia (Java) in 1951, where it was found to be responsible for large-scale casualties in young tea fields (Thorne, 1961). The frequency of occurrence of this species was found to be very low in Darjeeling, when compared to other plant parasitic nematodes (Basu & Roy, 1976). In Sri Lanka, this species was first encountered in a tea nursery in Rakwana in 1960 and subsequently in 19 tea estates at low and mid-elevations, below 1200 m (Hutchinson & Vythilingam, 1963*b*). Although large numbers of nematodes were present in the root zone, no mature females could be detected and hence not much effort was made to study this pest. Surveys carried out recently have revealed that 78 amongst 342 estates were found infested by this species in the elevation range 200 to 900 m (Gnanapragasam, 1988).

Fig. 9. Young tea plant (TRI 2025) showing root damage and premature fruit setting caused by infestation with *Rotylenchulus reniformis*.

Symptoms of damage

In Sri Lanka, young plants infested with this species were found to be stunted with premature flowering and fruiting. Examination of the root system revealed that most of the feeder roots were clipped off due to feeding by this nematode (Fig. 9). Although a large number of juveniles and immature females were recovered from the root zone, no mature females have yet been recovered.

Other hosts

This species has a wide range of hosts, including several common weeds encountered in the tea plantations. Other perennial crops that are sometimes intercropped with tea, including pepper (*Piper nigrum*), coffee (*Coffea robusta*) and cloves (*Syzygium aromaticum*), as well as grass cover crops, including Guatemala (*Tripsacum laxum*). and Mana (*Cymbopogon confertiflorus*)that are planted in uprooted tea fields for a process of reconditioning, are good hosts to this species (Gnanapragasam,

1987*b*). Species of marigolds (*Tagetes* spp.) have also been reported to be suitable hosts to this nematode in India (Basu & Roy, 1976).

Economic importance

Damage by this species of nematode is often found in nursery plants and in newly planted young tea fields.

Other nematodes

Helicotylenchus

Both *Helicotylenchus dihystera* and *H. erythrinae* are commonly encountered in tea soils at all elevations in Sri Lanka (Hutchinson & Vythilingam, 1963*b*) and in Japan (Takaji, 1969). No positive evidence of pathogenicity have been reported to tea from these countries. In Queensland, Australia, *H. dihystera* have been reported to affect the growth of young tea seedlings up to 12 months old. No evidence of pathogenicity has been recorded on older plants (O'Brian pers. comm., 1988). In East Africa, this species of nematode has been reported to be the commonest nematode parasite in tea (Hainsworth, 1970). In Darjeeling, India, this species formed the bulk of the nematode fauna in tea soils at all altitudes. Soil samples collected from the rhizosphere of weak seedlings had significantly more numbers of nematode than from healthy seedlings. However, no positive evidence of pathogenicity has been demonstrated (Basu, 1967).

Paratylenchus curvitatus (Pin Nematode)

This is also one of the most commonest and most prevalent plant parasitic nematodes encountered in the rhizosphere of tea plants at all elevations in Sri Lanka (Hutchinson & Vythiligam, 1963*b*), in Japan (Kaneko & Ichinohe, 1963), and in N.E. India (Basu, 1967). Although large numbers of this ectoparasitic nematode are encountered in the root zone of both young and mature tea, no positive evidence of pathogenicity has yet been established.

Hoplolaimus, Rotylenchus

In N.E. India, these two genera have been found in the root zone of weak and stunted seedlings (Basu, 1967). These nematodes have seldom been encountered in tea soils in Sri Lanka and in locations where they have been found no correlation has been established between their occurrence and any set back to growth.

Xiphinema

Large numbers of this genus have been found in the soils of tea nurseries in N.E. India. They have been found to feed at the root tips of feeder roots resulting in slight swelling of the affected root tips. No further evidence of pathogenicity has been established in respect of this nematode (Basu, 1967).

Species of *Xiphinema* have also been reported from tea fields in S. Africa (Martin, 1962).

Control of nematode parasites in tea

In most countries, studies on the incidence and pathogenicity of nematodes in tea have been made mostly in nurseries and young tea fields. As such, methods of control have been largely confined to treatment of nursery soils. However, in countries like Sri Lanka and Japan, where plant parasitic nematodes pose a serious threat to the tea crop, various methods have been developed to mitigate their effects on the growth and productivity of tea. When adopting various measures of control in a perennial crop such as tea, the plant spacing, the manner of planting and other agronomic practices all tend to determine the economic feasibility of the adoption of the respective measures.

Cultural methods

As long as the tea plant can grow vigorously and produce fresh feeder roots to compensate for those that die prematurely on account of nematode damage, it will be able to withstand the parasitism to a significant extent. Therefore, those cultural methods that enhance growth and at the same time curtail soil populations, help sustain productivity at economic levels. Tea fields in which yields have declined, but not to uneconomic levels, benefit most from such practices.

Incorporation of organic matter

Besides helping in the retention of essential soil nutrients and the consequent better nutrient status of the tea plant, large inputs of organic matter, including dung and well decomposed plant residue, has been reported to suppress the population level of *P. loosi* (Loos, 1953*a*; Takaji, 1969).

The incorporation of specific oil cakes, such as Margosa seed cake (*Azadirachta indica*), coconut copra residue, as well as decomposed waste tea, help to curtail pathogenicity caused by the root-lesion nematode, *P. loosi* (Sivapalan, 1980; Gnanapragasam, 1984, 1987).

Soil cultivation (forking)

Soils with increasing acidity have a tendency to form a hard pan, which impedes the rate of normal replenishment of damaged and dying feeder roots. Tea plants subject to such conditions suffer most from nematode infestation. Regular forking of such soils helps to break the hard pan formation and improve soil aeration and feeder root growth. Tea fields with hard pan and heavily infested with the root-lesion nematode, *P. loosi*, have recovered remarkably following such treatments (Sivapalan, 1972).

Fertilizer applications

The provision of balanced fertilizer mixtures influence the physiological status of the plant, which in turn influences the population dynamics of plant parasitic nematodes. An unbalanced input of potash fertilizer (in proportion to increasing levels of nitrogen) was found to enhance the pathogenicity caused by *P. loosi* in tea. The reverse effect was induced by increasing the dosage of potash fertilizer, which also brought about a decline in the population level of this species of nematode (Fig. 10) (Gnanapragasam, 1982).

The type of nitrogenous fertilizer applied to tea also influenced the population dynamics of *P. loosi* in tea. Application of nitrogen in the form of urea brought about a significant suppression in the population (Sivapalan, 1980).

Cultivation of cover crops

It is customary to plant a grass cover crop for a period of two years following uprooting of old tea fields, prior to replanting with young tea. These grasses are meant to improve the physical structure of the soil, improve soil aeration and at the same time add substantial amount of organic matter that is provided through regular loppings of such grasses. The grasses used for such soil reconditioning include, Guatemala grass (*Tripsacum laxum*) and Mana (*Cymbopogon confertiflorus*), both of which suppress populations of *P. loosi* (Visser, 1959; Hutchinson, 1962; Kerr & Vythilingam, 1966).

The planting of *Eragrostis curvula* (African weeping love grass), which is planted mainly to prevent soil erosion in steep sections and in vacant areas in tea fields, has been found to suppress populations of both *P. loosi* (Gnanapragasam, 1981) and *R. similis* (Gnanapragasam, 1986*b*). This grass has also been reported to suppress populations of *Meloidogyne* sp. in tea fields in Malawi (Anon. 1960).

Planting of trap crops

The vacant areas amongst nematode-infested seedling tea fields are sometimes planted to marigolds (*Tagetes erecta* and *T. patula*)to help reduce nematode populations, prior to infilling such areas with young tea. Since marigold competes for soil moisture and nutrients, this practice is discouraged in

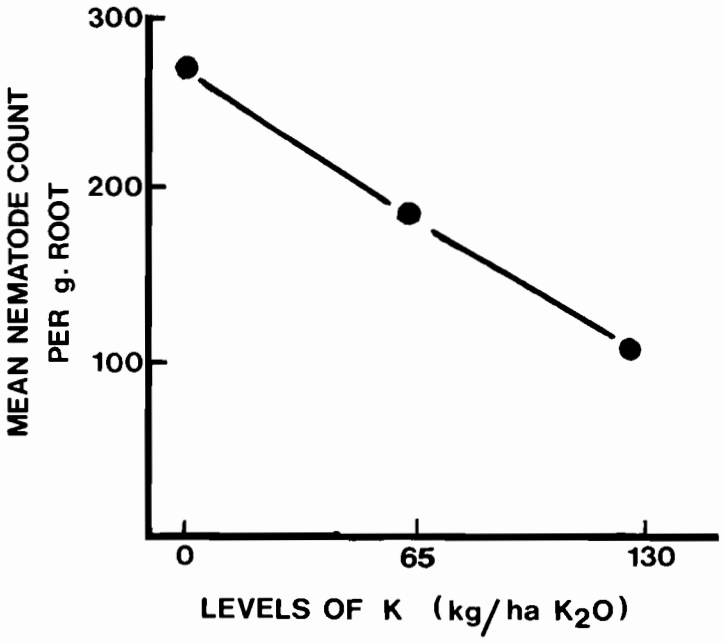

Fig. 10. Influence of potash fertilizer level on root population of *Pratylenchus loosi* in mature tea.

young tea fields (Hutchinson, 1961; Hainsworth, 1970; Sivapalan, 1972). The nematode suppressing activity of marigold is most effective only during its vegetative growth and prior to flowering.

Irrigation

Nursery plants that are irrigated with water collected from ravines that course through infested sections of tea plantations, have been found infested with nematodes (Fig. 11) (Gnanapragasam & Jebamalai, 1982). In order to circumvent this danger, it is a recommended practice to sediment irrigation water for 48 h in areas that are prone to nematode infestation.

Resting of tea fields

Tea fields are pruned regularly once every two to six years, depending on the ambient temperature of the locality. This is a drastic operation, the recovery from which is dependent on the physiological status of the plant. When the plant is subject to various forms of stress, including nematode parasitism, the affected plants recover poorly, mainly on account of low carbohydrate reserves. In order to tide over this, such fields are rested prior to pruning, for periods ranging from six to eight weeks.

Replanting old tea

Tea fields that are uneconomical for further retention are uprooted and replanted to selected tea varities with specific virtues. If such fields are known to be infested with nematodes, the removal of the old tea has to be carried out in such a manner to ensure the extraction of as many residual roots as is possible. Large root fragments left in the soil harbour nematodes in the periphery of the lesions and such populations are known to remain viable for as long as two to three years (Hutchinson, 1960*a*, 1962). It is, therefore, very necessary to ensure a thorough cleaning up of all residual roots following uprooting. Large-scale failures in newly planted tea areas have been traced to re-infestation from residual old roots (Sivapalan, 1967*b*).

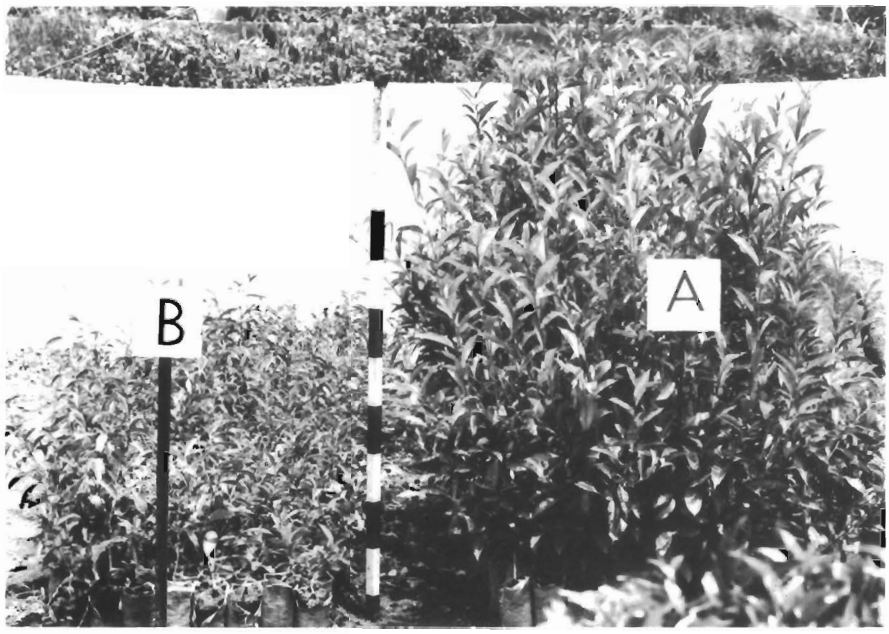

Fig. 11. Heavy infestation and stunting of nursery plants infested with nematode contaminated water (B) compared with similar age plants irrigated with clean sedimented water (A).

Physical control

The only physical control method adopted for controlling nematodes in tea is in nurseries. Nursery soil used for propagating young tea plants in India is sometimes heated by spreading the soil on galvanized sheets to temperatures ranging from 60–62°C for five minutes (Rao, 1976; Basu, 1978). This method of nursery soil treatment is not practical for large nurseries.

Resistance and tolerance

Tea clones have been assessed to have varying degrees of natural tolerance and resistance to different species of parasitic nematodes in Sri Lanka (Loos, 1953*a*; Hutchinson, 1960*b*). Large numbers of tea clones have been screened for resistance and tolerance to the root-lesion nematode of tea in Sri Lanka (Kerr & Vythilingam, 1967; Sivapalan, 1967*a*, 1972). Since of late, several clones are also being screened against *R. similis* in this country (Gnanapragasam, 1984, 1985) (Table 4).

Chemical control

In a perennial crop that is grown for as long as 50 to 60 years, chemical control generally proves to be uneconomical, since such costly treatments have to be repeated from time to time to sustain populations below economic thresholds. This form of treatment is thus confined to eradicating nematodes from nursery soils and in reducing soil populations in the field at the time of planting the young tea.

Chemical control in nurseries

Infested nursery plants are an important source of spread of nematode infestation to fields that may hitherto have been free of infestation. In areas prone to such infestation it is a routine practice to

chemically treat all nursery soils. Nursery soils are treated with fumigants such as methyl bromide,

TABLE 4. Tea clones resistant/tolerant to (A) *Pratylenchus loosi* (B) *Radopholus similis*.

(A)	TRI 62/5	TRI 3049	Balangoda MT 18
	TRI 62/7	TRI 3055	Balangoda DG 7
	TRI 62/9	TRI 3059	Coombewood CW 21
	TRI 2025	TRI 3061	Diyanilakelle DK 1
	TRI 2142	TRI 3065	Diyanilakelle DK 16
	TRI 3013	TRI 3069	Dunsinane DUN 7
	TRI 3014	TRI 3070	Kenilworth KEN 16/3
	TRI 3016	TRI/NEM 9	Mooloya MO 116
	TRI 3017	Diyagama DN	Mooloya 146
	TRI 3018	Downside DW 12	Nayabedde NAY 3
	TRI 3019	Drayton DT 1	Passara MPA 1
	TRI 3020	Drayton DT 95	Ragalla B 275
	TRI 3022	Kirkoswald K 145	Walaha WY
	TRI 3024	Norwood N 2	Waltrim WT 26
	TRI 3047	Park PK 2	
	TRI 3048	Tangakelle CY 9	
		Welimada W 1/1	
(B)	TRI 2023		
	Balangoda DG 7		
	Balangoda DG 39		
	Diyagama DN		
	Tangakelle CY 9		

DD soil fumigant and Dazomet (Kerr, 1963*b*; Akbar & Ali, 1965; Sivapalan, 1969; Nara *et al.*, 1973; Sivapalan *et al.*, 1980*a*). Following such chemical treatment, the cuttings or seeds are planted after an appropriate interval as specified for the respective chemical. In certain countries like India, granular nematicides are added to soils bearing young nursery plants (Rao, 1976; Basu, 1979; Basu & Gope, 1985).

Chemical control at planting

Despite soil rehabilitaion and minimizing residual populations in the soil and further confining replanting to those cultivars that have proven tolerance or resistance to nematode infestation, chemical treatment of planting holes, at planting time, is now being routinely practised in Sri Lanka, as a measure of insurance against a possible setback to the establishing young plants. The chemicals recommended include fenamiphos 5%G and carbofuran 3%G, at 7g per planting hole (Sivapalan, *et al.*, 1980*b*).

In Japan, pre-planting nematode control has been achieved by fumigating the planting area with ethylene dibromide or DD at 200–300 l/ha at a depth of 20 to 30 cm (Takaji, 1969).

Chemical control in mature tea

Routine chemical treatment of mature tea is an uneconomical exercise. Nevertheless, each time the tea is pruned, a significant amount of feeder roots decay and at the time of recovery from pruning, there is a significant growth of new feeder roots that are susceptible for rapid re-infestation, and this has a significant deleterious effect on the rate of recovery from prune. Therefore, in Sri Lanka, for fields that still have a high yield potential, but are subject to moderate to heavy nematode infestation, the current recommendation is to apply one application of nematicide (fenamiphos 5%G) at 10g per plant, mixed along with the first application of fertilizer following pruning of such fields (Gnanapragasam, 1987*c*).

Biological control

Very little information is available with regard to control of plant parasitic nematodes in tea by biological agents. Kaneko and Ichinohe (1963) have reported that as much as 30% reduction in the population of adult females of *H. kanayaensis* is brought about by a phycomycete fungus.

Summary of control methods

Although nematodes cannot be eradicated in a field, it is essential to reduce them below the economic damage threshold to help avert a reduction in the productivity. Any one of the above cited control methods by themselves may not be adequate to reduce the population level to that below the economic damage threshold in the field planted to young and mature tea. In Sri Lanka, the management strategy is, therefore, geared to integrate the appropriate methods of control most suited for a given environment. The most useful resources of management include; limited use of enviromentally accepted chemicals with short soil persistence; planting of nematode tolerant and resistant clones; proper soil management to maintain soil pH within the range of 4.5 to 5.0; using fertilizer mixtures enriched with potash; enriching the soil with various organic matter and cultivation of soils by regular forking.

Methods of diagnosis

As is the case with other crops, the above-ground damage symptoms on tea brought about by nematodes is often confused with similar symptoms induced by other factors that tend to restrict root growth. Positive diagnosis is made by sampling both soil and roots from affected sections.

Soil sampling

Sampling of tea soils in Sri Lanka is carried out for the three commonly encountered nematodes, *P. loosi, R. similis* and the juveniles and immature females of *R. reniformis*. Sampling is usually carried out when the soil is adequately moist and at a depth of 15 to 25 cm and at a distance of 15 cm from the base of the plant. Several samples are collected from a given field, with approximately 25 to 30 samples per two hectares. When collecting the samples, it is necessary to sample the weak as well as the moderately healthy plants, since the very weak plants carry only a small population during growth decline. It is essential to include the small root fragments that come with the soil and these should not be discarded.

Besides collecting the above species of plant parasitic nematodes, several other species of tea nematodes could also be recovered from these samples. However, for a proper sampling of *H. kanayaensis*, sampling should be done at a depth of 30 cm (Kaneko, 1963; Takaji, 1969).

Root sampling

When a newly planted young tea clearing is to be sampled for nematode infestation (young tea fields less than five years old), it is necessary to collect feeder roots from as many as 25 to 30 random points per ha. A few grammes of feeder roots will have to be collected from the rhizosphere of these respective points of sampling and bulked together to form a composite sample.

Conclusions and Future Prospects

Other than in the countries where studies on nematode problem in tea have been carried out to some depth, preliminary surveys will have to be carried out in other tea growing areas to estimate the presence of different species of nematodes and to determine the extent of pathogenicity caused by the dominant species.

In countries where intensive studies have been carried out, further work needs to be done on the role of nematodes in disease complexes, biological control methods as well as controlling these pests at the physiological level using pheromones and specific metabolic disruptors.

References

Abrego, L. (1974). Ensayos de selectividade de nematici das en el combate del *Pratylenchus coffeae* en almaciqueras de café. *Nematropica*, 4:17.

Alolami, S. O. (1981). Symptoms of root-knot nematode infectionon *Theobroma cacao* L. – A preliminary investigation 148 - 156pp. In: *Proceedings of the third research planning conference on root-knot nematodes, Meloidogyne sp. November 16–20.* Ibadan. Nigeria, 275pp.

Akbar, K. & Ali, M. A. (1965). Studies on the control of eelworms in tea nurseries: effect of fumigation with Shell DD on the population of eelworm in the soil. *Tea Journal of Pakistan*, 3:14–18.

Alvarenga, A. (1973). Determinaçâ0 preliminar da longevidade no solo, do nematóide *Meloidogyne exigua* . In: *Congresso Brasileiro de Pesquisas Cafeeiras* , IBC – GERCA (EMBRAPA), Poços de Caldas, 2:45.

Anonymous (1960) Tea Research Station, Tea Association of Nyasaland, Rhodesia *Quarterly Newsletter.* 18.

Anonymous. (1966). India Coffee Board. (26th). Bangalore, 199p.

Anonymous. (1968). *Principles of plant and animal pest control* . Vol. 4 – Control of plant parasitic nematodes. National Academy of Sciences. Publ. N° 1696. Washington, D.C. 172p.

Anonymous. (1974). India Coffee Board. 33rd Annual Report 1972–1973 (1st April 1972 to 31st March 1973). Bangalore, India XXIV + 269p.

Anonymous. (1977). Kenya Coffee Research Foundation. Annual Report 1975–1976. Ruiru. 131p.

Anonymous. (1985). Instituto Brasileiro do Café. Cultura do Café no Brasil. Setor de programação visual e gráfica (IBC/GERCA). 580p.

Aragon, B. C. A. Gomes, M. B. & Caicedo, J. E. (1978). Plantas de la zona cafetera colombiana hospedantes de espécies de *Meloidogyne* Goeldi, 1887. *Cenicafé*, 29:35–45.

Arulpragasam, P. V. & Adaikkan, S. (1983). Soft-root-rot. A new disease of tea? *Tea Quarterly* , 52:52–55.

Ayala, A. (1976). State of knowledge of *Meloidogyne* in Puerto Rico. In: *Proceedings of the Regional Conference of the International Meloidogyne Project* . Regional I, Panamá: 93–95.

Bally, W. & Reydon, G. A. (1931). De tegenwoordige stand van het Vraagstuk van de Wortelaaltjes in de Koffiecultur. *Archf Voor de Koffiercultur, Indonesie,* 2:23–216

Banerjee, B. (1967). Eelworm as soil-borne pests of tea. *Proceedings of the 23rd Tocklai Conference.* 1–8.

Barber, C. A. (1901). A Tea Eelworm diseasse in S. India. *Tropical Argiculturist*, 21 p.238.

Barriga, R. (1976). Reports by regional investigators: B. South America. In: *International Meloidogyne Project. Proceedings of the research planning conference on root knot nematodes Meloidogyne spp* . N.C.S.U. USA: 7–9

Basu, S. D. (1967). Eelworm in tea: some important groups. *Two & A Bud*, 14:84–85.

Basu, S. D. (1968). Eelworms – A Progress Report on a few more groups found in N. E. Indian Tea Soils. *Two & A Bud*, 15:70–71.

Basu, S. D. (1976) Root-knot nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood on stem of tea, seedling. *Two & A Bud*, 23:23.

Basu, S. D. (1978). Heat the soil and kill nematodes. *Two & A Bud*, 25:42.

Basu, S. D. (1979). Control of *Meloidogyne incognita* on tea seedlings with some systemic nematicides. *Indian Journal of Nematology*, 9:84.

Basu, S. D. & Gope, B. (1985). Control of root-knot nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood on tea seedlings with some systemic nematicides. *Two & A Bud* , 32:32–35.

Basu, S. D. & Roy, S. K. (1976*a*). Preliminary Note on Nematode survey in Darjeeling. *Two & A Bud.*, 23:58.

Basu, S. D. & Roy, S. K. (1976*b*). A new ectoparasitic nematode in tea soils. *Two & A Bud*, 22 :17.

Baujard, P. (1986). Ecologie des nématodes dans le bassin arachidier du Sénégal. *Revue de Nématologie 9* :288.

Braudeau, J. (1970). El Cacao. Editorial Blume, Barcelona. 297p.

Bridge, J. (1984). Coffee nematode survey of Tanzania. Report on a Visit to Examine Plant Parasitic Nematodes of Coffee in Tanzania, February/March 1984. Commonwealth Institute of Parasitology, 22p.

Bridge, J. (1988). Plant parasitic nematode problems in the pacific islands. *Journal of Nematology*, 20:173–183.

Bridge, J. & Page, S. L. J. (1984). Plant nematode pests of crops in Papua New Guinea. *Journal Plant Protection in the Tropics* ,1:99–109,

Bridge, J., Page, S. L. J. & Waller, J. M. (1982). Plant parasitic nematodes and diseases of crops in the Santa Cruz department of Bolivia. U.K. Overseas Development Administration Report. 60p. (Printed materials).

Campos, V. P. & Lima, R. D. (1986). Nematoides parasitas do cafeeiro. In: Rena, A.B.; Malavolta, E.; Rocha, M. & Yamada, T. (Eds). *Cultura do Cafeeiro, fatores que afetam a produtividade* . Associação Brasileira para Pesquisa da Potassa e do Fosfato. Piracicaba, SP. Brazil: 379–389.

Campos, V. P.; Lima, R. D. & Almeida, V. F. (1985). Nematoides parasitas do cafeeiro. *Informe Agropecuário Belo Horizonte,* 11:50–58.

Campos, V. P.; Lima, R. D. & Almeida, V. F. (1987). Nematóides parasitas de grandes culturas identificado em lo calidades de Minas Gerais e São Paulo. *Nematologia Brasileira*, 11:226–232.

Campos, V. P. & Melles, C. C. A. (1987). Ocorrência e distribuição de espécies de *Meloidogyne* em cafezais dos Campos das Vertentes e do Sul de Minas. *Nematologia Brasileira*, 11:233–241.

Campos, V. P. & Resende, I. C. (1988). Efeito de nematicidas no ciclo de vida de *Meloidogyne exigua* em mudas de café (*Coffea arabica*). *Ciência e Prática.* (In press).

Campos, V. P.; Resende, I. C. & de Faria, M. A. (1988). Flutuação populacional de *Meloidogyne exigua* em cafezais tratados com nematicidas. *Fitopatologia Brasileira*.(In press).

Carneiro, R. G. & Carneiro, R. M. D. G. (1982*a*). Levantamento preliminar dos nematóides do gênero Meloidogyne associados á cultura do café no norte do Paraná, no período de 1978 a 1980. *Nematologia Brasilieira* , 6:133–139.

Carneiro, R. G. & Carneiro, R. M. D. G. (1982*b*). Seleção preliminar de plantas para rotação de culturas em áreas infestadas por *M. incognita* nos anos de 1979 e 1980. *Nematologia Brasileira*, 6:141–148.

Caveness, F. E. (1967). Nematology studies 1960/1965. Ministry of Agriculture and Natural Resources. US AID project, Lagos, Nigeria, 135pp.

Chevalier, A. (1947). *Lés caféiers du globe. III. Systématique des caféiers et faux-caféiers, maladies et insectes nusibles,* Encyclopédie Biologique no. 28. Paris, Paul Lechevalier. 356p.

Chitwood, B. G. & Berger, C. A. (1960). Preliminary report on nemic parasites of coffee in Guatemala with suggested and interim control measures. *Plant Disease Reporter,* 44:841–847.

Corbett, D. C. M. (1961). *Report of Department of Agriculture 1959/1960. Part II. Nyasaland:* 157–158.

Corbett, D. C. M. 91967). Nematodes as plant parasites in Malawi. *PANS*, 13:151–162.

Cotterel, G. S. (1930). *Bulletin Department of Agriculture, Accra Gold Coast*, 22p.

Curi, S. M. (1973). Novas observações sobre um nematóde do cafeeiro. *O Biológico*, 39:209–207.

Curi, S. M.; Carvalho. A.; Moraes, F.P.; Monaco, L.C. & Arruda, H.V. de (1970). Novas fontes de resistência genética de *Coffea* no controle de nematóde do cafeei ro, *Meloidogyne exigua*. O Biológico , 36:293–295.

Curi, S. M.; Monteiro, L. G. E.; de Bona, A. de & Cintra, A. F. (1969). Levantamento do nematóide do cafeeiro *Meloidogyne coffeicola* no estado de São Paulo. *O Biológico*, 35:41–44.

Curi, S. M.; Silveira, S. G. P. da & Elias Jr., E. G. (1977). Resultados de produção e da proteção do sistema radicular de cafeeiros sob controle quíco do nematóide *Meloidogyne incognita* (Kofoid & White, 1969) Chitwood 1949, em condiçõe̊s de campo. *Nematologia Brasileira*, 2:93–99.

D'Antonio, A. M.; Libeck, P. R.; Coelho, A. J. E. & Paula, V. de. (1980). Levantamento de nematóides parasitas do cafeeiro que ocorrem no sul de Minas Gerais. In: *Congresso Brasileiro de Pesquisas Cafeeiras, Campos do Jordão*. Rio de Janeiro, IBC/GERCA: 440.

D'Souza, G. I. & Screenivasan, C. S. (1965). A note on the reniform nematode *Rotylenchulus reniformis* , on arabica coffee in South India. *Indian Coffee*, 29:11–13.

Edwards, E. E. (1955). Further observations in the occurrence of nematodes of the genus *Meloidogyne* in Gold Coast. *Journal of helminthology*, 29:153–170.

Elmiligy, I. A. (1968). Three new species of the genus *Meloidogyne*. Goeldi, 1887. (Nematoda:Heteroderidae). *Nematologica*, 14:577–590.

Fazuoli, L. C. (1986). Genética e melhoramento do cafeeiro. In: Rena, A.B.; Malavolta, E.; Rocha, M. &

Yamada, T. (Eds). *Cultura do cafeeiro, fatores que afetam a produtividade.* Associação Brasileira para Pesquisa da Potassa e do Fosfato. Piracicaba, SP. Brazil: 87–113.

Ferraz, E. (1979). Nematódes do cacueiro. *IV Curso Internacional de Cacau. Centro de Pesquisa do Cacau. Itabuna, BA, Brazil*, 24p.

Figueroa, A. (1978). Efectos de Carbofuran 5G en la productividade del café Caturra. *Nematropica*, 8:26–33.

Figueroa, A. & Perlazo, F. (1982). Investigacion sobre *Meloidogyne* en Costa Rica. In: *Proceedings of the third Research & Planning Conference on Root-Knot Nematodes, Meloidogyne spp.* January 11–15, Region I: 12–25.

Flores, J. M. & G. Yépez T. (1969). *Meloidogyne* in coffee in Venezuela. In: Peachey, J. E. (Eds). *Nematodes of Tropical Crops.* Technical Communication n° 40. Commonwealth Bureau of Helminthology St. Albans, Herts. England: 251–256.

Fluitter, H. J. & Mulholland. J. J. (1941). Gegevens, Verkregen biji het onderzoek naar de waardplanten van *Tylenchus coffeae. Bergcultures,* 15:1588–1593.

Food and Agriculture Organization of the United Nations (1986). FAO Statistics series no. 76. FAO Production Yearbook. Rome. Vol. 40.

Gadd, C. H. (1939). A destructive root disease of tea caused by the nematode, *Anguillulina pratensis. Tea Quarterly, 12*: 131–139

Gadd, C. H. & Loos C. A. (1946). The problem of nematode control in tea plantations. *Tea Quarterly* 18:3–11.

Ghesquiere, J. (1921). Nouveaux parasites du cacoyer. Maladie vermiculire du cacaoyer *Tylenchus (Heterodera) radicicola).* Greef.] et relation aves la maladie du *Diplodia. Bullentin de e Agriculture,* 12:709–718.

Gnanapragasam, N. C. (1981). The influence of cultivating *Eragrostis curvula* in nematode infested soil, on the development on the subsequent build-up of populations in replanted tea. *Tea Quarterly*, 50:160–162.

Gnanapragasam, N. C. (1982). Effect of potassium fertilization and of soil temperature on the incidence and pathogenicity on the root-lesion nematode, *Pratylenchus loosi* Loof on tea *Camellia sinensis* L). *Tea Quarterly*, 51:169–174.

Gnanapragasam, N. C. (1984) *Report on the Tea Research Institute of Sri Lanka* – 1984, 67–75.

Gnanapragasam, N. C. (1985). *Report on the Tea Research Institute of Sri Lanka* – 1985, 82–96.

Gnanapragasam, N. C. (1986) *Report on the Tea Research Institute of Sri Lanka* – 1986, 69–78.

Gnanapragasam, N. C. (1987*a*) Effect of soil acidity on the population levels of *Pratylenchus loosi, International Nematology Network Newsletter* 4:23–24.

Gnanapragasam, N. C. (1987*b*). *Report of the Tea Research Institute of Sri Lanka* – 1987: 70–83.

Gnanapragasam, N. C. (1987*c*. Integratede strategies to manage nematodes in tea. *Proceedings of the International Conference on Tea Quality & human Health.* China (Hangzhou), November, 1987: 117–183.

Gnanapragasam, N. C. (1988). Limitation on growth and productivity of tea by plant parasitic nematodes. *Proceedings of the Regional Tea Scientific Conference, Sri Lanka* (In Press.)

Gnanapragasam, N. C., Ariaratnam, V. & Navaratne, N. (1987). *Rotylenchulus reniformis*, the new nematode species causing damage to tea in Sri Lanka. *Tea Bulletin*, 7:34–39

Gnanapragasam, N. C. & Jebamalai, A. S. (1982). Nematode infestation of nursery plants through irrigation water. *Tea Quarterly*, 51:31–33.

Gnanapragasam, N. C. & Manuelpillai, M. E. K. (1981). Relative rates of egg hatch of the root-knot nematode of mature tea, *Meloidogyne brevicauda,* in relation to other species of the nematode. *Tea Quarterly,* 50:160–162.

Gnanapragasam, N. C. & Manuelpillai, M. E. K. (1984). Influence of inoculum level and temperature on the population build-up and pathogenicity of the root-lesion nematode *Pratylenchus loosi* Loof of tea. *Tea Quarterly.*, 53:19–22.

Göldi, E. A. (1889). Der kaffeenematode Brasiliens (*Meloidogyne exigua* G.). *Zoologische Jahrbücher, Abt. Systematik R*, 4:261–267.

Göldi, E. A. (1892). Relatório sobre a moléstia do cafeeiro na Província do Rio de Janeiro. *Archivos do Museu Nacional Rio de Janeiro* , 8 (1987): 7–123.

Gomez, J. (1980). Resultados preliminares sobre distribuição de fitonematodes en la zona cafetera de los departamentos de Caldas, Risaralda y Quindio en Colombia. *Nematropica* , 10:67.

Gonçalves, W. & Ferraz, L. C. B. (1987). Resistência do cafeeiro à nematóides II. Testes de progênies e híbridos para *Meloidogyne incognita* raça 3. *Nematologia Brasileira*, 9:125–142.

Gonçalves, W.; Thomaziello, R. A.; Moraes, M. V.; Fernandes, J. A. E.; Costa, A. M.; Corsi, T.; Jungueira, C. A. & Lacerda, L. A. O. (1978). Estimativas de danos ocasionados pelos nematóides do cafeeiro. In: *6º Congresso Brasileiro de Pesquisas Cafeeiras de Ribeirão Preto, São Paulo*. Brazil – IBC/GERCA: 182–186.

Guerra Neto, E. G. & D'Antonio, A. M. (1984). Nematóides parasitas em lavouras cafeeiras do sul de Minas Gerais. In: *11º Congresso Brasileiro de Pesquisas Cafeeiras, Londrina*. IBC/GERCA: 171.

Guerra Neto, E. G.; D'Antonio, A. M.; Almeida, S. R. & Lordello, L. G. E. (1983). Ocorrência do nematóide *Meloidogyne coffeicola* Lordello & Zamith, 1960, em lavouras de café no sul do estado de Minas Gerais. *Revista de Agricultura*, 58:45–48.

Gutierrez, G. & Jimenez, Q. M. F. (1970). Algumas observaciones sobre la infestacion del cafe practicada en Guatemala y El Salvador como medio para el control de nematodes. *Revista Cafetera, Guatemala*, 98:35–47.

Hainsworth, E. (1970). Tea. *J. Tea Boards E. Africa*, 11:15–17.

Huan Jin (1984). The identification of some species of root-knot nematodes (*Meloidogyne*) on tea seedlings in Zheijiang Province. *Acta Zheijiang Ag. University*, 9:343–350.

Huang, S. P.; Resende, I. C.; Souza, P. E. de & Campos, V. P. (1983). Effect of aldicarb, ethoprop and carbofuran on control of coffee root-knot nematode, *Meloidogyne exigua. Journal of Nematology*, 15:510–514.

Hutchinson, M. T. (1960a). Nematode samples from estates. *Tea Quarterly.*, 31:116–118.

Hutchinson, M. T. (1960b). Resistance and tolerance of tea to nematodes. *Tea Quarterly.*, 31:13–18.

Hutchinson, M. T. (1962). Rehabilitating tea soils – susceptibility of plants now in use to the root-lesion nematode, *Pratylenchus loosi. Tea Quarterly*, 33:138–14.

Hutchinson, M. T. & Vythilingam, M. K. (1963a). The distribution of *Pratylenchus loosi* among tea estates in Ceylon, with particular reference to altitude. *Tea Quarterly*, 34:68–84.

Hutchinson, M. T. & Vythilingam, M. K. (1963b). Distribution of plant parasitic nematodes in the soils of tea estates in Ceylon. *Tea Quarterly.*, 34:119–126.

Hutton, D. G.; Eason-Heath, S. A. E. & Coates-Beckford, P. L. (1982). Control of *Meloidogyne incognita* affecting coffee. In: *Proceedings of the third Research & Conference on Root-Knot Nematodes Meloidogyne spp.*, January 11–15, Region I: 109–113.

Jaehn, A. (1984). Viabilidade do uso de nematicidas em cafezal novo, instalado em solo infestado por *Meloidogyne incognita. Nematologia Brasileira*, 8:275–283.

Jaehn, A. & Rebel, E. K. (1984). Sobrevivência do nematóide de galhas *Meloidogyne incognita* em substrato infestado, para produção de mudas de cafeeiros sadios. *Nematologia Brasileira*, 8:319–324.

Jaehn, A.; Rebel, E. K. & Lordello, L. G. E. (1980). A origem do nematóide *Meloidogyne coffeicola. Nematologia Brasileira*, 4:159–161.

Jaehn, A.; Rebel, E. K. & Matiello, J. B. (1984). Viabilidade de recuperação de mudas de cafeeiro infestadas por *Meloidogyne incognita* através de nematicidas. *Nematologia Brasileira*, 8:295–300.

Jiménez-Saenz, E. (1971). Relacion entre el ataque de nemátodos y la muerte súbita del cacao (*Theobroma cacao* L.) en Bahia, Brasil. *Turrialba*, 19:225–260.

Jobert, C. (1878). Sur une maladie du caféier observée au Brésil. *Comptes-Rendus de la Societé de Biologie, Paris*, 87:941–943.

Kaneko, T. & Ichinohe, M. (1963). Notes on the nematode species and their bionomics associated with tea roots in Japan. *Japanese Journoul of Applied Entompology & Zoology*, 7:165–174.

Keetch, D. P. & Buckle, N. H. (1984). A check list of the plant parasitic nematodes of Southern Africa. *Technical. Communication No. 195. Department of Agricultral Report of S. Affrica.*

Kerr, A. (1963a). *Report of Tea Research Institute of Ceylon* – 1963:95–102.

Kerr, A. (1963b). Fumigation of nursery soils. *Tea Quarterly*, 34:150–151.
Kerr, A. & Vythilingam, M. K. (1966). Replanting eelworn infested areas. *Tea Quarterly*, 37:67–72.
Kerr, A. & Vythilingam, M. K. (1967). Resistance of tea clones and seedlings to the root-lesion eelworm (*Pratylenchus loosi*). *Tea Quarterly.*, 38:42–51.
Krug, C. A. (1969). *Estudio Mundial del Cafe*. FAO: Estudios Agropecaurios nº 76. Organizacion del las Naciones Unidas para la Agricultura y la Alimentacion. 507p.
Kumar, A. C. (1982). Evaluation of Nemacur 5G against the coffee root-lesion nematode, *Pratylenchus coffeae*. *Journal of Coffee Research*, 12:1–7.
Kumar, A. C. (1984). Resistance in coffee to *Meloidogyne* spp. and occurrence of intersexes in *M. thamesi*. *Nematologica*, 30:108–110.
Kumar, A. C. & Viswanathan, P. R. K. (1972). Studies on physiological races of *Pratylenchus coffeae*. *Journal of Coffee Research*, 2:10–15.
Lima, R. A.; Campos, V. P.; Huang, S. P. & Melles, C. A. A. (1985). Reprodutividade e parasitismo de *Meloidogyne exigua* em ervas daninhas que ocorrem em cafezais. *Nematologia Brasileira*, 9:63–72.
Lima, R. D. (1984). Embriogenese, desenvolvimento pósembriogênico e caracterização morfométrica de *Meloidogyne exigua*, Goeldi, 1887. Viçosa, MG, UFV. (MS Thesis).
Loof, P. A. A. & Sharma, R. D. (1980). *Discocriconemella* species from Bahia state, Brazil (Nematoda: Criconematidae). *Mededelingen Fakulteit Landbouwwetenschappen Rijksunivérsiteit*. Gent, 45:795–805.
Loos, C. A. (1951). Pathological problems. *Tea Quarterly.*, 22:27–30.
Loos, C. A. (1953*a*) Eelworms *Tea Quarterly.*, 24:34–38.
Loos, C. A. (1953b). *Meloidogyne brevicauda* n. sp. a cause of root-knot nematode of mature tea in Ceylon. *Proceedings of the helminthological Society of Washington*, 20:83–91.
Lordello, L. G. E. (1964). Contribuição ao conhecimento dos nematóides que causam galhas em raízes de plantas em São Paulo e estados vizinhos. *Anais Escola Superior de Agricultura Luiz de Queiroz*, 21:181–218.
Lordello, L. G. E. (1967). O nematóide coffeicola inváde São Paulo. *Revista de Agricultura*, 42:162.
Lordello, L. G. E. (1968). Nematoides associados a uma doença do cacaueiro. *Revista de Agricultura, Piracicaba (Brazil)*, 43:154.
Lordello, L. G. E. (1972). Nematode Pests of Coffee. In: Webster, J. M. (Ed.). *Economic Nematology*. Academic Press, London & New York: 268–282.
Lordello, L. G. E. (1980). Estado atual do nematóide reniforme como parasita do cafeeiro. *Revista de Agricultura, Piracicaba, Brasil*, 55:62.
Lordello, L. G. E. (1982). Nova ocorrência do nematóide *Meloidogyne hapla* em cafeeiro. *Revista de Agricultura, Piracicaba, Brasil*, 57:6.
Lordello, L. G. E. (1984). *Nematóides das plantas cultivadas*. 8º Edição. Livraria Nobel S. A. 314p.
Lordello, L. G. E.; Carneiro Filho, I.; Rebel, E. K.; Guidolin, J. A. & Lordello, R. R. A. (1974). Identificação de nematóides em cafezais do estado do Paraná. *Nematologia Brasileira*, 1:16–24.
Lordello, R. R. A. & Fazuoli, L. C. (1980). *Meloidogyne decalineata* parasita cafeeiro na ilha de São Tomé. *Revista de Agricultura, Piracicaba, Brasil*, 55:238.
Lordello, L. G. E. & Hashizume, H. (1971). Suscetibilidade da variedade Kouillon de *Coffea canephora* a um nematóide. *Revista de Agricultura*, 46:157–158.
Lordello, L. G. E. & Lordello, R. R. A. (1972). *Meloidogyne incognita* ataca cafeeiro no Paraná. *O Solo*, 64:27.
Lordello, L. G. E. & Lordello, R. R. A. (1972). Duas plantàs hospedeiras novas do nematóide *Meloidogyne coffeicola*. *Anais da Escola Superior de Agricultura Luiz de Queiroz*, 29:61–62.
Lordello, L. G. E. & Mello Filho, A. T. (1969). O capim pangola difunde nematóides. *Revista de Agricultura, Piracicaba*, 44:122.
Lordello, L. G. E. & Mello Filho, A. T. (1970). Mais um nematóide ataca o cafeeiro. *Revista de Agricultura*, 45:102.
Lordello, L. G. E.; Monteiro, A. T. & D'Arce, R. D. (1968). Distribuição geográfica dos nematóides nocivos do cafeeiro. *Revista de Agricultura*, 43:79–82.

Lordello, L. G. E. & Zamith, A. P. L. (1960). *Meloidogyne coffeicola* sp. n., a pest of coffee trees in the state of Paraná, Brazil, (Nematoda, Heteroderidae). *Revista Brasileira de Biologia*, 20:375–379.

Luc, M. & de Guiran, G. (1960). Les nématodes associés aux plantes de l'Ouest Africain. Liste préliminaire. *L'Agronomie Tropicale Nogeut*, 15:434–449.

Macedo, M. C. M. (1974). Suscetibilidade de cafeeiros ao nematóide reniforme. *Solo*, 66:15–16.

Martin, G. C. (1960). Plant parasitic nematodes associated with tea production in the southern province of Nyasaland. *Proceedings of first Inter-African Plant Nematology Conference I.A.P.S.C. Publ.* 86.

Martin, G. C. (1961). Plant species attacked by root-knot nematodes (*meloidogyne* spp) in the Federation of Rhodesia and Nyasaland. *Nematologica*, 6:130–134.

Martin, G. C. (1962). Population levels of nematodes in roots and soil around the root zone of tea, sugar cane, tobacco and wheat grown in the Federation of Rhodesia & Nyasaland. *Rhodesia Agricultural Journal*, 62:28–35.

Medina Filho, H. P.; Fazuoli, L. C. & Costa, W. M. da (1981). Identificação das raças 2, 3 e 4 de *Meloidogyne incognita* parasitando cafeeiros. In: *Nono Congresso Brasileiro de Pesquisas Cafeeiras, São Lourenco, MG:* 161–168.

Mendes, B. V. (1977). Observações histopatholófgicas de raízes de cafeeiros parasitadas por Meloidogyne exigua Goeldi, 1887. *Nematologia Brasileira*, 2:207–229.

Monteiro, A. R. & Lordello, L. G. E. (1974). Encontro do nematóide *Pratylenchus coffeae* atacando cafeeiro em São Paulo. *Revista de Agricultrua, Piracicaba*, 49:164.

Moraes, M. V. de & Lordello, L. G. E. (1977). Estudo de três populações de nematóides nocivos ao cafeeiro. *Nematologia Brasileira*, 2:249–255.

Moraes, M. V.; Lordello, L. G. E.; Lordello, R. R. A. & Piccinin, O. A. (1973). Novas pesquisas sobre plantas hospedeiras do nematóide do cafeeiro, *Meloidogyne exigua* Goeldi, 1887. *Anais da Escola Superior de Agricultura Luiz de Queiroz*, 30:71–75.

Moraes, M. V.; Lordello, L. G. E.; Piccinin, O. A. & Lordello, R. R. A. (1972). Pesquisas sobre plantas hospedeiras do nematóide do cafeeiro *Meloidogyne exigua* Goeldi, 1887. *Ciência e Cultura*, 24:628–660.

Moraes, M. V. de; Lordello, L. G. E.; Piccinin, O. A. & Lordello, R. A. (1973*a*). Suscetibilidade de cafeeiros ao ataque por um nematóide. *Nematologia Mediterranea*, 2:107–110.

Moraes, M. V.; Lordello, L. G. E.; Reis, A. J.; Thomaziello, R. A. & Gonçalves, W. (1977*b*). Ensaio de rotação de culturas para reaproveitamento com cafeeiros de terras infestadas por *Meloidogyne exigua. Nematologia Brasileira*, 2:257–265.

Moraes, M. V.; Thomaziello, R. A.; Lordello, L. G. E. & Krinski, J. (1977). Ensaios de tratamento de solo por produtos químicos para uso em viveiro de café. *Nematologia Brasileira*, 2:231–244.

Mukerjea, B. & Dasgupta, M. K. (1982). Community analyses of plant-parasitic nematodes in tea plantations in W. Bengal. *Nematologia mediterranea*, 10:1–7.

Nakasono, K. & Ichinohe, M. (1961). *Hemicriconemoides kanayaensis* n.sp associated with tea roots in Japan (Nematoda: Criconematidae). *Japanese Journal of applied Entomology and Zoology*, 5:273–276.

Nara, J., Wargadipura, R., Sukandis, K. Ruswanda. (1973). The efficacy os several nematicides in the soil media of tea cutting nurseries. *Menara Perkebunan Batania*, 4:297–301.

Nickle, W. R. (1984). *Plant and Insect Nematodes*. New York & Basel. Marcel Dekker, Inc. 925p.

Palanichamy, L. (1973). Nematode problems of coffee in India. *Indian Coffee*, 37:99–100.

Pinochet, J. & Raski, D. J. (1976). *Discocriconemella repleta* n.sp. and the male of *Criconemoides inusitatus* Hoffmann, 1974 (Criconematidae: Nematoda). *Journal of Nematology*, 8:327–330.

Ponte, J. J. (1977). Nematóides das galhas: espécies ocorrentes no Brasil e seus hospedeiros. Coleção Mossoroense, ESAN, RN. 99p.

Ponte, J. J. & de Castro, F. E. (1975) Lista adicional de plantas hospedeiras de nematóides das galhas, *Meloidogyne* spp. no estado do Ceará (Brasil) referente a 1969/74. *Fitossanidade*, 1:29–30.

Rahm, G. (1929). Nematóides parasitas e semiparasitas de diversas plantas cultivadas no Brasil. *Archivos do Instituto Biológico*, 2:67–137.

Rao, G. N. (1976). Control of nematodes in nursery soils. *Planters' Chronicle. S. India*, 7:257–259.

Raski, D. J.; Jones, N.O.; Hafez, S. L.; Kissler, J. J. & Luvisi, D. A. (1981). Systemic nematocides tested as alternatives to DBCP. *California Agriculture*, 35:10–12.

Rong, W. Z., Juan, J. & Zheng, K. S. (1984). Study of Tea seedling disease caused by root-knot nematode, Meloidogyne spp. *Acta.Phytopathologica Sinca*, 14:225–232.

Sabrego, L. (1971). Nematodes, problem in coffee plantations of El Salvador. *Nematropica*, 1:1.

Salas, L. A. & Echandi, E. (1961). Parasitic nematodes in coffee plantations of Costa Rica. *Coffee*, 3:6–9.

Schieber, E. (1971). The nematode problems of coffee in Guatemala. *Nematropica*, 1:17.

Schieber, E. & Grullon, L. (1969). El problema de nematodos que atacam el café (*Coffea arabica* L.) en la Republica Dominicana. *Turrialba*, 19:513–517.

Sharma, R. D. (1971). Nematode associated with cacao and rubber in Bahia, Brazil. *Revista Theobroma* (Brazil), 1:43–45.

Sharma, R. D. (1973). Plant parasitic nematodes in the São Francisco Valley, Pernambuco, Brazil. *Nematropica*, 3:51–54.

Sharma, R. D. (1975). Effect of partial soil sterilization on the growth of the cacao (*Theobroma cacao* L.) seedling in the nursery. Arquivos do Instituto Biológico, São Paulo, Brazil, 42:23–30.

Sharma, R. D. (1979). Informe técnico – Setor de nematologia 56–60. CEPEC-CEPLAC, Itabuna, Bahia, Brazil.

Sharma, R. D. (1982). Nematodes associated with cocoa hybrids and clones in Bahia, Brazil. *Nematologia Brasileira*, 6:85–91.

Sharma, R. D. & Ferraz, E. C. A. (1977). Eficácia de nematicidas sistêmicos e não sistêmicos no controle aos nematóides fitoparasitas associados a mudas de cacaueiro. *Nematologia Brasileira*, 2:139–147.

Sharma, R. D. & Loof, P. A. A. (1974). Nematódes of the cocoa region of Bahia, Brazil. III – Plant Parasitic and free-living nematodes in the rhizospheres of six different plant species. *Revista Theobroma*, 4:39–43.

Sharma, R. D. & Maia, M. A. Z. (1976). Pathogenicity of the root-knot nematode *Meloidogyne incognita* on cocoa. *Revista Theobroma*. 6:56–65.

Sharma, R. D. & Sher, S. A. (1973*a*). Nematodes associated with coffee in Bahia, Brazil. *Archivos do Instituto Biológico de São Paulo*, 40:131–135.

Sharma, R. D. & Sher, S. A. (1973*b*). Nematodes of the cocoa region of Bahia, Brazil. II. Occurrence and distribution of plant parasitic nematodes associated with cocoa (*Theobroma cocao* L.). *Revista Theobroma*, 3:17–24.

Sharma, R. D. & Sher, S. A. (1974). Nematoides da região cacaueira do Espírito Santo, Brasil. I. Nematoides associados ao cacaueiro (*Theobroma cacao* L.). *Revista Theoborma*, 4:26–31.

Sivapalan, P. (1967*a*). Nematodes and Tea. *Tea Quarterly*, 38:178–185.

Sivapalan, P. (1967*b*). Nematode problems in tea. *Tea Quarterly*, 38:260–268.

Sivapalan, P. (1968). Association of *Radopholus similis* with decline in young tea fields. *Plant Disease Reporter*, 52:528.

Sivapalan, P. (1971). The effects of infestation by *Pratylenchus loosi* and of soil fumigation on the growth of young tea plants in different soil types. *Tea Quarterly*, 42:131–137.

Sivapalan, P. (1972). Nematode Pests of Tea. In Webster, J. M. [Ed.]: *Economic Nematology*. New York & London Academic Press: 285–310.

Sivapalan, P. (1980). *Report of Tea Research Institute of Sri Lanka* – 1980:83–96.

Sivapalan, P. & Gnanapragasam, N. C. (1975). The effect of soil temperature and infestation by *Pratylenchus loosi* on the growth and nutrient status of a susceptible variety of young tea (*Camellia sinensis* L.). *Tea Quarterly*, 45:29–35.

Sivapalan, P., Gnanapragasam, N. C. & Jebamalai, A. S. (1980*a*). Treatment of nursery soils with Dazomet 98% G (Basamid) as an alternative method of control of the root-lesion nematode, *Pratylenchus loosi* in new plantings. *Tea Quarterly*, 49:134–136.

Sivapalan, P., Gnanapragasam, N. C. & Jebamalai, A. S. (1980*b*). Chemical control of the root-lesion nematode, *Pratylenchus loosi* in new tea plantings. *Tea Quarterly*, 49:30–36.

Sosamma, V. K., Koshy, P. K. & Sundararaju, P. (1980*a*). Nematodes associated with cacao – A review. *Plant*

Protection Committee for the South East Asia and Pacific region, Technical Document N° 123. 14p.

Sosamma, V. K.; Koshy, P. K. & Sundararaju, P. (1980*b*). Plant parasitic nematodes associated with cocoa. *Cocoa Growers Bulletin*, 29:27–30.

Souza, P. (1977). *A disease complex of coffee involving* Meloidogyne exigua *and* Rhizoctonia solani. Thesis, North Carolina State University Graphics, 144p.

Steiner, G. & Buhrer, E. (1933). The nematode *Tylenchus similis* Cobb as a parasite of tea plant (*Thea sinensis*), its sexual dimorphism, and its nemic associates in the same host. *Zeitschrift Parasitenkunde*, 5:412–420.

Stuart-Light, S. (1928). Pests of Nurseries: A warning. *Tea Quarterly*. 1:19–22.

Swai, I. S. (1981). Root-knot nematodes, *Meloidogyne* species, in Tanzania. In: *Proceedings of the third Research Planning Conference on Root-Knot Nematodes, Meloidogyne* spp. November 16–20, Ibadan, Nigeria: 28–30.

Takaji, K. (1967). Control of nematodes in Tea. *Shokubutsu Boeki*, 2:429–432.

Takaji, K. (1969). Nematodes confronts tea plantations in Japan. *Japanese Agricultural Research Quarterly*, 4:27–2.

Tarjan, A. C.; Jimenez, M. F. & Soria, J. (1973). Increasing yields of cacao by application of nematocides. *Turrialba*, 23:138–142.

Taylor, A. L. & Sasser, J. N. (1978). *Biology, identification and control of root-knot nematodes* (*Meloidogyne* species). International *Meloidogyne* Project. North Carolina State University Graphics. 111p.

Thorne, G. (1961). *Principles of Nematology*, New York, Toronto & London. McGraw Hill Co. Inc., 553p.

Thorold, C. A. (1975). *Disease of cocoa*. Oxford. Clarendon Press. 423p.

Torrealba, P. A. (1969). Survey of plant parasitic and free-living nematode genera from Venezuela. In: Peachey, J. E. [Ed.]. *Nematodes of Tropical Crops*. St. Albans, U. K. Commonwealth Agricultural Bureaux, Technical Communication n° 40. 257–263.

Urquhart, D. H. (1955). *Cocoa*. Longmans, Green and Co. London – New York – Toronto, 230p.

Valdez, R. B. (1968). Stubby roots of coffee seedlings caused by *Rotylenchulus reniformis. Philippines Agriculture*, 51:672–679.

Van Doorsselaere, R. & Samsoen, L. (1981). Some tylenchids from coffee-fields of Ivory Coast, with the description of *Hemicriconemoides snoecki* sp. (Nematoda: Tylenchida). *Revue de Nématologie*, 4:51–63.

Van Gundy, S. D. & McKenry, M. V. (1977). Action of nematocides. In: Horsfall, J. G. & Cowling, E. B. [Eds]. *Plant Disease – An advanced treatise. Vol. 1.*New York, Academic Press: 263–283.

Vaquerano, G. M. (1980). Estudio del ciclo biologico del *Pratylenchus coffeae* (Zimm.). In: *Resumenes di investigaciones en café 1979 – 1980*. Nueva San Salvador, El Salvador, C. A.; Instituto Salvadoreño de Investigaciones del café: 36–37.

Vega, M. C. (1982). Informe sobre la situacion nematologica en Nicarágua. In: *Proceedings of the third Research & Planning Conference on Root-Knot Nematodes Meloidogyne* spp. January 11–15, Region I: 66–68.

Venkata Ram, C. S. (1963). *Annual Report of the United Planters' Association of Southern India:* Scientific Department. Appendix: 31–36.

Vernalha, M. M.; Zappia, O.; Mansur, R. & Rodrigues, S. (1967/1970). Sobre a ocorrência de nematóides do cafeeiro no estado do Paraná. *Arquivos de Biologia e Technologia*, 13:33–38.

Visser, T. (1959). Observations on the prevalence and control of parasitic eelworms in tea. *Tea Quarterly*, 30:96–107.

Visser, T. & Vythilingam, M. K. (1959). Effect of marigolds and some other crops on the *Pratylenchus loosi* and *Meloidogyne* populations in tea soils. *Tea Quarterly*, 30:30–38.

Vovlas, N. 91987). Parasitism of *Teophotylenchulus obscurus* on coffee roots. *Revue de Nématologie*, 10:337–342.

Way, J. I. (1981). *Meloidogyne* species in Zimbabwe susceptible crops other than tobacco, taxonomy and resistant crops. In: *Proceedings of the third Research Planning Conference on Root-Knot nematodes Meloidogyne* spp. November 16–20, Region IV. Ibadan, Nigeria: 13–20.

Whitehead, A. G. (1959). The root-knot nematode of east Africa. *Nematologica*, 4:272–278.

Whitehead, A. G. (1968*a*). Taxonomy of *Meloidogyne* (Nematodea: Heteroderidae) with descriptions of four new species. *Transactions Zoological Society, London*, 31:263–401.

Whitehead, A. G. (1968*b*). Nematodea. In: Le Pelley, R. H. [Ed]. *Pests of coffee*. Longmans, Green and Co. Ltd., London and Harlow: 407–422.

Whitehead, A. G. (1969*a*). The distribution of root-knot nematodes *Meloidogyne* spp. in Tropical Africa. *Nematologica*, 15:315–333.

Whitehead, A. G. (1969*b*). Nematodes Attacking Coffee, Tea and Cocoa and their control. In: Peachey, J. E. [Ed]. *Nematodes of Tropical Crops*. Technical communication n° 40. Commonwealth Bureaux of Helminthology. St Albans, Herts. England: 238–250.

Yu Sheng Fu & Zia Bing (1987). Preliminary results of identification of causal root-knot nematodes of tea seedlings in Yunnan. *Journal of Yunnan Agricultural University*, 2:35–40.

Zimmermann, A. (1899). Het voorkomen van nematoden in de wortels van sirihen thee I. De aaltjesziekte der sirih (piper betle L) II. *Tylenchus acutocaudatus* Zn in de thee. *Teysmannia*, 10:523–531.

Chapter 13

Nematode Parasites of Bananas, Plantains and Abaca

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Bananas thrive in the lowland tropical regions where rainfall is in excess of 1250 mm per year and there is a mean minimum temperature above 15°C (Simmonds, 1966; Stover & Simmonds, 1987). Significant areas of production exist outside these climatic zones such as in the East African highlands, several subtropical countries and in warmer localities beyond the 30° latitudes (Stover & Simmonds, 1987). Bananas originate in Southeast Asia and the western Pacific Islands where several wild seed bearing *Musa* spp. still exist in the natural vegetation. There is no firm botanical distinction between the different types of banana and they are best classified by dividing the many different types into those which are sweet and eaten as a dessert fruit and those which can be eaten only after cooking, or fermented to produce a nutritious type of beer. In many countries the cooking bananas are known as plantains but the term is sometimes used ambiguously. Many edible bananas are sterile, the most important varieties are triploid and are propagated vegetatively. Of the very great number of recognized clones (Simmonds, 1966) some are derived from *Musa acuminata* Colla and others from natural hybridisations of *M. acuminata* and *M.balbisiana* Colla. Currently accepted nomenclature of clones indicates ploidy and genomic origin with A for *acuminata* and B for *balbisiana* (Table 1).

TABLE 1. Names and genomic origin of some important banana clones.

1. DESSERT BANANAS
Musa AAA Cavendish sub-group: Robusta, Poyo, Grand Nain, William hybrid, Lacatan, Giant Cavendish, Dwarf Cavendish.
Red, Green red.
Gros Michel
Musa AAB Silk, Mysore, Pome, Prata.
Musa AA Sucrier.
Musa AB Ney Poovan, Lady's Finger.
2. COOKING BANANAS
Musa AAA Lujugira, Mutika.
Musa AAB French plantain, Horn plantain, Pisang raja.
Musa ABB Bluggoe, Pisang awak.

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds) © CAB International 1990

International trade in dessert and cooking bananas amounts to 7.5 million t (FAO, 1987*b*) and this is about 12–15% of the estimated world production of 69 million t (FAO, 1987*a*) of this, Africa produces 24 million t, South America and Asia each produce 18 million t, and Central America produces 9 million t. Most bananas are grown for local consumption in mixed cropping systems or as a subsistence crop in gardens. Pure stands of cooking and dessert types are usually where there is access to urban markets or where the fruit is the major contribution to the diet.

Abaca, *Musa textilis* Nee, which closely resembles bananas, is grown for its hard, water and salt resistant fibres known as Manila hemp which are particularly useful for marine rope and fish nets. Most abaca is produced in the Philippines where the area under cultivation in 1971 was 173 000 ha, about 100 000 ha less than 1938 (FAO, 1950, 1972). Small areas (less than 10 000 ha) have been cultivated in parts of Central and South America since 1925.

The banana root system

Bananas are herbaceous perennials with short underground rhizomes from which grow an adventitious root system. Most roots grow laterally from the rhizome (corm) in the superficial soil layer (Champion & Sioussaram, 1970). Fewer roots grow vertically or deeper (Summerville, 1939) although rooting density and distribution is influenced by the texture and depth of the topsoil (Irrizary *et al.*, 1981; Weckx, 1982).

New roots are produced continously until flowering (Beugnon & Champion, 1966) which may occur from 7–9 months after planting a new crop of the commercial AAA cultivars. The duration of the vegetative phase may be considerably longer if climatic or soil conditions are less favourable and may last more than 1–2 years in the cooler upland regions of East Africa where cooking cultivars are cultivated (INIBAP, 1986).

After flowering, the developing inflorescence is sustained by a declining root system in which natural senescence is hastened by the activity of root pathogens. The increasing root growth of the daughter plant (sucker) may be of benefit during this critical phase by providing additional anchorage to the mother plant and also as a supplementary source of nutrients for the maturing fruit (Lavigne, 1987).

Some AAB cooking bananas may have less extensive root systems than dessert AAA types. This major difference may partially explain the relatively low productivity of many cooking bananas (Swennen *et al.*, 1986).

Swennen *et al.* (1986) recognize two types of primary root according to their proximal diameters and overall length. Those that are thinner (approximately 4–5 mm), longer and bearing greater numbers of secondary roots are considered as the feeder roots, the roots that are relatively thick (approximately 7–8 mm) and shorter such as those produced on rapidly growing sword suckers are the pioneer roots. Generally, there are twice as many feeder roots as there are pioneer roots. Secondary roots develop on primary roots in the proximal root zones and short tertiary roots develop on the secondaries. A proportion of the secondary roots of some AAB cooking cultivars may not develop tertiary roots. Studies of the proportion of primary, secondary, and tertiary roots as a percentage of the total root length have shown that diploids and AAA types have greater numbers of tertiary roots than the AAB dessert and cooking cultivars (Swennen *et al.*, 1986).

Cropping systems

Bananas may be grown as a permanent crop or on a system of re-planting every 3–8 years or longer (Stover & Simmonds, 1987). In many countries, particularly in the Caribbean, Surinam, Ivory Coast, Cameroon and the Pacific islands, bananas and plantains soon become unproductive for reasons related to the soil structure, fertility, drainage and severity of pathogens, so frequent replanting is necessary (Lassoudière 1978; Dartenucq *et al.*, 1978; Stover & Simmonds, 1987).

Crop longevity is extended if plants are mulched regularly with organic wastes and manures (Wilson *et al.*, 1986) which may explain the long established banana gardens in many parts of Central and East Africa (Ruthenberg, 1980) and elsewhere. The soil conditions for banana cultivation are

ideal in the major exporting countries of Latin America and the Philippines and once established, may remain in production more or less indefinitely.

Cultivation techniques

The intensity of inputs and management for the different farming systems are quite varied and depend on the market or use for which fruit is destined.

Bananas for export

All of the dessert fruit and some cooking bananas grown for the international export trade is managed intensively to ensure high yields of fruit of the correct size, free of skin blemishes and post harvest diseases. Such fruit is usually produced in pure stands at densities maintained at 1700–2000 plants /ha. Routine field operations involve pruning surplus suckers, removal of dead foliage, fruit bunch protection, propping fruiting stems and a regular use of fertilizers, fungicides, nematicides and when needed, herbicides and insecticides. Irrigation is applied where rainfall is inadequate, a minimum of 100 mm of rain per month is considered ideal.

Non-export bananas

Bananas are a useful component in mixed farming systems providing continuity of food, income and employment throughout the year. Fruit can be harvested close to maturity and minor attention is given to fruit size and skin blemishes. Field operations may be done only if necessary to prevent crop loss although production and fruit quality will be dependent on the extent of sucker pruning, use of fertilizers and crop protection measures.

Bananas as a subsistence crop

Bananas are a valuable subsistence crop and there can be few household gardens anywhere in the tropics that do not have one or more clumps of bananas requiring minimal attention other than propping those stems with maturing fruit. Many other crops will thrive alongside bananas benefiting from the shade and the large amount of leaf material that is available for mulching and soil improvement.

Nematodes of bananas, plantains and abaca

The species of nematodes found to be most detrimental to these crops are those which are involved in the destruction of the primary roots, disrupting the anchorage system and resulting in toppling of the plants. The most widespread and important are *Radopholus similis*, some species of *Pratylenchus* and *Helicotylenchus multicinctus*. As for most tropical crops, nematode parasitism in banana plants is characterized by simultaneous infestations by several species. It is also very common to find some sedentary endoparasites such as *Meloidogyne* spp. and *Rotylenchulus reniformis* parasitising the root system.

In addition to these five major nematodes parasitic on roots of *Musa* spp., there are 146 species belonging to 43 other genera of nematodes associated with *Musa* spp. throughout the world. None of these species are until now considered as serious pests damaging the banana root although they may be important in some areas where their densities are very high. These potentially important species include *Hoplolaimus pararobustus, Helicotylenchus microcephalus, H. mucronatus* and *Cephalenchus emarginatus*. Additional research is needed to establish the degree of pathogenicity of these species.

For the banana plant, in addition to the main functions of absorption and conduction of solutes, the continuous development and elongation of its primary roots is vital to the major requirement of providing a firm anchorage in the soil.

According to the mode of parasitism of the different species, the symptoms will differ from the

most severe such as toppling, to the less obvious and subtle such as prolonging of the vegetative cycle.

Radopholus similis

The disease of banana caused by *R. similis* is known throughout the world by different names, the most common are "black head toppling disease" and "toppling disease". The burrowing nematode, *R. similis*, was first observed by Cobb in necrotic tissue of the roots of *Musa* sp. sent to him in New South Wales from Fiji in July, 1891. Since this first record, it has subsequently been found widespread in all the tropical and subtropical banana and plantain growing regions of the world except Israel, the Canary Islands, Cape Verde Islands, Cyprus, Crete, Mauritius and Taiwan. It also appears to be absent from some of the important areas of production in the highlands of Eastern Africa.

Symptoms of damage

The most obvious symptom of attack of *R. similis* on banana is the toppling over or uprooting of plants (Plate 11C) especially those bearing fruit, but there is a range in gradation in the severity of damage, from the lengthening of the vegetative cycle to the drastic reduction in bunch weight. This reveals two types of damage that can occur in banana plantations; that affecting the anchorage of the plant, and less apparent, the effect on the ability to take up water and nutrients.

Macroscopically, several dark red lesions appear on the outer part of the root penetrating throughout the cortex but not in the stele (Plate 11B); adjacent lesions may coalesce and the cortical root tissue atrophies and later turns black (Plate 11D). In heavy infestations the lesion girdles the roots. Nematodes can migrate from infected roots into the corm causing diffuse black lesions which may then spread around the corm (Loos & Loos, 1960*b*). Roots emerging become infected as they grow out of the corm. Uprooting occurs commonly in windstorms or if heavy rains loosen the soil. The mechanical stresses on the root system are often increased by the natural angle of leaning which develops as fruit bunches grow. The presence of a number of fungi in nematode induced lesions probably hastens the destruction of roots and may contribute to toppling disease because fungi colonise the stele which is not penetrated by *R. similis* (Stover, 1972).

Biology and life cycle

R. similis is a migratory endoparasitic species which is able to complete its life cycle within the root cortex.

The histopathology of banana roots attacked by *R. similis* was studied by Blake (1961, 1966) and Loos (1962). Penetration occurs mostly near the root tip, but nematodes can invade along the entire length of the root; females and all juvenile stages are infective although males, morphologically degenerate (without stylet), are probably non parasitic. After entering the roots of banana, the nematodes occupy an intercellular position in the cortical parenchyma where they feed on the cytoplasm of nearby cells, causing cavities which then coalesce to appear as tunnels. Invasion of the stele is never observed even in heavily infected roots. Migration and egg-laying are governed by nutritional factors, as females move in search of healthy tissue away from the necrosis. It is within infected tissues that females lay their eggs, with an average of four to five eggs per day for two weeks. The complete life cycle from egg to egg spans 20 to 25 days at a temperature range of 24°C to 32°C, the eggs hatch after 8 to 10 days and the juvenile stages are completed in 10 to 13 days (Loos, 1962).

Pathotypes/races/biotypes

Until recently *R. similis* was considered to have two races one attacking banana but not citrus and a "citrus race" pathogenic to both (DuCharme & Birchfield, 1956). These two races are now designated as sibling species (*R. similis sensu stricto* and *R. citrophilus*) on the basis of genetic, biochemical, behavioural and minor morphological differences (Huettel *et al.* 1984; Huettel &

Yaegashi, 1988). However, in studies of populations from plantain in Puerto Rico, Rivas and Roman (1985) found that the chromosome numbers were the same as for those attacking citrus in Florida. The criteria for describing populations of *R. similis sensu lato* from different hosts and localities would appear to require further clarification.

Physiological differences in reproductive capabilities and morphological variations of *R. similis* on bananas in Central and South America suggest the existence of different biotypes or isolates, on the basis of host preferences and the rate of reproduction (Pinochet, 1979; Tarté *et al.*, 1981).

Survival and means of dissemination

The survival of *R. similis* in banana soil depends on the effectiveness of the destruction and removal of infected banana stools, rhizomes and roots in the soil before a fallow period. Tarjan (1961) and Loos (1961) demonstrated that *R. similis* did not survive in the soil for more than 6 months in the absence of hosts roots or pieces of live corms. *R. similis* will survive on corms and roots of a previous crop for a long time and, within planting material, it is the major means of reinfestation.

While *R. similis* now occurs in most tropical and subtropical areas of the world, the genus *Radopholus* is indigenous to Australia and New Zealand (Sher, 1968). Its worldwide distribution is relatively recent (beginning of the 19th century) and is due to the transfer of infected plant material (banana sets) from country to country for commercial purposes. The wide distribution of *R. similis* seems often to be correlated with the areas where banana sets of the sub-group Cavendish (AAA) were imported. Adaptation may cause the development of a wider host range as it spreads on different AAA, AAB and ABB clones in Africa and on ornamental plants which increasingly are being exported to regions outside the tropics.

Other hosts of *R. similis*

Most of the banana and plantain cultivars of the edible *Musa* varities AA, AAA, AB, AAB, ABB are attacked by *R. similis* (Luc & Vilardebó, 1961; Wehunt *et al.*, 1978; Davide & Marasigan, 1985) as well as abaca (Taylor & Loegering, 1953) and other seeded *Musa* species. In the Americas *R. similis* seems to be confined to *Musa* spp. and to a few other plants, including five weed species (Edwards & Wehunt, 1971). O'Bannon (1977) listed agronomic and edible horticultural crops that are susceptible to *R. similis*. Information is scarce on the host range of *R. similis* outside Florida and Central America. In the Ivory Coast it has been found associated with *Asystasia gangetica* L., *Amaranthus viridis* L., *Cleome ciliata* Schum, & Thonn., *Commelina benghalensis* L., *Phyllanthus amarus* Schum. & Thonn., *Solenostemon monostachys* B., *Portulaca oleracea* L., *Talinum triangulare* J. and *Fleurya aestuans* L. (unpublished data from ORSTOM). Elsewhere it attacks several crop plants which are important in world commerce and subsistence type agriculture (Bridge, 1987).

Pratylenchus

Eight species of *Pratylenchus* root lesion nematodes, have been reported attacking *Musa* spp. throughout the world. Among these species, only two are relatively widespread and recognised as damaging pathogens. These are *P. coffeae* and *P. goodeyi*.

P. coffeae was first observed in roots of plantains in Grenada and described as *Tylenchus musicola* by Cobb in 1919. The demonstration of its pathogenic activity in extensive lesions in the root cortex of abaca was done by Taylor and Loegering (1953) in Costa Rica. *P. goodeyi*, was first observed in banana roots in the Canary Islands by de Guiran and Vilardebó (1962) with *P. coffeae* and *P. thornei*. *P coffeae* seems to be widespread throughout the world. *P. goodeyi* has been observed in every banana growing area of East Africa (Gichure & Ondieki, 1977; Walker *et al.* 1984; Bridge, 1988) suggesting that it is indigenous to this area.

Symptoms of damage

Root lesion nematodes cause symptoms of damage similar to those observed with *R. similis*: stunting of plants, lengthening of the vegetative cycle, reduction in size and number of leaves and in bunch weight, reduction of the productive life of the plantation, and toppling (Plate 11A).

Roots heavily infested by *P. coffeae* have extensive black or purple necrosis of epidermal and cortical tissue often accompanied by secondary rotting and root breakage. Similar necrosis can be observed on the outer parts of the corm (Plate 11E) (Bridge & Page, 1984).

In the Canary Islands, de Guiran and Vilardebó (1962) observed that *P. goodeyi* penetrates the cortical parenchyma of banana roots forming small brownish-red elongated flecks. These feeding areas enlarge and eventually coalesce, so most of the cortical parenchyma is destroyed, impairing root function.

Biology and life cycle

P. coffeae and *P. goodeyi* are migratory endoparasites of the root cortex and banana corm. Nematodes of both sexes and all juvenile stages are invasive. The life cycle is completed within the root. Pinochet (1978) described the histological changes after inoculation of *P. coffeae* on roots of AAB clones. After entering the roots, the nematodes migrate between and within the cells, occupying a position parallel to the stele. They feed on the cytoplasm of neighbouring cells, eventually causing cavities which coalesce. The destruction of the cortical parenchyma of plantain roots by *P. coffeae* is very similar to those effects described by Blake (1961, 1966) for *R. similis* on dessert bananas, except there was no cell enlargement or increase in size of cell nucleus or nucleolus. The life cycle has been discussed in detail on other host plants (Zimmerman, 1898; Gotoh, 1964) and the average life cycle from egg to egg is about 27 days at a temperature range of 25°–30°C.

Pathotypes/races/biotypes

There is scarce information on "biotypes", "isolates" or "races" of *P. coffeae*. Wehunt and Edwards (in Stover, 1972), mention the existence of different biotypes or isolates from Honduras and Panama, stated in terms of host preferences related to the infection index on test plants of abaca, plantain and banana.

Survivial and means of dissemination

In Central America, a fallow period of 6 months after destruction of all abaca eliminated *P. coffeae* and *R. similis*. Root lesion nematodes have also been observed infesting the corm, so dissemination occurs in the same way as described for *R. similis*. Records of the risk of this type of dissemination are reported from Ivory Coast for *P. coffeae* on dessert bananas and plantains (Adiko, 1988; Fargette & Quénéhervé, 1988) and from East Africa for *P. goodeyi* on highland bananas (Walker *et al.*, 1984; INIBAP, 1986; Bridge, 1988; Sikora *et al.*, 1989).

Other hosts of *Pratylenchus* spp.

Many other hosts of *Pratylenchus spp.* have been recorded, several of which may be found in banana plantations. Fluiter and Mulholland (1941) mention the association of *P. coffeae* on weeds, *Alternanthera sessilis* L. and *Portulaca oleacera* in banana plantations. In the Ivory Coast this nematode has been found associated with *Asystasia gangetica*, *Amaranthus viridis*, *Commelina benghalensis*, *Phyllanthus amarus*, *Solenostemon monostachys* and *Borreria chartophyla* (Schum. & Thonn.) K. Schum. (unpubl. data from ORSTOM).

Helicotylenchus multicinctus

After *R. similis* the spiral mematode, *Helicotylenchus multicinctus*, is probably the most widespread and numerous nematode on all bananas. The first evidence of substantial losses in yield due to *H. multicinctus* was shown in the Jordan valley by Minz *et al.* (1960). This nematode has also been

recorded as damaging to plantains in Cuba (Stoyanov, 1967). Recent literature on *H. multicinctus* as a parasite of banana has been reviewed by McSorley and Parrado (1986). *H. multicinctus* and *R. similis* are often encountered together in many banana growing regions of the world, particularly where bananas are grown under optimal conditions. *H. multicinctus* is often regarded as the main parasitic nematode on bananas where environmental conditions are suboptimal for the crop (and also for *R. similis*) in relation to latitude, temperature and rainfall.

Symptoms of damage

The damage symptoms, on both banana and plantain, caused by *H. multicinctus* are very similar to those observed with other serious root parasites such as *R. similis*: stunting of plants, lengthening of the vegetative cycle, reduction in size of the plant and in bunch weight, and reduction of the productive life of the plantation. Toppling may also occur in situations where there are heavy infestations.

The nematodes attack and feed on the outer cells of the root cortex and produce small, characteristic necrotic lesions (Luc & Vilardebó, 1961). Development of root lesions caused by *H. multicinctus* is slow relative to those produced by *R. similis*. Lesions on primary roots are shallow and superficial, like numerous small dashes, reddish brown to black in colour. However, in heavy infestations, those lesions can coalesce, causing extensive root necrosis in the outer cortex (Plate 11F) and dieback; lesions can also be found in the corm (Quénéhervé & Cadet, 1985*a*).

Biology and life cycle

H. multicinctus is regarded as an endoparasitic species which is also able to complete its life cycle within the cortical part of the root where both sexes and all juvenile stages, including eggs, can be found (Zuckerman & Strich-Harari, 1963). The host-parasite relationships of *H. multicinctus* were studied by Blake (1966) who observed that four days after inoculation of banana roots, the nematodes were wholly embedded within the cortex, sometimes to a depth of four to six cells. Nematodes fed on the cytoplasm of surrounding cells in the root cortex. Infected tissues show various types of cellular damage such as, contracted cytoplasm, distorted or ruptured walls and enlarged nucleus but, in contrast to those observed with *R. similis*, histological changes are confined to parenchyma cells close to the epidermis. Damaged cells were often discoloured and became necrotic.

Pathotypes/races/biotypes

Until now there is no available information on "biotypes", "isolates" or "races" of *H. multicinctus*, but this topic requires further study.

Survival and means of dissemination

Little information exists on the survival of *H. multicinctus* in the absence of a susceptible host. As with *R. similis* survival occurs on infected corms or on tissue remaining from the previous crop. Infected planting material is also the main means of dissemination.

Other hosts of *H. multicinctus*

Most of the banana and plantain cultivars of edible *Musa* cultivars of differing ploidy are attacked by *H. multicinctus* (Luc & Vilardebó, 1961; Gowen, 1976; Zem *et al.*, 1981; McSorley & Parrado, 1983). This nematode is also recorded to have a wide host range (Goodey *et al.*, 1965; Stoyanov, 1967). In the Ivory Coast this nematode has been found associated with *Asystasia gangetica, Alternanthera sessilis, Amaranthus viridis, Eupatorium odoratum* L., *Commelina benghalensis, Phyllanthus amarus, Solenostemon monostachyus, Portulaca oleracea, Talinum triangulare, Borreria chartophyla, Fleurya aestuans* and *Clerodendrum splendens* D. (unpubl. data from ORSTOM).

Meloidogyne

Root-knot nematodes are worldwide in distribution attacking many economically important crops. At least five identified species have been reported on *Musa* spp. in the warm tropical and subtropical areas or in particular conditions as in Morocco where bananas are grown in greenhouses (Ammati, pers.comm.). The species most commonly found associated with bananas and plantain are *Meloidogyne incognita, M. arenaria, M. javanica* and *M. hapla*. Different species can be observed in the same gall (Pinochet, 1977) and 18–25% of root-knot infestations in West Africa have been found to be of mixed species (Netscher, 1978; Fargette, 1987). This genus is the second most abundant to be found in banana roots in South Africa (Jones & Milne, 1982) and is the only one in Taiwan (Lin & Tsay, 1985) and in North Yemen (Sikora, 1979) involved in nematode damage to banana plants. It also occurs on abaca in the Philippines (Ocfemia & Calinson, 1928).

Symptoms of damage

The most obvious symptoms are galling on primary and secondary roots (Fig. 1) sometimes causing them to bifurcate and distort. Stunted growth has been attributed to root-knot nematodes in India (Sudha & Prabhoo, 1983) and Taiwan (Lin & Tsay, 1985). Sikora (1979) observed higher levels of root rot in plantations in Yemen where *M.incognita* and *Fusarium solani* or *Rhizoctonia* sp. were present concomitantly.

Biology and life cycle

The life cycle, histopathology and etiology of the disease do not differ significantly on bananas from that reported on other hosts in recent reviews to which the reader is referred (Bird, 1979; Huang, 1985). In thick, fleshy primary roots, egg-masses may not protrude outside the root surface and multiple cycles can be completed within the same root, depending on the longevity of this root and

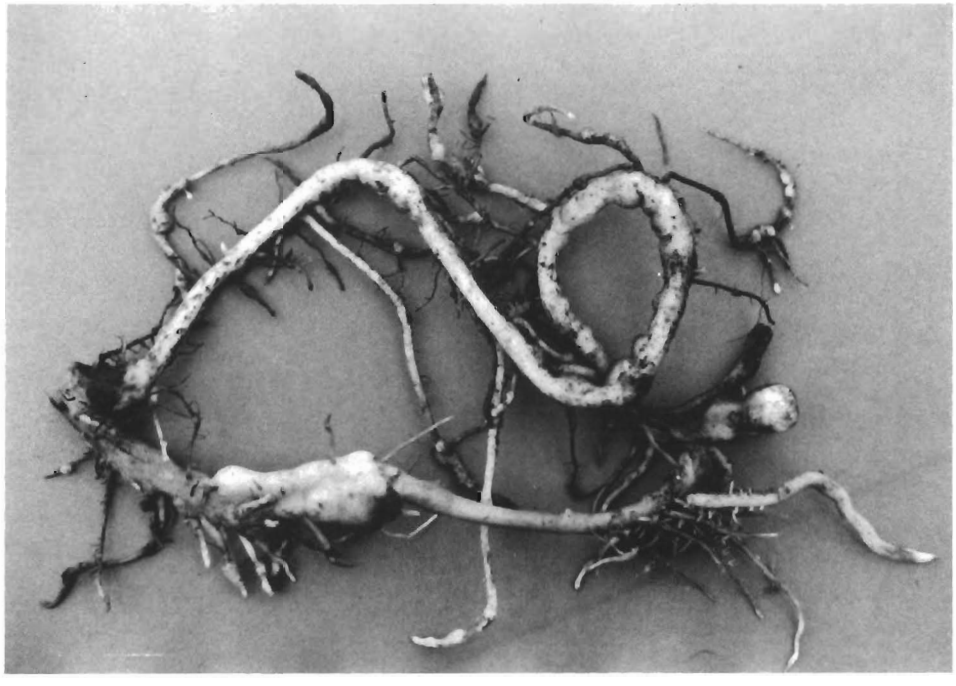

Fig. 1. Root galling caused by *Meloidogyne* sp. on a Cavendish AAA cultivar.

the severity of necrosis. Pinochet (1977) suggests that, in mixed infestations, the area of influence of this nematode would start between 60 and 90 cm from the rhizome because of the competition with *R. similis* in suppressing or replacing the *Meloidogyne* population. This had also been shown by Luc and Vilardebó (1961).

Survival and means of dissemination

Root-knot nematodes have a wide host range, especially on dicotyledonous plants, which are usually present in most soils in which bananas are growing. As for other nematodes associated with bananas, survival and dissemination also occurs with the planting material on infected roots and corms (Quénéhervé & Cadet, 1985*a*).

Other hosts

Because of the wide host ranges of root-knot nematodes associations with weeds in banana plantations are more numerous than for other major nematode parasites. Special attention would be needed in maintenance of weed free fallow or selection of cover crops or associate crops in intercropping systems.

Other nematodes

Of the many other species of plant parasitic nematodes found associated with bananas some are thought to be potentially damaging but there is no conclusive evidence to show their pest status. Invariably, these nematodes are in mixed communities with species already established as key pests.

Rotylenchulus reniformis

Since the first records of *R. reniformis* on bananas in Puerto Rico by Ayala and Roman (1963) this nematode has now been reported in numerous banana growing areas. The life cycle and the histopathology and etiology of the disease do not differ significantly on bananas from that reported on other hosts (Sivakumar & Seshadri, 1974). Juveniles of *R. reniformis* are commonly extracted from the soil and it is generally observed that permanent feeding positions occur mostly on the secondary roots (Ayala, 1962; Edmunds, 1968). As for *Meloidogyne* sp., the effect of this nematode is probably influenced by the presence of other root parasitic nematodes.

Hoplolaimus pararobustus

This species has been found within roots and corms of dessert bananas in different areas of the Ivory Coast (Quénéhervé & Cadet, 1985*a*; Quénéhervé, 1989 *a, b*). Population densities in roots of mature plants have been as high as 200 individuals per gram of root (Mateille *et al.*, 1988*b*). This nematode is also abundant around plantain roots in some localities in the Ivory Coast (Adiko, 1988).

Helicotylenchus mucronatus and *H. microcephalus*

Each of these nematodes has been found to be the cause of root necrosis and stunted growth of bananas at separate sites in Papua New Guinea (Bridge & Page, 1984). In Makira, Solomon Islands, *H. mucronatus* has been found associated with *R. similis* in root lesions on dessert bananas (Gowen & Hunt, unpubl.).

Cephalenchus emarginatus

This ectoparasite has been found at populations of up to 9000 per litre of soil taken from around the roots of dessert bananas in the Ivory Coast (Mateille *et al.*, 1988*b*; Quénéhervé, 1989 *a, b*) and has also been found associated with plantains (Adiko, 1988).

Environmental factors affecting parasitism of banana nematodes

On bananas grown under humid, tropical conditions, the major factors affecting nematode populations are abiotic, such as soil type and climate, and biotic such as plant host status, growth stage, competition with other nematode species and other pests. In subtropical or highland countries, soil temperature is an additional factor influencing parasitism.

The parasitism of banana root systems is somewhat different from that of other perennial crops because of the growth habit of the root system in which a succession of fleshy, relatively short lived roots are produced.

Unthriftiness of bananas may result from shallow or poorly drained soils, drought, nutrient deficiency or nutrient imbalance, and symptoms may show on aerial parts of the plant. Such conditions may also cause restriction of root development and in these situations the presence of nematodes may increase the incidence of toppling as well as exacerbate foliar symptoms. If drainage is poor, high or fluctuating water tables can considerably curtail root growth (Lassoudière & Martin, 1974). Roots in soil saturated for more than 24 hours die and rot rapidly but detailed observations of the roots can differentiate this damage from that of nematode damage. The combination of poor drainage and a nematode problem may result in nematodes and roots being concentrated in the upper layer of soil resulting in more severe nematode damage.

Influence of soil type

The influence of soil type on nematode community composition has been reviewed by Ferris and Ferris (1974), and Vrain (1986) reviewed the effect of soil moisture content on population dynamics. In general, most information concerning banana nematodes deals with the relation between soil type and density of nematode species on commercial bananas (Stover & Fielding, 1958; Ayala & Roman, 1963; Varghese & Nair, 1968; Guérout *et al.*, 1976; Davide, 1980; McSorley & Parrado, 1981). In the Ivory Coast, Quénéhervé (1988) showed that, in an organic soil, *H. multicinctus* is predominant in both soil and roots while on mineral soils *R. similis* predominates. The major differences in nematode community structure occur in the soil. *R. similis* seems less affected by the soil variables possibly because it is strictly an endoparasite. *H. multicinctus* is more frequent in soils characterized by high levels of clay, silt or organic matter and low pH. *Hoplolaimus pararobustus* is more commonly found in coarse volcanic or sandy soils and *M. incognita* is most abundant in sandy soils.

Influence of climatic factors

Most extended studies of population dynamics have shown a decline in numbers of *R. similis* during the wet season (Jimenez, 1972; Melin & Vilardebó, 1973; Jaramillo & Figueroa, 1974; Shafiee & Mendez, 1975; McSorley & Parrado, 1981; Hugon *et al.*, 1984; Hunt, in Ambrose, 1984; Quénéhervé, 1989 *a, b*), but the opposite effects have also been reported (Marcelino *et al.*, 1978; Davide & Marasigan, 1985).

Similar attempts have been made to correlate population densities of *H. multicinctus* with rainfall with variable results (Hutton, 1978; McSorley & Parrado, 1981; Badra & Caveness, 1983; Quénéhervé, 1989 *a, b*) but it is a general trend that greater populations can be found in the rainy season.

The discrepancies in the relationships between population densities and rainfall may be attributed to difference in soil type, soil temperature and incidence and intensity of rainfall.

Influence of the host

Gowen (1976) showed that *R. similis* and *H. multicinctus* can invade and reproduce on banana clones of differing ploidy. Of some experimental tetraploids, clone "A", was a less favourable host, in terms of nematode population density, than were the other tetraploids and triploid clones. Growth habit, root system and vigour of banana clones of differing ploidy can strongly influence the dynamics

of nematode populations. This subject needs further investigation in respect to breeding programmes and screening bananas and plantains for resistance to nematodes is required (Pinochet, 1988).

Influence of the root system and physiology of the plant

A relationship has been reported between successive annual peaks in the numbers of *R. similis* in the roots and the active growth of the plant (Jaramillo & Figueroa, 1974), which coincides with the emergence of the banana flower (Melin & Vilardebó, 1973). In Guadeloupe, Hugon *et al.* (1984) observed a relation between the physiological stage of the banana plant and such climatic factors as temperature and rainfall.

Pruning of excess suckers is practised in commercial plantations and this may influence the relative numbers of *R. similis* and *H. multicinctus* in the roots and corms (Mateille *et al.*, 1984).

In a study, conducted both on mineral and organic soils in the Ivory Coast, Quénéhervé (1989 *a, b*), has shown differences in the behaviour of the nematodes encountered. *R. similis* acts as the primary root invader, and levels of infestation decrease as the root system ages or decays. Blake (1961) and Loos (1962) showed that migration and egg-laying are governed by nutritional factors and that the nematodes "do not move out of a root so long as they are able to invade healthy tissue". *R. similis* is able to complete its life cycle in the cortical tissue of the root or the rhizome without a soil phase. After flowering there is little or no new root emergence from the main rhizome (Lavigne, 1987), but on the rhizomes of the suckers, prolific root emergence occurs once they have achieved self-reliance (change of the lanceolate leaves to enlarged leaves). In fact all the factors, endogenous or exogenous, which favour root emergence on banana plants contribute to the build up of *R. similis* populations.

Influence of the competition with other parasites

In addition to the various nematodes, other parasites such as fungi and bacteria are present in the roots and this complex is the cause of root decay. Infestations by nematodes like *H. multicinctus, H. pararobustus* and *P. coffeae* may accelerate root decay, thereby restricting the availability of healthy tissue to another endoparasite such as *R. similis*. An important aspect of the behaviour of *R. similis* is its ability to infest the corm and to build up to a high population level which can become a source for reinfestation. Such population increases appear not to be affected by adverse soil conditions that are unfavourable to banana growth. In organic soil, the competition with the other nematode species appears to be the most important factor involved in the dynamics of *R. similis* (Quénéhervé, 1989*b*). *H. multicinctus* and *R. similis* often occur together on bananas and plantains in those tropical regions best suited for growth of the crop. Vilardebó and Guérout (1976) noticed that high populations of *H. multicinctus* built up when *R. similis* is locally absent. In the Ivory Coast, it appears that on organic soil, even though *H. multicinctus* follows the primary infestations by *R. similis*, it is able to build up and become the most dominant parasite.

P. coffeae has a similar parasitic behaviour to *R. similis* and may compete directly with it (Quénéhervé, 1989*a*). In some parts of the world this nematode might be the more damaging parasite such as in Papua New Guinea or like *P. goodeyi* in Canary Islands (de Guiran & Vilardebó, 1962) or on highland bananas in East Africa (Gichure & Ondieki, 1977; Bridge, 1988).

The banana weevil, *Cosmopolites sordidus*, can confuse the diagnosis of a nematode problem because symptoms of damage are similar. With fungi, the problem becomes even more complex as nematodes and fungi occur within the same cells and infestations result in the same types of discoloration and necrosis. Often the problem is to define which is the primary or major pathogen.

The fungi associated with nematode lesions on plantains are the same ones found on dessert bananas (*Cylindrocarpon* spp., *Fusarium* spp. and *Rhizoctonia* spp.). Nematode induced lesions create a food base for weak, unspecialized fungal parasites, enabling them to invade the stele and to increase the amount of root necrosis. Differentiation is possible between the deep lesions due to *R. similis*, mainly associated with *Fusarium* sp., and the shallow and outer lesions of *H. multicinctus*, mainly associated with *Rhizoctonia* sp. (Blake, 1963; Laville, 1964; Stover, 1966; Sikora & Schlosser,

1973; Booth & Stover, 1974; Pinochet & Stover, 1980). Those fungi acting as secondary parasites can increase root breakage and consequently toppling.

One of the most devastating fungal diseases affecting commercial bananas (*Fusarium* wilt or Panama disease) caused by *Fusarium oxysporum f. cubense* was formerly observed on the susceptible cultivar Gros Michel and forced growers to change to the resistant Cavendish group cultivars between 1950 and 1960. Newhall (1958) and Loos (1959) concluded that the expression of Fusarial wilt on cv. Gros Michel was considerably increased in the presence of *R. similis*, although this was not confirmed from work in the Philippines (Epp, 1987). Three races of *Fusarium* attacking edible banana cultivars have been identified, the latest also infects Cavendish cultivars (Hwang *et al.*, 1984; Stover & Simmonds, 1987).

Economic importance

It is uncommon for bananas to be parasitised by monospecific populations and the relative importance of the different species is not fully understood. In addition to *R. similis, H. multicinctus, Pratylenchus* spp., *R. reniformis* and *Meloidogyne* spp., populations of other migratory endoparasites i.e. *H. pararobustus* or ectoparasites i.e. *Cephalenchus emarginatus* may reach high levels (Quénéhervé, 1989 *a, b*). Most evidence of crop loss from field experimentation comes from the use of nematicides which usually decrease populations of all species and can possibly cause other beneficial plant growth effects. The yield responses reported with nematicide applications to dessert and cooking bananas have been up to 275% greater than untreated controls (Tables 2 & 3). The differences in response may be due to several factors, in particular, soil type, nematode species and biotype, and climate, and may reflect the losses through uprooting as well as differences in the weights of harvested bunches.

Control measures

The importance of *R. similis* as a widespread cause of banana losses was reported by Leach (1958) and the early investigations into techniques for its control were made by Vilardebó (1959), Loos and Loos (1960*a*), Luc and Vilardebó (1961) and Blake (1961). Meanwhile Minz *et al.*, (1960) were applying DBCP for control of *H. multicinctus* in the Jordan valley. Control of the other major endoparasitic genus *Pratylenchus* in the Canary Islands was reported by de Guiran and Vilardebó (1962). Initially, much attention was given to the elimination of nematodes from planting material as it was realised that this was the principal source of infestation by which *R.similis* and other species were distributed through banana growing regions. The concept of providing nematode-free plant nurseries (Loos & Loos, 1960*a*) was technically sound but was never widely successful in practice.

Between 1960 and 1978 the non-phytotoxic fumigant nematicide DBCP was used extensively on commercial bananas particularly in Central and South America. Treatments were normally applied twice a year usually by hand held injectors in which the fumigant was injected in 6–8 points at 30–40 cm around individual plants. Less commonly, DBCP was applied through irrigation systems. Hand injection of DBCP was a laborious task requiring constant supervision. Consequently the easier to apply non-volatile nematicides began to be used commercially before DBCP was withdrawn from use.

Cultural and chemical techniques for controlling nematodes in replanted banana systems are continuing to be developed.

Cultural practices

In those areas where bananas are grown continuously, normally without replanting, the opportunity for controlling nematodes by cultural techniques is somewhat limited. In replanted crop systems, control of the populations can be done by creating a fallow or by rotating with non-host crops. Fallows may need to last six months or longer (Fig. 2) (Tarjan, 1961; Loos, 1961) and it is essential

TABLE 2. Principal nematode parasites and yield improvement as result of nematicide treatment in different countries producing *Musa* AAA Cavendish dessert bananas.

Country	Species	Soil type	Yield improvement % *	
Panama	Rs	Alluvial	86	Wehunt & Edwards, 1968
Honduras	Rs		15	Wehunt & Edwards, 1968
Costa Rica	Rs		132	
Ecuador	Rs	Alluvial	71	INIAP, 1978 (Unpubl.)
St Lucia	Rs Hm Rr	Alluvial	46	Gowen, 1975
St Vincent	Rs	Volcanic	267	Winban, 1977 (Unpubl.)
Guadeloupe	Rd Hm	Volcanic	30	
Martinique	Rs Hm	Clay and Volcanic	29–35	Hugon pers. comm.
Ivory Coast	Rs Hm	Heavy clay	72	ORSTOM (Unpubl.)
	Rs Hm	Peat	16–57	ORSTOM (Unpubl.)
	Rs Hm	Ferralitic	101–263	ORSTOM (Unpubl.)
	Rs Hm Pc	Loam	119–161	ORSTOM (Unpubl.)
Cameroon	Rs Hm Hp	Volcanic	30–40	Lassoudière pers. comm.
South Africa	Mel sp		5	Jones & Milne, 1982
	Mel sp			
	Prat sp			
	Rs		38	Jones & Milne, 1982
Malawi	Rs Hm Mel	Alluvial	6–49	Daudi pers. comm.
Israel	Hm	Alluvial	18	Minz *et al.*, 1960
Cyprus	Hm Mel sp Prat sp	Alluvial	30–40	Phillis pers. comm.
Taiwan	Mj Mi	Volcanic	7–70	H. Chiang pers. comm.
Australia	Rs	Alluvial		R. Broadley
		Volcanic	5–30	I. Ingllis pers. comm.

* Over 1 or more crop cycles: data based on gross yield ha^{-1} or weights of harvested bunches.
Rs – *R. similis*; Hm -*H. multicinctus*; Rr – *R. reniformis*; Mel sp – *Meloidogyne* species; Mi – *M. incognita*: Mj – *M.javanica* Hp – *H.pararobustus*; Pc – *P. coffeae*; Hel sp – *Helicotylenchus*; Prat sp – *Pratylenchus* sp.

TABLE 3. Yield improvements resulting from chemical control of nematodes infesting cooking bananas.

Country	Nematode Species	Soil type	Yield improvement % *	
Puerto Rico (*Musa* AAB maricongo)	Rs Hel spp Prat spp Rr	Clay	207–275*	Roman *et al.*, 1977
Jamaica	Rs Hel spp Mel sp Rr	Clay	119	Hutton & Chung, 1973
Ivory Coast (*Musa* AAB Horn)	Rs Hel sp	Sandy	51–74	Adiko, pers. comm.
(*Musa* AAB French)	Rs Mel sp	Sandy	100	Adiko, pers. comm.
Nigeria (*Musa* AAB Agbagba)	Hm, Mj	Sandy loam	61–98	Caveness & Badra, 1980

* Yield improvement over 3 years. No harvest from some untreated plots after 1 year.
Rs – *Radopholus similis*; Hm – *Helicotylenchus multicinctus*; Mj – *Meloidogyne javanica*; Mel sp – *Meloidogyne* sp; Prat spp – *Pratylenchus* spp: Rr – *Rotylenchulus reniformis*; Hel spp – *Helicotylenchus* spp.

Fig. 2. Fallowing as practised in Ivory Coast. Weed cover, free of banana volunteers in background; replanted Cavendish plants in foreground.

Fig. 3. Replanted Cavendish bananas on land previously cleared prior to being flooded for 5–6 weeks – Ivory Coast.

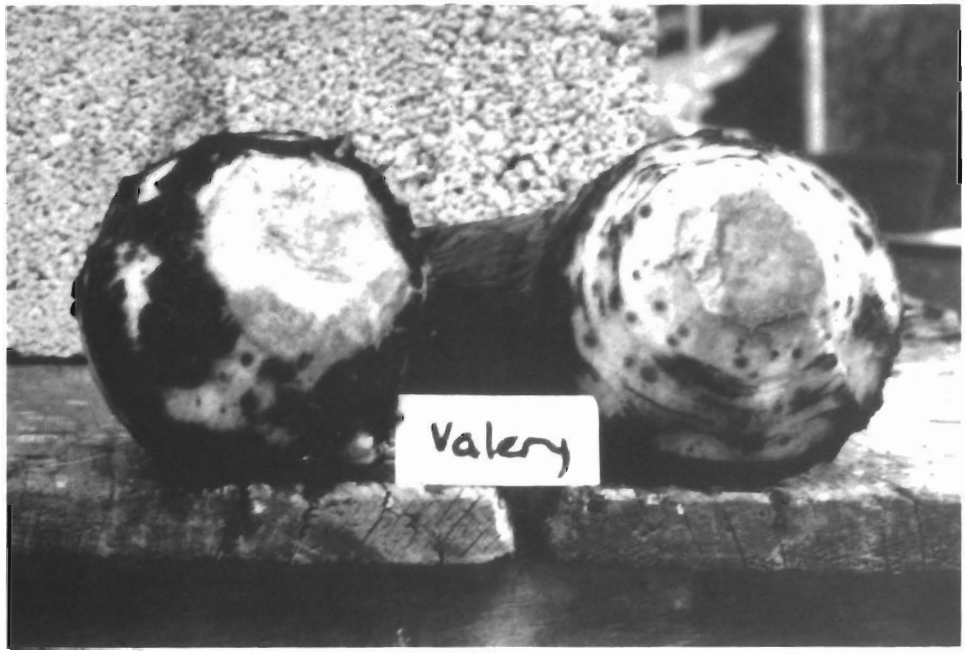

Fig. 4. Cavendish suckers cv Valery: left – heavily infected with *R. similis*; right – infection removed by paring.

that all banana roots and suckers are destroyed which in practice is a difficult task. In some commercial plantations this is done chemically with the herbicide 2,4-D. Beneficial results may also be obtained by flooding (Fig. 3) (Maas, 1969; Sarah *et al.*, 1983; Mateille *et al.*, 1988*a*), although the areas where this may be possible are very restricted. *R. similis* may be absent from many areas not previously cultivated with bananas. Unwanted introduction of the nematode can be avoided by use of disease free planting material (Loos & Loos, 1960*a*) but more reliable is the use of disease-free plants grown by the meristem culture technique (Berg & Bustamante, 1974; Cronauer & Krikorian, 1984).

Fallowing is practised in parts of West Africa where there is available land and *R.similis* is present but this technique may be less effective for control of species with wide host ranges. Where bananas are grown continuously, i.e. Latin America, or where it would be uneconomic to leave land fallow, i.e. the Caribbean, crop rotation is generally not practised. In Israel, where *H. multicinctus* and *Meloidogyne* spp. are the main parasites, wheat may be grown for 2–3 years between cycles of banana. In such cases the land is deep ploughed before the cereal is sown. In Taiwan, rice may be grown in rotation with bananas.

Since the work of Loos and contemporaries, most recommendations for banana planting include instructions for the selection and preparation of disease-free suckers. Some growers or organizations may maintain 'disease-free' nurseries from which new planting material, usually sword suckers is collected. Perhaps more commonly planting material is taken from existing banana fields and these are more likely to be infested with nematodes and weevils (*C. sordidus*). If the external tissue of the corm has purple or reddish-brown lesions these, together with root stumps and adhering soil should be removed with a machete (pared) until only white corm tissue is exposed (Fig. 4). The practice of paring suckers should be done away from the field, and corms with severe lesioning should be discarded. Similarly, deep lesions and tunnels caused by the weevil larvae should be removed. The paring technique although useful, may never be totally effective in removing all

nematode infection and this treatment is often complemented by dipping suckers in a nematicidal solution or more effectively by coating them with a nematicidal mud (see below). In the Ivory Coast, it is recommended practice to store large corms in the sun for two weeks prior to planting (Fig. 5). Populations of *R. similis* in the corm tissue decline by as much as 80% (Quénéhervé & Cadet, 1985*a*, *b*).

Physical treatments – hot water

The immersion of banana suckers in water held at a constant 55°C for periods of 15–25 min has been a commercial practice in Australia and Central and South America (Stover, 1972). Although hot water treatments are considered superior to nematicidal dips, the technique is quite difficult to manage because of the critical balance required between a temperature that is lethal to nematodes in the corm tissue and one that causes permanent damage to the plant. This factor can also be important if suckers are not of uniform size.

Resistance or tolerance

There is no widely grown clone that is known to be resistant to the important nematodes and genetic improvement in the past has been hindered by the difficulties in breeding new banana varieties (Menendez & Shepherd, 1975).

New techniques and a new optimism for exploiting genetic resources have developed in recent years (Persley & De Langhe, 1987) and breeding objectives now extend beyond the requirements of the international dessert banana trade.

Field observations have sometimes led to the belief that the Cavendish AAA clones are more susceptible to *R. similis* than the AAA clone Gros Michel, the Panama disease-susceptible clone which they replaced in many banana exporting countries (Leach, 1958). This may be so but Gros Michel is not resistant and it is possible that earlier introductions and dissemination of plants were from sources of material free of *R. similis*. In 1976, old commercial plantings of Gros Michel in Ecuador were found not to be infected with *R. similis* in an area where Cavendish varieties were infected (Gowen, unpubl.).

One of several tetraploid AAAA genotypes developed by the Banana Breeding Scheme in Jamaica derived from cv Highgate, a mutant of Gros Michel, was found to be marginally less susceptible than other clones (Gowen, 1976) and casual observations suggested that tetraploids were less vulnerable to falling over in winds or wet weather. It is possible that the relatively greater stature of some tetraploids and perhaps more vigorous root systems confer some tolerance to uprooting.

Resistance to *R. similis*, but not *Pratylenchus coffeae*, has been found in diploid *Musa* AA clones in the United Fruit Company banana collection in Honduras (Pinochet & Rowe, 1978; Pinochet, 1988) and it is possible that this resistance could be incorporated in commercially valuable cultivars of all types of banana (Shepherd *et al.*, 1987).

Chemical

Nematicides are widely used by growers producing fruit for the international export trade. Less specialised production serving local markets may not justify the high cost of chemical treatment. A number of organophosphate, oxime carbamate and carbamate nematicides are used on bananas either as granular or emulsifiable concentrate formulations. The use of DBCP, once the only fumigant nematicide available for application to a growing crop, was discontinued for toxicological reasons in the USA in 1977 and has subsequently been replaced in most other countries.

The method and timing of treatments may vary according to cultural practices (Gowen, 1979), climate (Jaramillo & Figueroa, 1976), crop damage and knowledge of the nematode population dynamics. Best results are often obtained if chemical treatments begin from the time of planting (Gowen, 1979). In this system nematode populations may be prevented from increasing to damaging levels. However in many banana exporting countries, particularly in Central and South America, the replanting of banana fields is uncommon and nematicide treatments may begin on established crops supporting high nematode population densities. Under such conditions the benefits of nematicide use may take several crop cycles to become apparent (Gowen, 1979).

Fig. 5. Cavendish suckers stacked in sun for 14 days prior to planting – Ivory Coast.

In new plantations, nematicides are applied in the planting hole or mixed with the soil when filling in around the plant. Alternatively, planting material may be coated with mud containing nematicide (Guérout, 1975; Mateille *et al.*, 1988*b*).

Dosages of 2–3 g a.i. per plant are generally used. Post planting applications are made in a 45–100 cm radius around the plant but are not incorporated in the soil. Established bananas are treated with nematicide every 4–5 months. In mature fields, the granular formulations may be sprinkled in a half circle around the selected follower sucker and not entirely surrounding the mother plant (Fig. 6).

Emulsifiable concentrate formulations are available in some countries for use in drip irrigation systems eg. in the Canary Islands, Martinique, Ivory Coast, Colombia. In the Caribbean, oxamyl 24% EC is used with a spot-gun spray applicator directly from disposable containers.

Yield loss may be attributed to smaller size of bunch harvested but more severe losses occur where banana stems are not propped and the incidence of uprooting is high. Another component of loss is the duration of the vegetative phase which may be up to two months longer in untreated plants over two crop cycles of a replanted banana field infested with *R. similis* and *H. multicinctus* (Gowen, 1975).

The loss of residual activity with repeated use of nematicides can arise from the development of adaptive strains of soil micro-organisms and it is recommended that different nematicides be used alternately although there is a possibility that cross-adaptation can develop (Suett & Walker, 1988).

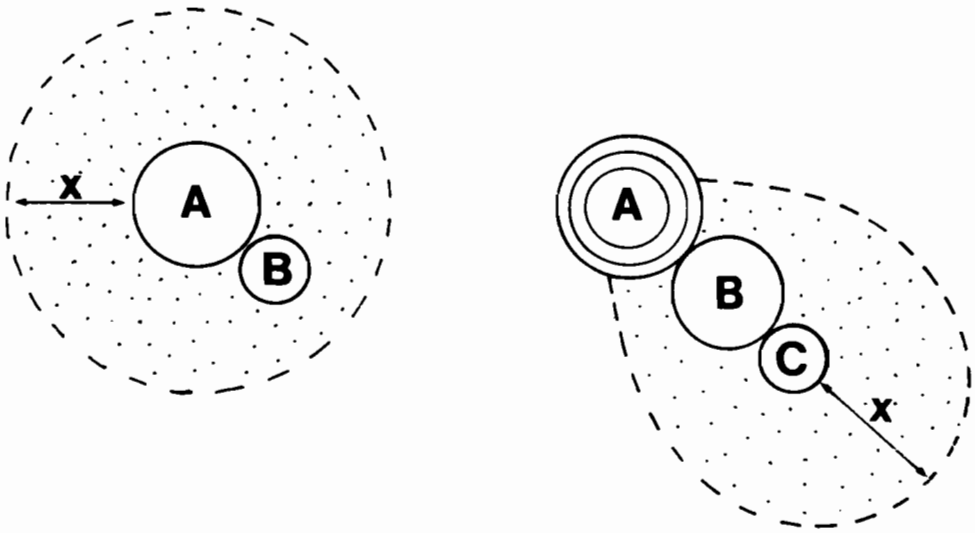

Fig. 6. Area of treatment when using granular nematicides on young plantation and on a ratooning crop.
A Mother plant
B Selected daughter sucker (1st ratoon)
C Selected daughter sucker (to produce second ratoon)
X Radius of treatment area 35–50 cm

Nematode populations might become sensitised or resistant to repeated applications of nematicides (Yamashita & Viglierchio, 1987) although in banana plantations the efficiency of soil application is unlikely to be so good as to exert continuous selection pressures on entire populations in roots and soil.

The degree of sorption of nematicides in different soil types may influence performance (Hague & Gowen, 1987) and, in light sandy or volcanic ash soils where sorption is low, phytotoxicity might occur (Gowen, unpubl.). Generally all types are equally effective in sandy or loamy soil but in peaty soils oxime carbamates may be better than organophosphates (Guérout, 1975; Moss *et al.*, 1975).

Biological control

No control techniques involving the field use of pathogens or parasites of the important nematodes of banana have yet been developed. With endoparasitic species that can complete their life cycles in roots and corm tissue the prospect of employing biological control agents seems remote.

Summary of control measures

The different practices used for controlling nematodes in bananas are summarised in Table 4. In permanent cultivation, the opportunities for control are limited to regular nematicide treatment, however in subsistence cultivation, the only realistic or economically justifiable techniques for preventing losses from nematodes may be by applying large quantities of mulch to stimulate root growth and by propping fruiting stems. Several of the techniques used for nematode control are also appropriate for controlling the banana borer which is a widespread pest causing damage to banana corms.

The selection of appropriate control techniques will depend largely on the local conditions, availability and reliability of workers and economic considerations. Most control methods depend on the skill and experience of the operators and may be of little value if the work is not well supervised.

TABLE 4. Established practises for decreasing nematode populations in different banana growing systems.

REPLANTED SYSTEM

1. Rotation with alternative crops for 2–3 years.
2. Flooding for 8 weeks after having destroyed previous banana crop.
3. Fallow in absence of banana 'volunteers' for 10–12 months.
4. Selection of disease-free suckers.
5. Use of *in vitro* produced plants.
6. Paring diseased tissue from corm.
7. Paring and leaving large corms in sun for 14 days.
8. Immersing corms in hot water.
9. Coating corms with nematicide in mud.
10. Applying nematicide to planting hole and in-fill soil.
11. Regular spot applications with granular or liquid nematicide formulations.

PERMANENT PLANTATIONS

Regular spot applications with granular or liquid nematicide formulations.

Heavy mulches with organic wastes may have beneficial root growth effects and propping fruiting stems with poles or with string guy ropes may prevent plants uprooting.

Methods of diagnosis

Sampling

The root systems of bananas are unlike those of short-cycle and other perennial crops, and methods for sampling have to be modified accordingly. Some of the basic principles of sampling are reviewed by Southey (1986) and McSorley (1987).

The growth habit of the banana plant is a clump consisting of a mother plant and a number of lateral (daughter) suckers. The intensity of suckering varies between the different clones, some producing very few (Stover & Simmonds, 1987). A succession of roots develop from the corm of the mother plant and from its suckers until the time of flowering, thereafter the new root growth is only from the daughter suckers.

In the field, primary roots may be caused to branch extensively when the dominance of the root apex is disrupted by infection or attack by soil organisms or even unfavourable soil conditions (Lassoudière, 1978).

Samples taken near to the base of the stem of the mother plant will contain roots of different ages and vigour and consist predominantly of primary roots with relatively smaller quantities of secondary and perhaps no tertiary roots. It is in this region that roots will contain high populations of root cortex destroyers which usually are the "key pests" (Thomason & Caswell, 1987) against which most control techniques are directed. In an organic soil in the Ivory Coast where *R. similis* and *H. multicinctus* are the principal nematodes, studies of the relative populations in the roots of the different parts of the clump have shown that greater numbers of *R. similis* occur in the roots of the most actively growing suckers. *H. multicinctus* is relatively more numerous in roots of older suckers and harvested plants (Fig. 7). In Israel, greater numbers of *H. multicinctus* were found in the proximal 30–50 cm of primary roots (Strich-Harari *et al.*, 1966).

By separating primary roots from the others Edmunds (1968) showed that by weight the "secondary" and "tertiary" roots contained the greater numbers of a mixed population of *R. similis, H. multicinctus, R. reniformis* and *Meloidogyne* sp. It is possible however, that the terminology of root types described by Edmunds does not correspond with that described by Swennen *et al.* (1986) who studied root systems of bananas grown hydroponically. Root samples containing large quantities of thin, branching primary roots may therefore contain relatively greater numbers of nematodes than equivalent weights of root consisting of thicker unbranched primaries.

Sucker	*Nematode g^{-1} root*	
	Rs	*Hm*
A mother plant (harvested)	18	690
B pruned sucker	3	330
C selected daughter sucker (1st ratoon crop unharvested)	39	241
D pruned sucker	276	67
E selected daughter sucker (to produce second ratoon crop)	320	119
F youngest sucker	4	37

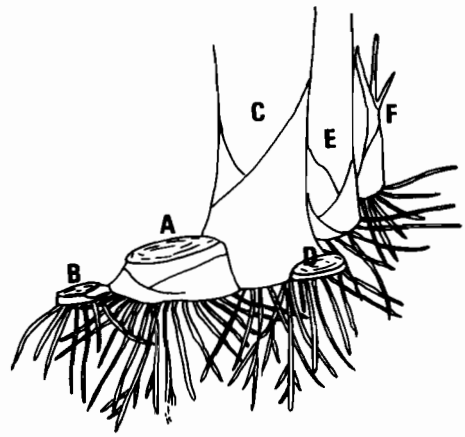

Fig. 7. The population levels of *Radopholus similis* (Rs) and *Helicotylenchus multicintus* (Hm) in the roots of the different components of a banana clump. From peaty soil, Niéky Valley, Ivory Coast (Quénéhervé unpubl.).

When sampling nematode control experiments in farmers' fields, quantities of roots with adjacent soil are taken from five to ten plants per plot and are bulked to form one composite sample. Samples are normally collected from close to the base of the principal pseudostem at a depth of 5–25 cm where there is an abundance of primary roots and which is within the area over which nematicide treatments are normally applied. Sampling may be done monthly or less frequently.

In more detailed studies of population dynamics of different species over one or more years, it may be desirable to analyse separately the roots originating from suckers of different stages of development on single plant clumps and the relative proportions of species along the length of the roots. This may involve the destructive sampling of entire plants (Quénéhervé & Cadet, 1986).

In localities where *R. similis* is known to be the only important root parasite, root sampling may be adequate to represent the population structure as the numbers in soil are relatively low. For other nematodes particularly *R. reniformis, Meloidogyne* spp., *H. multicinctus* and the ectoparasites, soil sampling will complement data from root samples.

It is generally accepted that the quality of nematode counts is only as good as the attention given to sampling and extraction. This is particularly true when sampling bananas as it is evident that the task requires careful supervision. In summary, the techniques of sampling bananas and plantains have to be within capabilities of the available personnel and laboratory facilities. The basic requirements are that sufficient representative plants are sampled (Vilardebó, 1974; Sarah, 1986), that there is consistency from where the roots (and soil) are taken in relation to position and growth stages of the plant, within samples, and between sampling dates. As a guideline, root sampling might be best done at the time of flowering when the phenology is clearly defined.

Extraction

Samples of banana roots and soil may be collected at locations far from the laboratory. Ideally, processing should be done as quickly as possible and samples should be kept cool and out of direct sunlight during collection and transit. The numbers of *R. similis* and *H. multicinctus* extracted may

be affected differentially by the conditions and period of storage prior to processing (Whyte & Gowen, 1974).

The techniques used to extract the nematodes of banana may depend on the available laboratory facilities and assistance, and use may be made of non-standard materials purchased locally. This should not prevent or discourage nematologists from adapting a technique which can be used routinely by different operators to give reproducible and equivalent results throughout a period of experimentation. Before initiation of a procedure it will be necessary to find the optima for sample weight, size of chopped roots, and periods of maceration, incubation, centrifugation or sieving (Alvarado-Soto & Lopez-Chavez, 1981).

Banana roots can present some difficulties in extraction if direct maceration and incubation techniques are used. The high levels of phenolic compounds released from chopped or macerated roots can cause a depletion in oxygen level and thus influence the recovery of nematodes because they may become inactive. This can be partly overcome by adding hydrogen peroxide to the extraction dishes (Gowen & Edmunds, 1973). However, direct recovery techniques by maceration and sieving (Vilardebó *et al.*, 1972; Quimi & Villacis, 1977), maceration, flocculation – flotation (Escobar & Rodriguez-Kabana, 1980; Hooper, 1986) will be more efficient. The mistifier extraction technique (Hooper, 1986) is used in some laboratories for recovering migratory endoparasitic species and efficiency in recovery improves if the roots are chopped in short (0.5 cm) sections (ORSTOM, unpubl. data). The recovery period may differ for the different species.

Whatever extraction procedure is used it is important to obtain a representative root sample which should be chopped in 0.5 cm lengths, mixed thoroughly and a 25 g subsample taken for processing. A 24 hour period of incubation is sufficient for macerated root samples. Chopped roots should be incubated for 2–4 days and mist extractions may be run for up to 14 days in some laboratories.

It is customary to report nematode populations per 100 g of fresh roots although this quantity is seldom used for extraction.

No specific techniques have been described for extraction or estimation of the sedentary endoparasites *R. reniformis* and *Meloidogyne* spp. in banana roots but those used for their extraction from other hosts and the many techniques for extracting migratory endoparasites from plant material and the free-living stages in the soil are given by Hooper (Chapter 2).

Visual assessments

Where nematologists or laboratory facilities are unavailable, nematode damage is sometimes assessed by recording incidence of uprooting per hectare per month (Tarté & Pinochet, 1981). This may also be correlated with assessments of necrosis on primary roots and on rhizomes taken from randomly selected plants from a plantation (Stover, 1972; Tarté & Pinochet, 1981; Bridge, 1988; Sikora *et al.*, 1989). Such techniques can be used by those who are familiar with nematode symptoms but care should be taken not to confuse lesions caused by plant parasitic nematodes with those resulting from other root infesting pests and pathogens.

Determination of populations and crop loss

Quantification of crop losses attributable to nematodes is difficult because of the close association between species, soil pests and pathogens and with environmental conditions (Ferris, 1981).

The nematode parasites of banana can be classified according to the damage caused. The most serious are those that destroy root cortex (*R. similis, Pratylenchus* spp., *H. multicinctus*). Damaged cortex then becomes colonised by fungi which penetrate vascular tissues and hasten the decline in root function. Typically, on an infested plant all gradations of root damage can be found. The parasitism of *Meloidogyne* spp. and *R. reniformis* may impede the efficiency of roots but does not usually lead to their rapid decomposition. Their location (particularly *R. reniformis*) on the thinner roots suggests that damage will affect absorption. Yield losses attributed to these nematodes have not been determined. Many ectoparasitic species probably only browse on the fine secondary and

tertiary roots. Despite the large populations recovered from soil there are no reports of damage causing yield loss.

The damage caused by nematodes in different soil types and the influence of wind exposure can, in terms of uprooting, be devastating. The mechanical stresses on the stem and corm of bananas bearing fruit at 2 m or more above the ground are probably considerable. Anchorage may be further impaired by the deliberate removal or suppression of suckers as part of agronomic practice. There may often therefore be direct relationships between nematode populations, root damage and uprooting. In many situations where uprooting occurs, corm necrosis (and consequent root damage) may result from borers (*C. sordidus*). Corm necrosis caused by borers and nematodes can be difficult to distinguish.

No universally agreed population damage thresholds have yet been suggested, probably because of the nature of the host plant and of its different parasites in different environments. The nematodes are generally on a continuous reproductive cycle influenced by the vigour of the plant and also by environmental conditions. Similarly the plant is in a continuous state of aerial growth and root proliferation also mediated by the environment and perhaps foliar and root pathogens. In such situations, it is difficult to introduce concepts of initial inoculum potential linked to crop losses and final population densities as can be shown with some other plant-parasite associations. Nevertheless, in long term banana experimentation with nematicides, regular sampling can describe population levels which can be compared with crop productivity. From such studies Guérout (1972) considered that 1000 *R. similis* per 100 g of roots was a damage threshold on the AAA cultivar Poyo in the Ivory Coast. It might be dangerous to use this value to consider thresholds on other cultivars of banana which may have more or less vigorous root systems. In Latin America, relatively less severe crop losses may be explained by differences in pathogenicity of *R. similis* populations (Pinochet, 1979). However, it is surprising that in Honduras, Costa Rica and Panama, populations as high as 20 000/100 g of roots of AAA cultivars are considered critical (Pinochet, 1987). In the Windward Islands yield losses can be severe when mixed populations of *R. similis* and *H. multicinctus* exceed 10 000/100 g roots. Despite these differences between regions (and in efficiency of extraction techniques) it is probably not unreasonable to consider root infestations in excess of 2000 per 100 g of roots as a potential cause of crop losses in all commercially grown cultivars.

There is always the likelihood of external influences or events causing crop loss by uprooting. Such losses might be far in excess of those that might be incurred through the general debilitation resulting from the parasitic burden of nematodes feeding in and on the root system.

Conclusions and Future Prospects

Many changes have occurred in the cultivation of bananas in recent years and, with increasing interest in the many different types of banana, it may be expected that the areas cultivated for local and regional markets will expand. Since 1961–5 the combined production of bananas and plantains has increased from 38 million tons to 69 million tons (FAO, 1977, 1987*a*). The relatively recent extension of banana cultivation in ecologically less favourable zones such as Sind province in Pakistan, Morocco and North Yemen is in response to the demands of expanding urban markets and, in some cases, restrictions on the importation of fruit.

The areas of dessert bananas grown for the international export trade will probably increase marginally but the spread of some serious diseases is a major threat to production and could destroy the export industry such as has happened in some of the islands of the Pacific (Fullerton, 1987). Export bananas are grown on plantations but the attention that is necessary for the production and presentation of high quality fruit is closer to that given for horticultural crops. Increasingly, banana plantations will require a well trained workforce that can adapt to changes in crop management techniques.

The wide variability that exists in the many different clones of both dessert and cooking bananas has not been exploited and may show desirable types suited to a broader range of ecological

conditions and with useful disease and pest resistance. The International Network for Improvement of Banana and Plantain (INIBAP) has been formed to co-ordinate the transfer and evaluation of *Musa* germplasm for disease resistance and genetic improvement. The freer movement of genetic material has been made possible by the development of *in vitro* culture techniques thus overcoming the fear of further continental and intercontinental movement of some, as yet, uncontrollable pests and diseases.

Despite the many years of effort, no new banana has been bred to satisfy the stringent demands of the major banana exporters. International trade is based on the minor variants of one genotype *Musa* AAA subgroup Cavendish. Renewed efforts in banana breeding (Shepherd *et al.*, 1987) may introduce good agronomic qualities along with pest and disease resistance to cultivars which have a wider acceptance in home or regional markets.

Exploitation of the resistance to *R. similis* in the diploid AA 'Pisang Jari Buaya' (Pinochet & Rowe, 1979; Pinochet, 1988) should be a major priority although plant characters such as root vigour that confer some tolerance to nematodes should also be considered, particularly in programmes for improvement of cooking cultivars.

The development of micropropagation enables the mass production of plants for new commercial plantings. This has considerable advantages over conventional techniques as it ensures that plantations are free (at least initially) from nematode parasites and borers. However, the incidence of undesirable somaclonal variants (Vuylsteke *et al.*, 1988) may become a cause for some concern. Micropropagation should be of benefit to nematologists who should be able to devise critical tests for pathogenicity of the different nematode species on breeding lines and new cultivars.

The procedures for studying population ecology of the nematode communities feeding in or on banana roots should be examined in greater detail. The importance of several ectoparasitic species, and the sedentary parasites *R. reniformis* and *Meloidogyne* spp. is not well understood. Such studies will almost certainly have to be separated from those established procedures for the regular sampling of experiments on chemical control. The traditional methods of sampling roots close to the corm were designed to evaluate the populations where nematicides are applied. This puts a bias on the importance of those parasites in the proximal portion of the primary roots and neglects those feeding on the thinner distal parts of the root system.

Nematodes will continue to be a major production constraint for most types of banana cropping system. There are no major banana growing regions in the tropics where *R. similis, H. multicinctus* or *Pratylenchus* spp. have not been found. *Meloidogyne* spp. appear to be more damaging in the few special production areas outside the tropics such as Morocco, N. Yemen and Cyprus, and in Taiwan.

Nematicides are the only available means of controlling nematodes in established plantations. The absence of new compounds with novel modes of activity that can be used economically on a large scale means that the use of existing products will continue for the foreseeable future, particularly by those growers supplying fruit to the high value markets.

The use of liquid formulations in irrigation will continue to increase as more commercial plantations install drip irrigation systems. This method has both labour saving and safety advantages. Further research is needed to establish the optimum dosages and frequencies of application.

Refinements in the efficiency of nematicide use may be devised whereby plants are treated individually at well defined events such as harvest when the growth of the sucker is stimulated.

Cost and high mammalian toxicities discourage nematicide use in most growing systems other than for international export.

Further research into the suitability of nematicides in certain soil types and environments will be necessary and greater attention will have to be given to the possible development of microbially active soils. With increased application efficiency, the selection of soil floras with enhanced ability to degrade nematicides may become a major technical problem requiring careful planning of nematicide rotations.

Acknowledgements

We thank the following for sending information from their countries: M. Amati, C. Bazirake, F. Caveness, H. Chiang, E. Cohn, A. Daudi, R. Hugon, I. Inglis, A. Lassoudière, B. Lubilanj–Tshibamba, Mauritius Ministry of Agriculture, D. Masaba, E. Mcharo, J. Meyers, F. Ngulu, B. Ngundo, J. Philis, S. Simon, and A. Wybou.

References

Adiko, A. (1988). Plant-parasitic nematodes associated with plantain, *Musa paradisiaca* (AAB), in the Ivory Coast. *Revue de Nématologie*, 11:109–113.

Alvarado-Soto, M. & Lopez-Chavez, R. (1981). Eficacia de dos metodos y sus modificaciones en la extracción de nemátodos endopárasitos migratorios de raices de piña y plátano. *Nematropica*, 11:129–136.

Ambrose, E. (1984). Research and development in banana crop protection (excluding Sigatoka) in the English speaking Caribbean. *Fruits*, 39:234–247.

Ayala, A. (1962). Pathogenicity of the reniform nematode on various hosts. *Journal of Agriculture, University of Puerto Rico*, 45:265–299.

Ayala, A. & Roman, J. (1963). Distribution and host range of the burrowing nematode in Puerto Rican soils. *Journal of Agriculture, University of Puerto Rico*, 47:28–37.

Badra, T. & Caveness, F. E. (1983). Effects of dosage sequence on the efficacy of nonfumigant nematicides on plantain yields, and nematode seasonal fluctuations as influenced by rainfall. *Journal of Nematology*, 15:496–502.

Berg, L. A. & Bustamente, M. (1974). Heat treatment and meristem culture for the production of virus-free bananas. *Phytopathology*, 64:320–322.

Beugnon, M. & Champion, J. (1966). Etude sur les racines du bananier. *Fruits*, 21:309–327.

Bird, A. F. (1979). Morphology and ultrastructure. In: Lamberti, F. & Taylor, C. E. (Eds): *Root-knot Nematodes (*Meloidogyne *species) Systematics, Biology and Control*. London, Academic Press: 59–84.

Blake, C. D. (1961). Root rot of bananas caused by *Radopholus similis* (Cobb) and its control in New South Wales. *Nematologica*, 6:295–310.

Blake, C. D. (1963). Root and corm diseases of bananas. *Agricultural Gazette of New South Wales*, 74:526–531.

Blake, C. D. (1966). The histological changes in banana roots caused by *Radopholus similis* and *Helicotylenchus multicinctus*. *Nematologica*, 12:129–137.

Booth, C. & Stover, R. H. (1974). *Cylindrocarpon musae* sp. nov., commonly associated with burrowing nematode (*Radopholus similis*) lesions on bananas. *Transactions of the British mycological Society*, 63:503–507.

Bridge, J. (1987). Control strategies in subsistence agriculture. In: Brown, R. H. & Kerry, B. R. (Eds): *Principles and Practice of Nematode Control in Crops*. Sydney, Australia, Academic Press: 389–420.

Bridge, J. (1988). Plant nematode pests of banana in East Africa with particular reference to Tanzania. *Nematodes and the Borer Weevil in Bananas: present status of research and outlook. Proceedings of a workshop held in Bujumbura, Burundi 7–11 December 1987*. 35–39.

Bridge, J. & Page S. L. J. (1984). Plant nematode pests of crops in Papua New Guinea. *Journal of Plant Protection in the Tropics* 1:99–109.

Caveness, F. E. & Badra, T. (1980). Control of *Helicotylenchus multicinctus* and *Meloidogyne javanica* in established plantains and nematode survival as influenced by rainfall. *Nematropica*, 10:10–14.

Champion, J. & Sioussaran, D. (1970). L'enracinement du bananier dans les conditions de la station de Neufchateau (Guadeloupe). *Fruits*, 25:847–859.

Cronauer, S. S. & Krikorian, A. D. (1984). Multiplication of *Musa* from exised stem tips. *Annals of Botany*, 53:321–328.

Darthenucq, A., Ganry, J., Lachenaud, J., Melin, P. & Meyer, J. P. (1978). Notes d'un voyage d'étude dans quelques zones bananières d'Amérique Latine (avril-mai 1977). *Fruits*, 33:157–165.

Davide, R. G. (1980). Influence of cultivar, age, soil texture and pH on *Meloidogyne incognita* and *Radopholus similis* on banana. *Plant Disease Reporter*, 64:571–573.

Davide, R. G. & Marasigan, L. Q. (1985). Yield loss assessment and evaluation of resistance of banana cultivars to the nematodes *Radopholus similis* Thorne and *Meloidogyne incognita* Chitwood. *Philippine Agriculturalist*, 68:335–349.

Ducharme, E. P. & Birchfield, W. (1956). Physiologic races of the burrowing nematode. *Phytopathology*, 46:615–616.

Edmunds, J. E. (1968). Nematodes associated with bananas in the Windward Islands. *Tropical Agriculture, Trinidad*, 45:119–124.

Edwards, D. I. & Wehunt, E. J. (1971). Host range of *Radopholus similis* from banana areas of Central America with indications of additional races. *Plant Disease Reporter*, 55:415–418.

Epp, M. D. (1987). Somaclonal variation in bananas: a case study with *Fusarium* wilt. In: Persley, G. J. & De Langhe, E. A. (Eds): *Banana and Plantain Breeding Strategies*: Proceedings of an International Workshop held at Cairns, Australia 13–17 October 1986, ACIAR, Proceedings No. 21: 140–150.

Escobar, J. & Rodriguez-Kabana, R. (1980). Comparacion de un método de flotacion con uno de tamizado para la determinacion de *Radopholus similis* en raices de banano. *Nematropica*, 10:86–88.

FAO (1950). Production Yearbook for 1949. *Vol. 3* Rome.

FAO (1972). Production Yearbook for 1971. *Vol. 25* Rome.

FAO (1977). Production Yearbook for 1976. *Vol. 30* Rome.

FAO (1987*a*). Production Yearbook for 1986. *Vol. 40* Rome.

FAO (1987*b*). Trade Yearbook for 1986. *Vol. 40* Rome.

Fargette, M. (1987). Use of the esterase phenotype in the taxonomy of the genus *Meloidogyne* 2. Esterase phenotypes observed in West Africa populations and their characterization. *Revue de Nématologie*, 10:45–56.

Fargette, M. & Quénéhervé, P. (1988). Populations of nematodes in soils under banana, cv Poyo, in the Ivory Coast. 1. The nematofauna occuring in the banana producing areas. *Revue de Nématologie*, 11:239–244.

Ferris, H. (1981). Dynamic action thresholds for disease induced by nematodes. *Annual Review of Phytopathology*, 19:427–436.

Ferris, V. R. & Ferris, J. M. (1974). Inter-relationship between nematode and plant communities in agricultural ecosystems. *Agro-Ecosystems* 1:275–299.

Fluiter, H. J. & Mulholland, J. J. (1941). Gegevens, verkregen bij het onderzoek naar de waardplantenvan *Tylenchus coffeae*. *Bergcultures*, 15:1588–1593.

Fullerton, R. A. (1987). Banana production in selected Pacific Islands. In: Persley, G. J. & De Langhe, E. A. (Eds): *Banana and Plantain Breeding Strategies:* Proceedings of an International Workshop held at Cairns, Australia 13–17 October 1986. ACIAR, Proceedings No. 21 57–62.

Gichure, E. & Ondieki, J. J. (1977). A survey of banana nematodes in Kenya. *Zeitschfrift für Pflanzenkrankheiten und Pflanzenschutz*, 84:724–728.

Goodey, J. B., Franklin, M. T. & Hooper, D. J. (1965). T. Goodey's *The nematode parasites of plants catalogued under their hosts*. Slough, UK Commonwealth Agricultural Bureaux, 214p.

Gotoh, A. (1964). The embryonic and larval development of *Pratylenchus coffeae* (Zimmerman) (Nematoda: Tylenchida). *Japanese Journal of Applied Entomology and Zoology*, 8:26–33.

Gowen, S. R. (1975). Improvement of banana yields with nematicides. *Proceedings 8th British Insecticide and Fungicide Conference, Brighton 1975*: 121–125.

Gowen, S. R. (1976). Varietal responses and prospects for breeding nematode resistant banana varieties. *Nematropica*, 6:45–49.

Gowen, S. R. (1979). Some considerations of problems associated with the nematode pests of bananas. *Nematropica*, 9:79–91.

Gowen, S. R. & Edmunds, J. E. (1973). An evaluation of some simple extraction techniques and the use of hydrogen peroxide for estimating nematode populations in banana roots. *Plant Disease Reporter*, 57:678–681.

Guérout, R. (1972). Relations entre les populations de *Radopholus similis* et la croissance du bananier. *Fruits*, 27:331–337.

Guérout, R. (1975). The soil and its importance on the effect of nematicidal treatments on banana yields. *Nematropica*, 5:22–23.

Guérout, R., Lassoudière, A. & Vilardebó, A. (1976). Efficacité des nématicides sur deux types de sol à caractéristiques particulières en Côte d'Ivoire. *Fruits*, 31:427–436.

de Guiran, G. & Vilardebó, A. (1962). Le bananier aux Iles Canaries. IV: Les nématodes parasites. *Fruits*, 17:263–277.

Hague, N. G. M. & Gowen, S. R. (1987). Chemical control of nematodes. In: Brown, R. H. & Kerry, B. R. (Eds) *Principles and Practice of Nematode Control in Crops*, Sydney, Australia, Academic Press: 131–178.

Hooper, D. J. (1986). Extraction of nematodes from plant material. In: Southey, J. F. (Ed.): *Laboratory Methods for Work with Plant and Soil Nematodes*, M. A. A. F. Reference Book 402, HMSO London: 51–58.

Huang, C. S. (1985). Formation, anatomy and physiology of giant cells induced by root-knot nematodes. In: Sasser, J. N. & Carter, C. C. (Eds): *An Advanced Treatise on* Meloidogyne. *Vol. 1 Biology and Control.* North Carolina State University: 155–164.

Huettel, R. N., Dickson, D. W. & Kaplan, D. T. (1984). *Radopholus citrophilus* sp. n. (Nematoda), a sibling species of *Radopholus similis. Proceedings of the helminthological Society of Washington*, 51:32–35.

Huettel, R. N. & Yaegashi, T. (1988). Morphological differences between *Radopholus citrophilus* and *R. similis. Journal of Nematology*, 20:150–157.

Hugon, R., Ganry, J. & Berthe, G. (1984). Dynamique de population du nématode *Radopholus similis* en fonction du stade de développement du bananier et du climat. *Fruits*, 39:251–253.

Hutton, D. G. (1978). Influence of rainfall on some plantain nematodes in Jamaica. *Nematropica* 8:34–39.

Hutton, D. G. & Chung, D. C. (1973). Effects of post-planting application of the nematicide DBCP to plantain. *Nematropica*, 3:46–50.

Hwang, S. C., Chen, C. L. & Wu, F. L. (1984). An investigation on susceptibility of banana clones to fusarial wilt, freckle and marginal scorch disease in Taiwan. *Plant Protection Bulletin (Taiwan)*, 26:155–161.

INIBAP (1986). *Banana Research in Eastern Africa. Proposal for a regional research and development network.* International Network for the Improvement of Bananas and Plantains). Montpellier, France.

Irizarry, H., Vicente-Chandler, J. & Silva, S. (1981). Root distribution of plantains growing on five soil types. *Journal of Agriculture, University of Puerto Rico*, 65:29–34.

Jaramillo, R. & Figueroa, A. (1974). Análisis armónico de la densidad de población de *Radopholus similis* (Cobb) Thorne en la zona bananera de Guápiles, Costa Rica. *Turrialba*, 24:402–407.

Jaramillo, R. & Figueroa, A. (1976). Relación entre el balance hídrico y la población de *Radopholus similis* (Cobb) Thorne en la zona bananera de Guápiles, Costa Rica. *Turrialba*, 26:187–192.

Jimenez, M. F. (1972). Fluctuaciones anuales de la población de *Radopholus similis* (Cobb) Thorne en la zona bananera de Potoci, Costa Rica. *Nematropica*, 2:33–40.

Jones, R. K. & Milne D. L. (1982). Nematode pests of bananas. In: Keetch, D. P. & Heyns, J. (Eds): *Nematology in Southern Africa*. Pretoria, Republic of South Africa: 30–37.

Lassoudière, A. (1978). Quelques espects de la croissance et du développment du bananier "Poyo" en Côte d'Ivoire. 2. Le système radical. *Fruits*, 33:314–338.

Lassoudière,A. & Martin, P. (1974). Problèmes de drainage en sols organiques de bananeraie (Agnéby, Côte d'Ivoire). *Fruits*, 29:255–266.

Lavigne, C. (1987). Contribution á l'étude du système racinaire du bananier. Mise au point de rhizotrons et premiers résultats. *Fruits*, 42:265–271.

Laville, E. (1964). Etude de la mycoflore des racines du bananier "Poyo". 1. Etude du système radiculaire. *Fruits*, 19:435–449.

Leach, R. (1958). Blackhead toppling disease of bananas. *Nature*, 181:204–205.

Lin, Yih-Yaw & Tsay, Tung-Tsan (1985). Studies on banana root-knot nematode disease in the central area of Taiwan. *Journal of the Chinese Society for Horticultural Science*, 31:44–46.

Loos, C. A. (1959). Symptom expression of *Fusarium* wilt disease of the Gros Michel banana in the presence of *Radopholus similis* (Cobb, 1893) Thorne, 1949 and *Meloidogyne incognita acrita* Chitwood, 1949. *Proceedings of the helminthological Society of Washington*, 26:103–111.

Loos, C. A. (1961). Eradictation of the burrowing nematode, *Radopholus similis*, from bananas. *Plant Disease Reporter*, 45:457–461.

Loos, C. A. (1962). Studies on the life history and habits of the burrowing nematode, *Radopholus similis*, the cause of blackhead disease of banana. *Proceedings of the helminthological Society of Washington*, 29:43–52.

Loos, C. A. & Loos, S. B. (1960*a*). Preparing nematode free banana seed. *Phytopathology*, 50:383–386.

Loos, C. A. & Loos, S. B. (1960*b*). The blackhead disease of bananas. *Proceedings of the helminthological Society Washington*, 27:189–193.

Luc, M. & Vilardebó, A. (1961). Les nématodes associés aux bananiers cultivés dans l'ouest Africain. *Fruits*, 16:205–219.

Maas, P. W. T. (1969). Two important cases of nematode infestation in Surinam. In: Peachey, J. E. (Ed): *Nematodes of Tropical Crops*. Slough, UK, Commonwealth Agricultural Bureaux: 149–154.

Marcelino, L. L., Viquez, M. & Tarté, R. (1978). Fluctuaciones estacionales de la densidades de poblacion de *Radopholus similis* en raices de banano "Valery" (*Musa acuminata* AAA) en la zona Pacifica de Panama. *Nematropica*, 8:52–55.

Mateille, T., Cadet, P. & Quénéhervé, P. (1984). L'influence du recépage du bananier cv. Poyo sur le développement des populations de *Radopholus similis* et d'*Helicotylenchus multicinctus*. *Revue de Nématologie*, 7:355–361.

Mateille, T., Foncelle, B. & Ferrer, H. (1988*a*). Lutte contre les nématodes du bananier par submersion du sol. *Revue de Nématologie*, 11:235–238.

Mateille, T., Quénéhervé, P. & Topart,P. (1988*b*). Nematicidal treatment of banana AAA cv. Poyo planting material by corm coating. *Revue de Nématologie*, 11:89–92.

McSorley, R. (1987). Extraction of nematodes and sampling methods. In: Brown, R. H. & Kerry, B. R. (Eds): *Principles and Practice of Nematode Control in Crops* Sydney, Australia, Academic Press: 13–47.

McSorley, R. & Parrado, J. (1981). Population fluctuations of plant-parasitic nematodes on bananas in Florida. *Proceedings of the Florida State Horticulture Society*, 94:321–323.

McSorley, R. & Parrado, J. L. (1983). The spiral nematode, *Helicotylenchus multicinctus*, on bananas in Florida and its control. *Proceedings Florida State Horticultural Society*, 96:201–207.

McSorley, R. & Parrado, J. L. (1986). Nematological Review: *Helicotylenchus multicinctus* on bananas: an international problem. *Nematologica*, 16:73–91.

Melin, P. & Vilardebó, A. (1973). Efficacité de quelques nematicides en bananeraie dans les sols volcaniques de la région du Mungo (Cameroun). *Fruits*, 28:3–17.

Menendez, T. & Shepherd, K. (1975). Breeding new bananas. *World Crops*, 27:104–112.

Minz, G., Ziv, D. & Strich-Harari, D. (1960). Decline of banana plantations caused by spiral nematodes in the Jordan Valley and its control by DBCP. *Ktavim*, 10:147–157.

Moss, S. R., Crump, D. & Whitehead, A. G. (1975). Control of potato cyst nematode *Heterodera rostochiensis* and *H. pallida* in sandy, peaty and silt loam soils by oxime carbamate and organophosphate nematicides. *Annals of Applied Biology*, 81:359–365.

Netscher, C. (1978). Morphological and physiological variability of species of *Meloidogyne* in West Africa and implications for their control. *Mededelingen. Landbouwhogeschool Wageningen*, 46:78–83.

Newhall, A. G. (1958). The incidence of Panama disease of banana in the presence of the root knot and burrowing nematodes (*Meloidogyne* and *Radopholus*). *Plant Disease Reporter*, 42:853–856.

O'Bannon, J. (1977). Worldwide dissemination of *Radopholus similis* and its importance in crop production. *Journal of Nematology*, 9:16–25.

Ocfemia, G. O. & Calinisan, M. R. (1928). The root knot of abaca or Manila hemp. *Phytopathology*, 18:861–867.

Persley, G. J. & de Langhe, (1987). *Banana and plantain breeding strategies:* Proceedings of an International Workshop held at Cairns, Australia 13–17 Oct. 1986. ACIAR Proceedings No. 21 187p.

Pinochet, J. (1977). Occurrence and spatial distribution of root-knot nematodes on bananas and plantains in Honduras. *Plant Disease Reporter*, 61:518–520.

Pinochet, J. (1978). Histopathology of the root lesion nematode, *Pratylenchus coffeae* on plantains, *Musa* AAB. *Nematologica*, 24:337–340.

Pinochet, J. (1979). Comparison of four isolates of *Radopholus similis* from Central America on Valery Bananas. *Nematropica*, 9:40–43.

Pinocheto, J. (1987). La variabilidad de *Radopholus similis* en banane en las diferentes regiones productoras del mundo. *Memorias VII Reunion ACORBAT Realizada en San José, Costa Rica Setiembre, 1985 CATIE, Costa Rica*, 175–182.

Pinochet, J. (1988). Comments on the difficulty in breeding bananas and plantains for resistance to nematodes. *Revue de Nématologie*, 11:3–5.

Pinochet, J. & Rowe, P. R. (1978). Reaction of two banana cultivars to three different nematodes. *Plant Disease Reporter*, 62:727–729.

Pinochet, J. & Rowe, P. R. (1979). Progress in breeding for resistance to *Radopholus similis* in banana. *Nematropica*, 9:76–78.

Pinochet, J. & Stover, R. H. (1980). Fungi lesions caused by burrowing nematodes on bananas and their root and rhizome rotting potential. *Tropical Agriculture, Trinidad*, 57:227–232.

Quénéhervé, P. (1988). Populations of nematodes in soils under banana, cv "Poyo", in the Ivory Coast. 2. Influence of soil texture, pH and organic matter on nematode populations. *Revue de Nématologie*, 11:245–251.

Quénéhervé, P. (1989*a*). Population of nematodes in soils under banana, cv. "Poyo", in the Ivory Coast. 3. Seasonal dynamics of populations in mineral soil. *Revue de Nématologie*, 12:149–160.

Quénéhervé, P. (1989*b*). Population of nematodes in soils under banana, cv. "Poyo", in the Ivory Coast. 4. Seasonal dynamics of populations in organic soil. *Revue de Nématologie*, 12:161–170.

Quénéhervé, P. & Cadet, P. (1985*a*). Localisation des nematodes dans les rhizomes du bananier cv Poyo. *Revue de Nématologie*, 8:3–8.

Quénéhervé, P. & Cadet, P. (1985*b*). Etude de la dynamique de l'infestion en nématodes transmis par les rhizomes du bananier cv Poyo en Côte d'Ivoire. *Revue de Nématologie*, 8:257–263.

Quénéhervé, P. & Cadet, P. (1986). Une nouvelle technique d'échantillonnage pour l'étude des nématodes endoparasites du bananier. *Revue de Nématologie*, 9:95–97.

Quimi, V. H. & Villacis, J. (1977). Estudio comparativo de dos métodos de extracción del nématodo *Radopholus similis* de las raices de banano. *Nematropica*, 7:44–47.

Rivas, X. & Roman, J. (1985). Oogenesis y reproduccion de una poblacion de *Radopholus similis* de Puerto Rico. *Nematropica*, 15:19–25.

Roman, J., Rivas, X., Oramas, D. & Rodriguez, J. (1977). Further experiments on the chemical control of nematodes in plantains (*Musa acuminata* X *M. balbisiana*, AAB). *Journal of Agriculture of University of Puerto Rico*, 61: 192–199.

Ruthenberg, H. (1980). *Farming Systems in the Tropics*. 3rd Edn. Oxford University Press. 424p.

Sarah, J-L (1986). Répartition spatiale des infestations racinaires de *Radopholus similis* en relation avec la croissance et le développement du bananier "Poyo" en Côte d'Ivoire. *Fruits*, 41: 427–435.

Sarah, J-L, Lassoudière, A. & Guérout, R. (1983). La jachère nue et l'immersion du sol: deux méthodes intéressantes de lutte intégrée contre *Radopholus similis* (Cobb) dans les bananeraies de sols tourbeux de Côte d'Ivoire. *Fruits*, 38: 35–42.

Shafiee, M. F. & Mendez, J. M. (1975). Estudios sobre tres poblaciónes y fluctuaciónes estaciónales de *Radopholus similis* en plátano, *Musa* sp. *Ciencias, Universito de la Habana, seria II, Sanidad vegetal (1975)*. 12: 12p.

Shepherd, K., Dantas, J. L. L. & Alves, E. J. (1987) Banana breeding in Brazil. In: Persley, G. J. & de Langhe, E. A. (Eds): *Banana and plantain breeding strategies:* Proceedings of an international Workshop held at Cairns, Australia 13–17 Oct. 1986. ACIAR Proceedings No 21: 78–83.

Sher, S. A. (1968). Revision of the Genus *Radopholus* Thorne, 1949 (Nematoda: Tylenchoidea). *Proceedings of the helminthological Society of Washington*, 35: 219–237.

Sikora, R. A. (1979). Observations on *Meloidogyne* with emphasis on disease complexes, and the effect of host on morphometrics. *Proceedings of the second research planning conference on root-knot nematodes, Meloidogyne spp.*, Athens, 93–104.

Sikora, R. A., Bafokuzara, N. D., Mbwana, A. S. S., Oloo, G. W., Uronu, B. & Seshu Reddy, K. V. (1989).

Interrelationship between banana weevil, root lesion nematode and agronomic practices and their importance for banana decline in Tanzania. *FAO Report* (in press.)

Sikora, R. A. & Schlösser, E. (1973). Nematodes and fungi associated with root systems of bananas in a state of decline in Lebanon. *Plant Disease Reporter*, 57: 615–618.

Simmonds, N. W. (1966). *Bananas*, 2nd Ed. London, Longmans, 512p.

Sivakumar, C, V. & Seshadri, A. R. (1974). Histopathology of infection by the reniform nematode *Rotylenchulus reniformis* Linford & Oliveira, 1940 on castor, papaya and tomato. *Indian Journal of Nematology*, 2 (1972) 173–181.

Southey, J. F. (1986). Principles of sampling for nematodes. In: Southey, J. F. (Ed) *Laboratory Methods for Work with Plant and Soil Nematodes*, London HMSO: 1–4.

Stover, R. H. (1966). Fungi associated with nematodes and non nematode lesions on banana roots. *Canadian Journal of Botany*, 44: 1703–1710.

Stover, R. H. (1972). *Banana Plantain and Abaca Diseases*. Kew: Commonwealth Mycological Institute: 316p.

Stover, R. H. & Fielding, M. J. (1958). Nematodes associated with root injury of *Musa* sp. in Honduras banana soils. *Plant Disease Reporter*, 42: 938–940.

Stover, R. H. & Simmonds, N. W. (1987). *Bananas* 3rd Edition. London, Longmans. 468p.

Stoyanov, D. (1967). Especies de nématodos parásitos del plátano en Cuba y posibilidades de su control. *Revista Agricultura, Habana*, 1: 9–47

Strich-Harari, D., Minz, G. & Peled, A. (1966). The spread of spiral nematodes in banana roots and their control. *Israel Journal of Agricultural Research*, 16: 89–94.

Sudha, S. & Prabhoo N. R. (1983). *Meloidogyne* (Nematoda: Meloidogynidae) induced root galls of the banana plant *Musa paradisiaca* a study of histopathology. *Proceedings of the Indian Academy of Sciences, Animal Sciences*, 92: 467–473.

Suett, D. L. & Walker, A. (1988). Accelerated degradation of soil-applied pesticides – implications for UK horticulture. *Aspects of Applied Biology 17 Association of Applied Biologists, Warwick, UK. 1988*: 213–222.

Summerville, W. A. T. (1939). Root distribution of the banana. *Queensland Agricultural Journal* 52: 376–392.

Swennen, R., de Langhe, E., Janssen, J. & Decoene, D. (1986). Study of the root development of some *Musa* cultivars in hydroponics. *Fruits*, 41: 515–524.

Tarjan, A. C. (1961). Longevity of *Radopholus similis* (Cobb) in host free soil. *Nematologica*, 6: 170–175.

Tarté, R. & Pinochet, J. (1981). Problemas nematologicos del banano. Contribuciones reciente a su conocimiento y combate. *Union Paises Exportadores Banano (UPEB), Panama*, 32p.

Tarté, R., Pinochet, J., Gabrielli, C. & Ventura, O. (1981). Differences in population increase, host preferences and frequency of morphological variants among isolates of the banana race of *Radopholus similis*. *Nematropica*, 11: 43–52.

Taylor, A. L. & Loegering, W. Q. (1953). Nematodes associated with root lesions in abaca. *Turrialba*, 3: 8–13.

Thomason, I. J. & Caswell, E. P. (1987). Principles of nematode control. In: Brown, R. H. & Kerry, B. R. (Eds): *Principles and Practice of Nematode Control in Crops*, Sydney, Australia, Academic Press: 87–130.

Varghese, K. C. & Nair, M. R. G. KJ. (1968). Studies on the population fluctuations of soil nematodes associated with banana in Kerala State. *Agricultural Research Journal Kerala*, 6: 108–112.

Vilardebó, A. (1959). Note sur la lutte contre les nématodes du bananier en Guinée. *Fruits*, 14: 125–126.

Vilardebó, A. (1974). Méthode d'essai d'efficacité pratique de nématicides étudiés sur *Radopholus similis* Cobb en bananeraie. *Société Francaise de Phytiatrie & Phytopharmacie, Comm. Essais biol.* No. 49: 29p.

Vilardebó, A. & Guérout, R. (1976). Nematode species in West Africa, Madagascar and Reunion, with some comments on their biology. *Nematropica*, 6: 53–54 (Abstr).

Vilardebó, A., Aubert, A., Beugnon, M., Melin, Ph., Guérout, R., Lassoudière, A., Martin, P. & Pinon, A. (1972). Techniques expérimentales et progrès dans la lutte contre les nématodes en culture bananiére. *Phytiatrie-Phytopharmacie*, 21: 129–139.

Vrain, T. C. (1986). Role of soil water in population dynamics of nematodes. In: Leonard, K. & Fry, W. (Eds). *Plant Disease Epidemiology*. New York, MacMillan: 101–128.

Vuylsteke, D., Swennen, R., Wilson, G. F. & De Langhe, E. (1988). Phenotypic variation among *in vitro* propagated plantain (*Musa* sp. cultivar 'AAB'). *Scientia Horticulturae*, 36: 79–88.

Walker, P. T., Hebblethwaite, M. J. & Bridge, J. (1984). Project for Banana Pest Control and Improvement in Tanzania. *EEC Report for the Government of Tanzania*. Produced by Tropical Development and Research Institute, London 129p.

Weckx, G. (1982). *Invloed van mulching en minerale bemesting op het wortelstelsel van plantaan-banaan*. Eindwerk, Faculty of Agriculture, Catholic University of Louvain, 98p.

Wehunt, E. J. & Edwards, D. I., (1968). *Radopholus similis* and other nematode species on bananas. In: Smart, G. C. & Perry, J. G. (Eds): *Tropical Nematology*. University of Florida Press: 1–19.

Wehunt, E. J., Hutchinson, D. J. & Edwards, D. I. (1978). Reaction of banana cultivars to the burrowing nematode *Radopholus similis*. *Journal of Nematology*, 10: 368–370.

Whyte, E. B. & Gowen, S. R. (1974). Recovery of nematodes from banana roots and soil samples. *Nematropica*, 4: 27–31.

Wilson, G. F., Swennen, R. & de Langhe, E. (1986). Effects of mulch and fertilizer on yield and longevity of a medium and giant plantain and a banana cultivar. *Proceedings of Third Conference of the International Association for Research on Plantain and Bananas. Abidjan, Ivory Coast 1985*, 109–111.

Yamashita, T. T. & Viglierco, D. R. (1987). Field resistance to nonfumigant nematicides in *Xiphinema index* and *Meloidogyne incognita*. *Revue de Nématologie*, 3: 327–332.

Zem, A. C. Alvez, E. J., Lordello, L. G. E. & Montero (1981). Susceptibilidade das bananeiras Prata e Mysore aos nematoides *Radopholus similis* e *Helicotylenchus multicinctus*. *Anais Escola Superior de Agricultura "Luis de Queroz."* 38: 569–578.

Zimmerman, A. W. P. (1898). Die nematoden der koffiewortels. *Mededelingen 's Lands Plantentuin (Buitenzorg)*, 27: 1–64.

Zuckerman, B. M. & Strich-Harari, D. (1963). The life stages of *Helicotylenchus multicinctus* (Cobb) in banana roots. *Nematologica*, 9: 347–353.

Chapter 14

Nematode Parasites of Sugarcane

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Sugarcane is one of the few crops to provide commercial quantities of food, fibre and fuel. It is grown in more than 80 countries throughout the tropics and subtropics and in some of these countries it is the principal source of revenue, for example in the Dominican Republic, Jamaica, Mauritius and Swaziland. The main product of sugarcane is, of course, sugar, the name given to crystals of sucrose.

From 1982 to 1987 mean annual world production of cane sugar exceeded 63 000 000 tons with Brazil being the largest single producer closely followed by Cuba and India (Ahlfeld, 1987). These three countries, together with Australia, China, Mexico, South Africa and Thailand produced more than 60% of the world total. Crude sugar is produced from sugarcane by peasant farmers in many countries, particularly India, Pakistan and Colombia. Crude sugar production does not appear in the statistics although it is estimated to account for one seventh of the world sugar supply (Smith, 1978). In addition to the sugar produced from cane, a further 38 000 000 tons were produced in 1986/1987 from sugar beet (Ahlfeld, 1987).

There are two economically important by-products in the manufacture of sugar from sugarcane, *viz*. bagasse and molasses. Bagasse is the fibrous residue from the cane stalks. It is used primarily as a fuel for the sugar factories but also, for example, in the manufacture of paper and several types of fibrous board. Molasses is the remaining liquor in the manufacturing process after separation of the crystalized sucrose. It is used to produce a range of alcohols and organic acids as well as yeast and animal feed (Barnes, 1974, 1978). In Brazil only one third of the more than 200 million tons of cane is used to produce sugar. The remainder is crushed and the juice fermented to produce ethyl alcohol for use in automotive engines; production in 1985 exceeded 11 billion litres (Reeser, 1987).

Sugarcane is a tall, perennial, thick stemmed grass. Modern cultivars are complex hybrids derived from *Saccharum officinarum* L., *S. barberi* Jesw., *S. sinense* Roxb. and *S. spontaneum* L. (Sreenivasan *et al.*, 1987). *Saccharum officinarum* and *S. spontaneum* probably originated from the New Guinea – East Indonesia area, *S. barberi* from India and *S. sinense* from China (Daniels & Roach, 1987).

Sugarcane plants grow in tufts or stools composed of varying numbers of stalks. At maturity the stalks are approximately 2 – 3m in length and 20 – 30mm in diameter. The stalk is composed of a series of nodes each of which carries an axillary bud and a leaf. Carbohydrate is stored in the internodes primarily as sucrose. Modern cultivars of sugarcane normally contain between 11 and 14% sucrose.

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds) © CAB International 1990

Cultivation

Sugarcane is propagated vegetatively by planting setts or stalk cuttings with two or more nodes. Within a few days roots develop from primordia around the nodes of the setts. These sett roots support the initial growth of the primary shoots which develop from axillary buds on the setts (Fig. 1). Subsequently tillers arise and these and primary shoots develop shoot roots which soon replace the sett roots. As the shoots grow they compete for light and space and a notable proportion die. Those that survive increase in diameter and length. Depending on temperature and available soil moisture, the crop is harvested after approximately 12 to 24 months, when the sucrose content of the stalk approaches its maximum concentration.

Soon after harvest new shoots emerge from axillary buds on the stubble and give rise to the ratoon crop. Initially the young shoots are dependent upon the roots of the previous crop (stool roots) but these are replaced by new shoot roots (Fig. 1). The crop cycle of sugarcane is normally composed of the plant crop and, typically, two to four ratoon crops (Smith, 1978). However, the actual number of ratoons harvested before the crop is replaced depends on growing conditions and local cultural practices. There is often a natural decline in yield which occurs, generally, after the first or second ratoon crop. A large proportion of the world's sugarcane is grown under irrigated conditions (Smith, 1978).

Rotating sugarcane with other crops is a common practice on the smaller farms in a number of countries; interplanting the cane rows with food crops is practiced on a small scale in many countries and, in particular, in Mauritius and Taiwan (Smith, 1978).

Nematodes of sugarcane

More than 275 species of 48 genera of endo- and ectoparasitic nematodes have been recorded from the roots and/or rhizosphere of sugarcane. Certain genera are particularly widespread in sugarcane fields, *viz Pratylenchus, Helicotylenchus* and *Tylenchorhynchus;* several others are common locally, e.g. *Meloidogyne, Xiphinema, Hoplolaimus* and *Paratrichodorus* (Table 1).

There seems to be little doubt that the plant parasitic nematode fauna of sugarcane fields is composed of species that are indigenous to the various countries; none has been introduced with the planting material as has been the case with, for example, *Radopholus similis* on banana, and *Tylenchulus semipenetrans* on citrus. Sugarcane is normally grown as a continuous monoculture with usually no more than a few months fallow between removing the old ratoon crop and replanting the field. Thus conditions tend to favour the development of relatively large populations of selected species.

Pratylenchus

Twenty species of *Pratylenchus* have been recorded from sugarcane. Collectively they are the most common plant parasitic nematodes associated with this crop (Table 1); worldwide *P. zeae* is the species most frequently encountered.

Symptoms of damage

P. zeae caused extensive necrosis and conspicuous red lesions within the cortex of roots of cane grown in pots (Harris, 1974; Valle-Lamboy & Ayala, 1980) and has been shown to cause a reduction in shoot and root mass and stalk length as well as a yellowing of the leaves (Khan, 1963; Gargantiel & Davide, 1973; Valle-Lamboy & Ayala, 1980). Fewer stalks developed on sugarcane growing in microplots infested with *P. zeae* than in uninfested plots (Tarte *et al.*, 1977). Onapitan and Amosu (1982) found that *P. brachyurus* caused damage to the vascular system and destruction of cortical cells but it did not affect root or shoot mass. In an earlier study *P. brachyurus* was reported to affect the length and mass of stalks although no symptoms of damage were evident on the roots (Koike

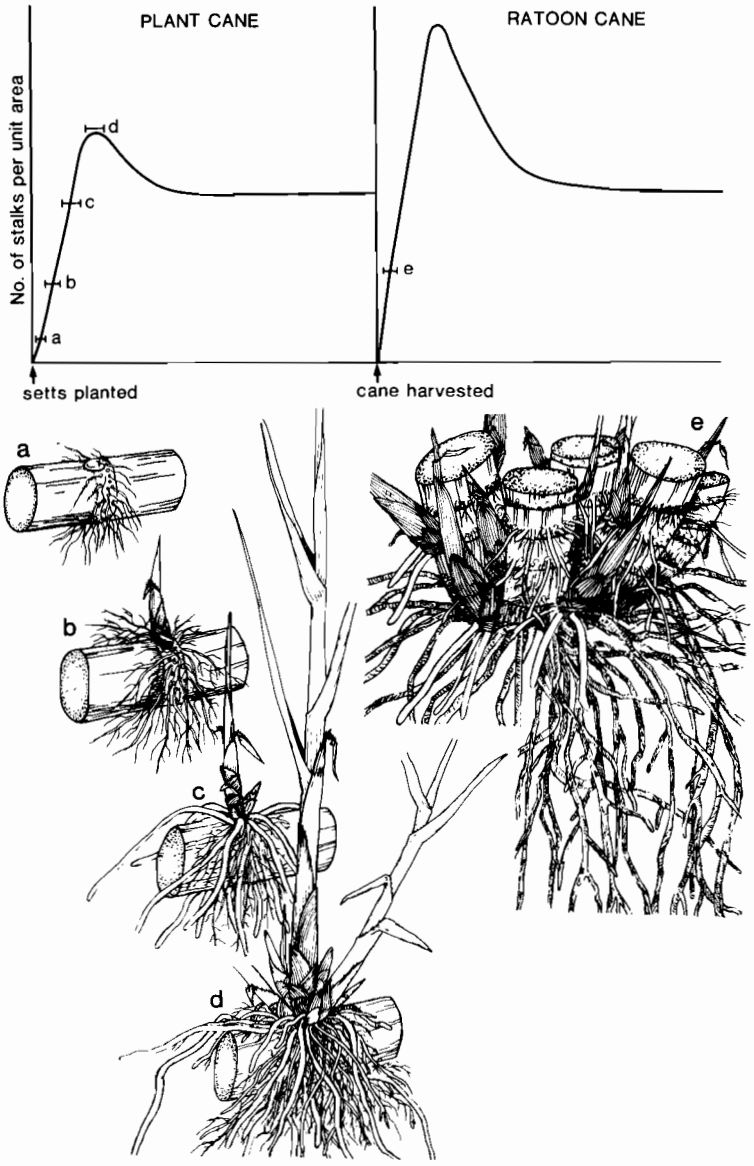

Fig. 1. Sequence of events in the early stages of development of plant and ratoon cane.
a. Appearance of sett roots.
b. Emergence of the bud and development of the primary shoot. Establishment of the sett root system.
c. Appearance of shoot roots on the primary shoot and initiation of tillers.
d. Maximum density of tillers, establishment of the shoot root system and disappearance of the sett root system.
e. Stool of ratoon cane showing new shoot arising from lateral buds on the stubble. Shoot roots develop at the base of the new shoots and eventually replace the stool roots (i.e. the shoot roots of the previous crop).

TABLE 1. Frequency of occurrence of the more common plant parasitic nematodes associated with sugarcane (%).

	Pratylenchus	*Heliotylenchus*	*Tylenchorhynchus*	*Meloidogyne*	trichodorids[a]	*Xiphinema*	*Hoplolaimus*	criconematids[b]	longidorids[c]	*Paratylenchus*	*Rotylenchus*	*Hemicycliophora*	*Scutellonema*	Size of survey: Reference
Barbados	64	77	16	27	9	+[d]	0	30	+	0	35	0	0	45 fields (Brathwaite, 1976)
Brazil	80	90	+	+	+	+	+	+	0	0	0	+	0	800 samples (Novaretti *et al.*, 1974)
Burkina Faso	89	99	74	71	52	74	92	25	0	52	+	+	+	47 fields (P. Cadet, unpubl.)
Colombia	94	87	42	17	4	0	0	13	31	0	6	0	0	74 fields (Andrade *et al.*, 1979)
Costa Rica	45	88	17	28	22	13	0	35	33	2	0	1	0	146 samples (Lainer Gonzalez, 1979)
Cuba	100	100	35	85	25	0	5	25	0	50	25	0	10	20 fields (Decker *et al.*, 1970)
Dominican Republic	+++	+++	+++	+++	++	++	0	+++	+	+	+	+	0	8 localities (Roman & Grullon, 1975)
Fiji	82	79	38	23	7	10	8	28	7	8	21	0	0	390 samples (Kirby & Kirby, 1977)
India	45	89	86	+	+	6	92	+	18	7	+	+	0	150 localities (Singh, 1967; Singh & Misra, 1974)
Indonesia	+++	+++	+	+++	+	++	+	+++	+	+	0	+	0	8 factory areas (Handojo *et al.*, 1980)
Ivory Coast	93	97	88	71	27	34	9	48	+	76	+	0	63	49 fields (Quénéhervé & Cadet, pers. comm.)
Japan	62	73	58	47	+	+	+	+	0	6	21	0	+	97 fields (Gotoh, 1965)
Kenya	+++	+++	+	+	+	+	0	++	0	+	0	+++	+	9 fields (Wolff Schoemaker, 1968)
Malaysia	100	50	71	36	14	14	71	36	43	21	+	0	7	14 fields (Razak, 1982)
Mauritius	+++	+++	+	+	+	+	0	++	+	+	+	+	+	– (Williams, 1963)
Mexico	63	13	37	0	0	8	54	17	0	4	0	0	0	24 fields (Riess, 1971)
Peru	68	93	94	72	+	+	+	+	+	0	0	83	0	10500 ha (Carbonell, 1978)
Philippines	99	75	74	12	4	83	45	4	48	2	15	18	11	168 samples (Gargantiel & Davide, 1973)
South Africa	96	95	30	71	93	94	8	75	72	9	99	11	97	124 fields (Spaull, 1981*a*)
Taiwan	85	71	89	62	76	16	50	25	1	+	0	+	0	17000 samples (Hu & Tsai, 1975)
Trinidad	100	91	91	0	0	9	18	0	0	0	0	0	0	11 fields (Brathwaite, 1980)
USA	++	+	++	++	++	0	+	+	0	0	0	0	0	– (Birchfield, 1969)
Venezuela	87	+	87	+	+	0	0	100	0	0	+	0	0	94 samples (Meredith & Castro, 1978)
Zimbabwe	85	41	67	41	81	78	19	22	22	0	15	11	59	27 sites (Martin, 1962)

a: trichodorids = *Trichodorus* and *Paratrichodorus*
b: criconematids = *Criconemella* and related genera
c: longidorids = *Longidorus*, *Longidoroides* and *Paralongidorus*
d: + = present in survey; ++ = common; +++ = widespread; 0 = not recorded

& Roman, 1970). Species of *Pratylenchus*, when present in large numbers, may destroy the root system of cane (Holtzmann, 1964).

Environmental factors affecting parasitism

Number of individuals and frequency of occurrence of species of *Pratylenchus* have been reported to be greater in clay soils than in light soils in West Africa and Taiwan (Hu *et al.*, 1968; Cadet, 1987), but in South Africa they were widespread in all soils (Spaull, 1981*a*). In Egypt much greater numbers of *P. thornei* were recorded from a field of recently planted cane and a field of mature cane than from a fallow field. In the fallow soil the population was concentrated at a depth of about 40 cm but under growing cane more individuals were recovered from the surface 10 cm of soil

(Oteifa *et al.*, 1963). In Zimbabwe the density of *P. zeae* in the soil was greater beneath the cane row than in the interrow, while the density in the roots was greater in the interrow (Martin, 1967). *P. zeae* was more numerous in the sett roots than the shoot roots of plant cane in Burkina Faso and South Africa (Cadet & Spaull, 1985) and in South Africa more individuals were recovered from the shoot roots than the stool roots of ratoon cane (Spaull, unpubl.). Numbers of *P. zeae* were positively correlated with soil moisture in Kenya (Wolff Schoemaker, 1968) and Brazil (Gomes Carneiro *et al.*, 1980) but not in the Philippines (Estioko & Reyes, 1984). Large differences were found in the suitability of different cane cultivars as hosts to *P. zeae*, many more individuals being recovered from the roots of some cultivars than of others (Tarte *et al.*, 1977). O'Relly and Milian (1978) noted that the diversity and relative abundance of species of *Pratylenchus* in Cuba differed from one locality to another.

Pratylenchus infected with spores of the bacterial parasite, *Pasteuria penetrans s.l.* were recorded in 30% of more than 100 sugarcane fields in South Africa (Spaull, 1981*b*); the level of parasitism in twenty fields ranged from 2 to 13%. *Pratylenchus brachyurus* and *P. zeae* are both hosts of the fungal parasite, *Catenaria vermicola*, which was abundant in sugarcane fields in Louisiana (Birchfield, 1960). The reproduction of *P. zeae* is affected by certain fungal pathogens of sugarcane. In glasshouse experiments the combined inoculation of sugarcane with *Phytophthora megasperma* and *P. zeae* favoured the multiplication of the latter (Khan, 1963) whereas in the presence of *Pythium graminicola* reproduction was reduced considerably (Holtzmann & Santo, 1971).

Disease complexes

The pathogenicity of *P. zeae* to sugarcane was not altered when inoculated with *Phytophthora megasperma* (Khan, 1963) but in combination with *Pythium graminicola, Meloidogyne incognita* or both these organisms simultaneously, *P. zeae* had significantly less effect on the mass of cane roots than in their absence (Valle-Lamboy & Ayala, 1980); necrosis of the roots was more than halved when one or both of the other pathogens was also present. However, according to Santo and Holtzmann (1970), when *P. zeae* was added to sugarcane seedlings 7 days before *Pythium graminicola* the seedlings were more severely affected than when the two organisms were added at the same time.

Economic importance

P. zeae is the primary nematode pathogen of sugarcane in Panama (Pinochet, 1987) and is among the most important nematodes associated with cane in N.E. Argentina (Costilla, 1973), Burkina Faso and South Africa (Cadet & Spaull, 1985, unpubl. data). According to Harper (1975), *P. pratensis* is one of the major pests of cane in Indonesia. Birchfield (1984) considered that the economic importance of species of *Pratylenchus* in sugarcane was exceeded only by the species of *Meloidogyne*.

Helicotylenchus

More than 30 species of *Helicotylenchus* have been recorded from around the roots of sugarcane; of these *H. dihystera* is the most common.

Symptoms of damage

Helicotylenchus feed ectoparasitically or semi-endoparasitically in the root cortex causing distortion and collapse of the cells (Carbonell, 1978; Brathwaite, 1980); root development is affected such that the primary roots become blunt and malformed with fewer lateral roots (Apt & Koike, 1962*a*; Rao & Swarup, 1975). Feeding may also result in the formation of brownish red lesions (Birchfield, 1984), or a general discolouration as a consequence of secondary infection by bacteria and fungi (Jensen *et al.*, 1959).

Environmental factors affecting parasitism

Species of *Helicotylenchus* are widespread, occurring in all types of soil, although in Taiwan, Hu *et al.* (1968) reported that they were more numerous in lateritic soils; and data presented by Estioko and Reyes (1984) indicated that in the Philippines *H. brachyurus* was more abundant in sandy loam than in clay soils. Numbers of *H. dihystera* were positively correlated with rainfall in Brazil (Gomez Carneiro *et al.*, 1980) but not in Kenya (Wolff Schoemaker, 1968). In Cuba the species diversity of *Helicotylenchus* was greater in older sugarcane fields (Decker *et al.*, 1970) and varied from one locality to another (O'Relly & Milian, 1978).

Economic importance

The pathogenicity of *H. dihystera* to sugarcane grown in pots has been demonstrated (Apt & Koike, 1962*a*; Rao & Swarup, 1975), but in the field this and other species of *Helicotylenchus* are probably mild pathogens (Birchfield, 1984). Indeed, observations made in Burkina Faso indicated that the number of *H. dihystera*, the dominant ectoparasite, was directly proportional to the yield of cane, thus suggesting that this species had no effect on the growth of cane (Cadet, 1986*a*).

Tylenchorhynchus

Twenty eight species of *Tylenchorhynchus* have been found associated with sugarcane. The genus is widespread in a number of countries particularly India, Ivory Coast, Peru, Taiwan and Venezuela (Table 1). *T. annulatus* has the widest geographical distribution.

Symptoms of damage

Species of *Tylenchorhynchus* are ectoparasitic, feeding on epidermal cells and root hairs. The root system of cane grown in pots and inoculated with *T. annulatus* appeared sparse with signs of necrosis and moderate to severe stunting of the lateral roots. There was a marked reduction in the number of root hairs and the sett roots died prematurely (Birchfield & Martin, 1956; Gargantiel & Davide, 1973; Harris, 1974). Height, top weight and root weight of potted sugarcane were all reduced by *T. annulatus* (Gargantiel & Davide, 1973).

Environmental factors affecting parasitism

In Taiwan species of *Tylenchorhynchus* were less numerous in sandy soils than in loam and clay soils (Hu *et al.*, 1968) but this may not be generally true, as, for example, in the Philippines (Estioko & Reyes, 1984).

Economic importance

Although *T. annulatus* affects the growth of cane in pots it is probably a mild pathogen in the field (Birchfield, 1984). The same is perhaps true of other species of *Tylenchorhynchus*.

Meloidogyne

The two common species of *Meloidogyne, M. incognita* and *M. javanica*, have been found in many sugarcane areas and at least some of the numerous records of unidentified *Meloidogyne* probably refer to one or both of these species. Four other species have been identified from cane: *M. arenaria* from Australia, Fiji, Puerto Rico, Taiwan and what was formerly known as the Federation of Rhodesia and Nyasaland (Malawi, Zambia and Zimbabwe); *M. thamesi* from the USA (Winchester, 1969*a*); *M. hispanica*[1] and *M. kikuyensis*[2] from South Africa. None of these four species is widespread.

1. = *Meloidogyne* sp. G in Spaull (1984); determination Fargette (1987).
2. = *Meloidogyne* sp. SC in Spaull (1984); determination Kleynhans (pers. comm.).

Symptoms of damage

The symptoms of damage are distinct but are usually less easily diagnosed than in many other susceptible crops. Galls formed by *M. incognita* and *M. javanica* develop on the tips of the sett roots and young shoot roots. Except in young plant cane they are often small and discrete and not easily detected. Williams (1969) illustrated elongated swellings on the tips of sugarcane roots and the proliferation of lateral roots immediately proximal to the gall. The tip of heavily infested terminal galls may necrose (Martin, 1967). In old suberized roots females may develop at various positions along the root without inducing galling (Martin, 1967). Dick and Harris (1975) reported that obvious galls developed on cultivar NCo376 but not on N53/216 although both cultivars were infested with females of *Meloidogyne*. Relatively large offset nodule-like galls were associated with *M. kikuyensis* (Fig. 2). The females invariably developed a feeding site among the primordial cells of lateral roots (Spaull, unpubl.). Cane roots infested with *M. incognita* or *M. arenaria* were distinctly curved compared with uninfested controls (Roman, 1961). In pot experiments, *M. incognita* and *M. javanica* reduced the top weight and root weight of sugarcane (Apt & Koike, 1962*c*; Khurana & Singh, 1971; Valle-Lamboy & Ayala, 1980; Novaretti, 1981). Species of *Meloidogyne* may also reduce the number of tillers developed by sugarcane (Hu, 1963; Salawu, 1986).

Environmental factors affecting parasitism

Species of *Meloidogyne* are more abundant and more frequently found in sandy soils than in finer texture soils (Williams, 1963; Hu & Chu, 1964; Roman, 1968; Roman & Grullon, 1975; Spaull, 1981*a*) although Parsons (1970) found *Meloidogyne* only in loam soils. Greater populations of *M. incognita* and *M. javanica* were recorded in sett roots than shoot roots of plant cane (Cadet & Spaull, 1985).

Fig. 2. Offset, nodule-like galls on sugarcane roots, cv NCo310, caused by *Meloidogyne kikuyensis*.

Disease complexes

Populations of root knot nematodes may be influenced by the presence of phytopathogenic fungi. Thus, far fewer *M. javanica* were recorded from the roots of sugarcane infected with the root rot fungus, *Curvularia lunata*, than from roots of uninfected plants (Khurana & Singh, 1971). Conversely the presence of other pathogens favoured colonization of sugarcane roots by *M. incognita*, many more galls being produced in the presence of *Pythium graminicola* than when the fungus was absent; and when *P. zeae* was also present even more galls were developed, although in both cases the size of the galls was smaller than normal (Valle-Lamboy & Ayala, 1980).

The pathogenicity of *Meloidogyne* may be influenced by the presence of other pathogens. Thus the effect of *M. javanica* and *C. lunata* on sugarcane was greater when the two organisms were inoculated together than when either was inoculated alone (Khurana & Singh, 1971). A similar interaction was recorded between *M. incognita* and *P. graminicola* on sugarcane seedlings (Apt & Koike, 1962*c*). However, in another study the combination of *M. incognita* plus *P. graminicola, M. incognita* plus *P. zeae* or all three species together had significantly less effect on root mass of sugarcane than when either of the nematodes was acting alone (Valle-Lamboy & Ayala, 1980). Yield loss in sugarcane was greater where growth was impaired by both *Clavibacter xyli xyli*, the causal agent of ratoon stunting disease, and root-knot nematodes than when only one pathogen was involved (Anon., 1977).

Economic importance

Together with *P. zeae, M. incognita* and *M. javanica* are probably the most important plant parasitic nematodes of sugarcane worldwide. Estimates of crop loss due to species of *Meloidogyne* in Mexico, Central and South America, the Caribbean and South East Asia ranged from 6 to 9% (Sasser, 1979). Based on sugar production data for 1985/86 (Ahlfeld, 1986) this represents a loss of approximately 2 700 000 t sugar.

Resistant cultivars

Species of *Meloidogyne* are highly specialized parasites of plants with an intimate relationship with the host. It is, therefore, not surprising to find that among the diverse array of sugarcane cultivars some are resistant (Table 2). In the Philippines Madamba *et al.* (1974) reported that of 40 cane cultivars tested 16 were resistant to *M. javanica* and 11 were resistant to *M. incognita*. Only four cultivars Q60, Q63, Q72 and F109, were resistant to both species (Table 2). Resistance to *M. incognita* was found in 30% of 236 young seedlings derived from controlled crosses between parent cultivars in the Louisiana sugarcane breeding programme; also, 13% of 85 cultivars in an advanced stage of selection were resistant (Anzalone & Birchfield, 1977). In Brazil, Novaretti and Nunes (1980) tested 29 clones and 13 commercial cultivars and found that 21% showed resistance to *M. javanica*. Significantly they observed that there was a tendency for resistance to be transferred from the parent to the seedling.

Biological control

Biological control of the *Meloidogyne* species that attack sugarcane has received little attention. The only recent experimental work on this topic was that reported by Novaretti *et al.* (1986) in Brazil. They incorporated the eggparasitic fungus, *Paecilomyces lilacinus* into sugarcane soil infested with *M. incognita* and *P. zeae* but found that it had no effect on the numbers of nematodes or the yield of cane. Naturally occurring parasites and predators of *Meloidogyne* have been recorded in sugarcane fields. *Catenaria vermicola*, a fungal parasite of several nematodes including a species of *Meloidogyne*, was abundant in cane soils in Louisiana (Birchfield, 1960). And, in Taiwan, Chu and Hsu (1965) isolated the nematode trapping fungus *Arthrobotrys oligospora* from cane fields in each of the 21 districts from which soil samples were collected. Three other species of *Arthrobotrys*, *Dactylella* sp. and *Dactylaria* sp. were also isolated but less frequently. In a pot experiment, the number of

TABLE 2. Sugarcane cultivars resistant to species of *Meloidogyne*.

Cultivar	Species	Country	Reference
CB40–13, CB46–47, CB53–98, Co740, IAC48–65, IAC50–134, IAC52–150, SP70–1143, SP71–1578, SP71–4156, SP72–4790.	*M.javanica*	Brazil	Novaretti & Nunes, 1980; Novaretti, 1982
CP26–116, F109, Q51, Q53, Q60, Q61, Q63, Q66, Q71, Q72, Q73.	*M.incognita*	Philippines	Madamba *et al.*, 1974
B37172, CP49–7, F109, F110, H49–262, I70, I226, K640, K641, Q52, Q55, Q60, Q62, Q63, Q72, Q82.	*M.javanica*	Philippines	Madamba *et al.*, 1974
CB36–14, N53216, NCo292, NCo382.	*M.incognita*	South Africa	Spaull, unpubl.
N8, NCo292, NCo382.	*M.javanica*	South Africa	Spaull, unpubl.
H68–2235, H72–1522, H72–6095, Q63.	*M.incognita* race 2	Taiwan	Hu & Tsai, 1983
CP36–105, CP48–103, L62–88, L62–98.	*M.incognita*	U.S.A.	Marcano, 1971 (in Birchfield, 1984)

Meloidogyne was reduced in soil inoculated with *A. oligospora* (Chu & Hsu, 1965).

Pasteuria penetrans was recorded in *Meloidogyne* from a number of sugarcane fields in South Africa (Spaull, 1984). Infected females were much more frequently found and the level of parasitism was greater in poor sandy soils than in heavier soils. At one site the level or parasitism of *M. incognita* and *M. javanica* increased as the number of nematodes increased, suggesting that *P. penetrans* was not limiting the populations. Besides *M. incognita* and *M. javanica, P. penetrans* also infected *M. hispanica* but not *M. kikuyensis. P. penetrans* was also recorded from *M. incognita* and/or *M. javanica* from sugarcane fields in Mauritius, Louisiana and Papua New Guinea (Williams, 1967; Birchfield, 1984; Bridge, 1986).

Trichodorus and *Paratrichodorus*

The trichodorids recorded from cane fields are predominantly species of *Paratrichodorus*, with *P. minor* being the most common. They are widespread in Burkina Faso, South Africa, Taiwan, the USA and Zimbabwe but infrequently reported in most other countries (Table 1).

Symptoms of damage

Like other trichodorids, *P. minor* feeds ectoparasitically on epidermal and sub-epidermal cells; the cells are killed and as a result of feeding at the apical meristem, the roots are typically stubby and lack fine feeder roots (Apt & Koike, 1962*b*). In a pot experiment in Hawaii the roots of sugarcane seedlings grown in soil infested with 1000 *P. minor* per plant were severely stunted (Fig. 3); shoot growth was also affected though to a lesser extent (Apt & Koike, 1962*b*). However, at the same density this species had no effect on sugarcane grown from cuttings in pots in South Africa (Harris, 1974).

Environmental factors affecting parasitism

Trichodorids are reported to be more frequently found and more numerous in the free draining sandy soils and rare or absent in fine textured soils (Winfield & Cooke, 1975). However in Taiwan they are as common in lateritic soils as in sands and loamy sands, though rare in clays (Hu *et al.*, 1968). In South Africa trichodorids are as numerous although a little less widespread in clays and sandy clays as in sandy soils (Spaull, 1981*a*). Cooke and Draycott (1971) noted that in sugar beet

Fig. 3. Stubby and swollen sugarcane shoot roots from soil infested with *Paratrichodorus* sp. and *Xiphinema elongatum*.

fields in England, numbers of *Trichodorus* increased with an increase in accumulated rainfall. Similar observations were made by Gomez Carneiro *et al.* (1980) who found that numbers of *Paratrichodorus porosus* in sugarcane fields in Brazil were positively correlated with rainfall and soil moisture. In the Philippines, however, numbers of *Trichodorus borneoensis* were correlated with rainfall in only one of four cane fields (Estioko & Reyes, 1984). Both Martin (1967) and Harris (1975) noted that the number of trichodorids declined sharply after soil was treated with fumigant nematicide, but that after 3 or 4 months the populations increased dramatically to levels well in excess of those present before fumigation. And in Puerto Rico, 9 months after fumigation, trichodorids increased from non-detectable levels to 6000 per dm^3 of soil (Roman, 1967). A similar but smaller response was recorded in Burkina Faso (Cadet, 1979).

Economic importance

In sandy soils in South Africa, large populations of *Paratrichodorus* were frequently associated with poorly growing cane with typical stubby root symptoms. Species of this genus were therefore considered among the most important nematode pests of cane in these soils (Spaull, 1981*a*). Similarly, *P. minor* and *P. porosus* were considered to be particularly damaging to sugarcane in Queensland (Holtzmann, 1964). In Zimbabwe, however, Martin (1967) found no evidence to suggest that even large numbers of trichodorids were a serious limiting factor in the growth of sugarcane, although earlier (Martin, 1962) he had recorded, on average, larger populations from stunted cane than from healthy cane. Apt and Koike (1962*b*) suggested that although *P. minor* had a sporadic distribution in Hawaii, where it occurred in relatively large numbers, it should be considered an important pest of sugarcane. This is probably applicable wherever cane is grown.

Xiphinema

Forty species of *Xiphinema* have been recorded from sugarcane fields, more than any other genus. As with the trichodorids, *Xiphinema* have a limited distribution (Table 1) although certain species

are widespread in some countries, eg. *X. attorodorum* in Burkina Faso, *X. insigne* in the Philippines and *X. elongatum* in South Africa (Cadet, unpubl. data; Estioko & Reyes, 1984; Spaull, unpubl. data).

Symptoms of damage

Data are lacking on the feeding behaviour of species of *Xiphinema* on sugarcane. Presumably however, as with other host plants, they are able to probe deep into the root tissue and feed on cells within or in the vicinity of the vascular tissues. In a pot experiment it was observed that the roots of cane plants inoculated with *X. elongatum* were coarse and sparse, with evidence of tissue decay and some of the root tips were swollen (Fig. 3); shoot and root mass were not, however, affected (Harris, 1974). Conversely, marked symptoms of damage were not observed on the roots of cane inoculated with *X. americanum s.l.* although shoot and root mass were reduced (Gargantiel & Davide, 1973).

Environmental factors affecting parasitism

Williams and Luc (1977) found that in Mauritius, *X. elongatum* was the most common species of *Xiphinema* associated with sugarcane, although it was largely confined to the lower altitudes where rainfall is less than 2500 mm per year. It was rarely found above 200 m in the central more elevated part of the island, where annual rainfall exceeds 2500 mm, and where *X. krugi* was widespread. The soils in both regions are predominantly silty clay loams. *X. elongatum* was also the most frequently encountered *Xiphinema* associated with sugarcane in South Africa. It was however far less common in clay and sandy clay soils than in lighter soils, and was slightly less common at altitudes greater than 150m (Spaull, unpubl.). *X. americanum s.l.* was not found in sugarcane fields in Hawaii above an altitude of approximately 230 m (Anon., 1961). *X. insigne*, the most common species of *Xiphinema* in cane fields in the central and southern Negros Occidental in the Philippines, was as abundant in clay soils as in sandy loams (Estioko & Reyes, 1984). Some cultural practices may influence *Xiphinema* populations. In Burkina Faso cane is normally cut at about 50 mm above the ground. When the cane was cut experimentally at ground level it was found that, over a period of 120 days, the number of *X. attorodorum* increased markedly compared with those associated with cane cut normally (Cadet, 1986*a*).

Williams (1967) collected *X. elongatum* infected with *Pasteuria penetrans s.l.* from around the roots of cane in seven of eight localities in Mauritius. The level of parasitism ranged from 3 to 50%. *P. penetrans s.l.* was also recorded from *X. elongatum* and *X.* cf *imitator* in South Africa (Spaull, 1981*b*).

Economic importance

Species of *Xiphinema* are among the most important nematodes of sugarcane in South Africa (Spaull, 1981*a*) and Young (in Holtzmann, 1964), considered *X. elongatum* to be one of the major parasites of cane in Australia.

Hoplolaimus

Hoplolaimus indicus is one of the most numerous and widespread plant parasitic nematodes associated with sugarcane in India (Singh, 1967; Singh & Misra, 1974) and *H. pararobustus* is among the most common nematodes of cane in Burkina Faso (Cadet & Merny, 1978). *Hoplolaimus* species, including *H. galeatus* and *H. seinhorsti*, are widespread in the Philippines (Gargantiel & Davide, 1973; Reyes & Beguico, 1978) and unidentified species have been reported from many localities in Malaysia (Razak, 1982), Mexico (Riess, 1971) and Taiwan (Hu & Tsai, 1975). Elsewhere *Hoplolaimus* is found only infrequently in cane fields (Table 1). Worthy of note is the report of *H. columbus* causing damage to sugarcane in Louisiana (Astudillo & Birchfield, 1980).

Symptoms of damage

Species of *Hoplolaimus* are migratory endoparasites of cane roots. Both *H. indicus* and *H. columbus*, restricted normal growth and development of the roots (Singh & Misra, 1976; Astudillo & Birchfield, 1980). Purple-red necrotic lesions were observed on roots invaded by *H. indicus* and in severe infestations the lesions girdled the roots. *H. columbus* caused necrosis of cortical cells. The mass of both the shoots and roots of sugarcane was reduced in pots inoculated with *H. indicus* (Singh & Misra, 1976; Nath *et al.*, 1976*a*) but this species had little effect on the growth of sugarcane seedlings (Nath *et al.*, 1975).

Environmental factors affecting parasitism

Reproduction of *H. indicus* was greater in sandy loam at 30°C than in sand or clay soil at higher or lower temperatures (Gupta & Atwal, 1971). *H. pararobustus* was more frequently found and more numerous in sandy soils in West Africa (Cadet, 1987) and in South Africa this species was quite common in sands but rare or absent in other soils (Spaull, 1981*a*). Very few *H. galeatus* were recorded in clay soils compared with sandy loams in the Philippines (Estioko & Reyes, 1984). In a trial conducted over a five year crop cycle the relative abundance of *H. pararobustus* increased from less than 10% of the endoparasites in the roots of the plant crop to more than 80% in the fourth ratoon (Cadet, 1985). During this period there was a corresponding decrease in the relative abundance of *Pratylenchus zeae*.

Disease complexes

Symptoms of root rot were observed on sugarcane inoculated with both *Fusarium moniliforme* and *H. indicus* but not when either pathogen was inoculated alone (Nath *et al.*, 1976*a*). Also the reduction in shoot and root mass was significantly greater when the two organisms were inoculated together.

Other nematodes

Although not common in many countries several other nematodes are widespread and/or numerically important in certain localities. In parts of Madagascar large numbers of *Scutellonema brachyurum* were associated with poorly growing cane (Luc, 1968). And species of *Scutellonema* were very widespread in South Africa though more numerous in heavier soils than in sands and loamy sands (Spaull, 1981*a*). This genus was also common in Zimbabwe and Ivory Coast but rare or absent in other countries (Table 1).

Species of *Hemicycliophora* were among the most widespread and abundant plant parasitic nematodes associated with sugarcane in Peru (Table 1). According to Carbonell (1978) they retarded the growth of the cane and caused distortion of the roots, which subsequently acquired a cork-like consistency; the smaller roots collapsed. *Hemicycliophora* was also commonly found in Kenya (Wolff Schoemaker, 1968). *Criconemella* and related genera were widespread in the Dominican Republic, El Salvador, Indonesia, South Africa and Venezuela (Interiana Munoz, 1971; Roman & Grullon, 1975; Meredith & Castro, 1978; Handojo *et al.*, 1980; Spaull, 1981*a*), and *Hemicriconemoides* and *Criconemella* were widespread and locally abundant in Fiji (Kirby & Kirby, 1977). *Criconemella xenoplax* was considered to be one of the more important pests of sugarcane in Indonesia (Harper, 1975).

Rotylenchulus, predominantly *R. parvus*, was very widespread in South Africa (van den Berg & Spaull, 1981). Unusually, a species of *Ditylenchus* was associated with stunted and chlorotic sugarcane in Brazil; some of the plants had died (Novaretti *et al.*, 1974).

In concluding this section on the more important nematode pests of sugarcane, it is as well to note that plant parasitic nematodes are not the only organisms that cause necrosis and impair the growth of cane roots. Such damage may also result from feeding by the larvae and adults of some Coleoptera, Diptera, Hemiptera, Coccoidea, Collembola, Thysanura and Myriapoda (Wilson, 1969). Also poor root growth may result from an imbalance of soil nutrients, e.g. high levels of aluminium

or low levels of phosphorus (Humbert, 1968), or from soil compaction or poor aeration. Only *Meloidogyne* can be diagnosed with confidence; if galls are present the female may be observed by dissecting the root. Thus it may not be prudent to link so called typical symptoms with one or other species of nematode when they are part of a complex of factors that can affect root growth. It should be added that there are some above ground symptoms that, although not diagnostic, are often associated with the damage caused by nematodes, *viz*: The shoots are reduced in number and are stunted, and the cane is slow to develop a canopy of leaves giving the cane rows a more open appearance; also the leaves curl longitudinally and appear spiky.

Nematode–sugarcane interaction

Thus far the nematodes have been considered in isolation; but roots of sugarcane are normally attacked simultaneously by a number of nematode species, some or all of which may cause serious damage. Furthermore the sugarcane plant itself interferes with the dynamics of the nematode populations, because one root system is replaced by another during the growth of the crop. Thus to understand the importance of the nematodes and to explain the mechanisms of damage to sugarcane it is necessary to consider the different components of the nematode community, in relation to both the development of the roots and to the evolution of those growth parameters which contribute to the yield of the crop. Yield of sugarcane is a function of the number, length and diameter of the stalks. Yield of sucrose is a function of the sucrose content of the stalks. Root damage by nematodes results in a reduction in the number and length of stalks; only occasionally does it have a significant influence on the diameter and sucrose content.

Plant cane

Cadet and Spaull (1985) found that in plant cane the reduction in the number of stalks takes place primarily during the period of maximum tiller development, that is while the cane plant is largely dependent upon the sett root system (Plate 12 C & D). A reduction in the length of stalks may also be apparent at this time and, in the presence of certain nematodes, this increases in magnitude through to harvest. Stalk length may thus be affected by damage to both the sett and the shoot roots (Cadet & Spaull, 1985).

The results of a number of field trials show that, in Burkina Faso, crop loss in plant cane was due more to a reduction in the number of stalks than to a reduction in the length of stalks, while the reverse was true in South Africa (Table 3). To explain this difference and to elucidate the roles played by the nematodes in limiting yield of plant cane in the two localities, Cadet and Spaull (1985) related the patterns of change in the nematode populations with the patterns of change in the development of the sugarcane crop. They deduced that:

1. In both Burkina Faso and South Africa damage to the sett roots by large numbers of *Meloidogyne* and *Pratylenchus* delayed the emergence, and retarded the development of many of the primary shoots, which either produced fewer tillers or were unable to compete successfully with those that developed more rapidly.
2. The suppression of tillering was greater in Burkina Faso than in South Africa because, in the former locality, there was a much greater rate of invasion of the sett roots by endoparasites.
3. *Xiphinema, Trichodorus* and *Paratrichodorus* caused extensive damage to the shoot roots in South Africa which restricted water uptake and thus limited stalk elongation.
4. Although nematodes caused some damage to the shoot roots in Burkina Faso, this had less effect on water uptake and thus on stalk elongation than in South Africa, because the cane was irrigated.
5. The dominant ectoparasite in Burkina Faso, *Helicotylenchus dihystera*, was a weak pathogen of sugarcane compared with species of *Xiphinema* and trichodorids.

Ratoon cane

Although plant parasitic nematodes have a marked effect on the plant crop in Burkina Faso they have little influence on the following ratoon crops (Cadet, 1985) (Table 3). In South Africa, however, ratoon cane is almost as badly affected by nematodes as is plant cane (Table 3). As was done with the plant crop, an attempt was made to understand the relationship between nematodes and ratoon cane by monitoring the nematode populations and the development of the cane in the two localities (Spaull & Cadet, unpubl.). It was noted that, as is usual with ratoon cane in South Africa, crop loss was due primarily to a reduction in the length of stalks. This was attributed to the considerable damage to the shoot roots caused by the ectoparasites, *Xiphinema* and *Paratrichodorus* species. The ectoparasites were also thought to be responsible for the reduction in the number of stalks in South Africa, since large numbers were present in the soil during the initial period of shoot development. During this short critical period very few endoparasites were present in the roots.

TABLE 3. Response of plant and ratoon cane to treatment with nematicides in Burkina Faso and South Africa (Spaull & Donaldson, 1983; Cadet & Spaull, 1985; Cadet, 1985; unpubl. data from SA Sugar Association Experiment Station).

	Plant cane		Ratoon cane	
	Burkina Faso (16)*	South Africa (21)	Burkina Faso (6)	South Africa (7)
Number of stalks (%)	46	20	15	13
Length of stalks (%)	21	35	2	25
Yield, t cane/ha (%)	65	80	11	66

*Number of observations

In Burkina Faso nematodes had relatively little effect on either the number or length of stalks. This was not altogether unexpected since very few endoparasites were recovered from the roots during the entire period of shoot establishment, and although present in large numbers the dominant ectoparasite *H. dihystera* is considered a weak pathogen of sugarcane.

Judging from the inactivity of the endoparasite populations during the early stage of growth in both localities, it appeared that the roots of ratoon cane were not attractive to or suitable for these nematodes. In South Africa this condition persisted for only 4 weeks but in Burkina Faso it lasted much longer. It was tentatively suggested that the lack of attraction by the roots was due to the initial inherent, low level of activity of the root system of young ratoon cane. That the activity of the roots in Burkina Faso should have remained at a low level for so long was attributed to the height at which the cane is cut in that country (Cadet, 1986*a*). Whereas in South Africa the stalks are cut at ground level and the shoots and shoot roots are initiated below the ground, in Burkina Faso they are cut approximately 50 mm above ground and most of the new shoots develop from the uppermost buds on the stubble. While the shoots in Burkina Faso develop rapidly it is some weeks before the shoot roots reach the ground. During this period the shoots are reliant upon the large but relatively inactive stool root system (Cadet, 1986*b*).

The growth and development of plant and ratoon cane in South and West Africa, and the corresponding fluctuations in the numbers of nematodes in and around the roots are summarized diagrammatically in Fig. 4. The direct and indirect consequences of this interaction on the two main components of cane yield are summarized in Fig. 5.

Control measures

In most countries sugarcane is cultivated on soils with a relatively high clay or silt content where nematodes have little apparent effect on growth; sandy soils constitute only a small proportion of the total world area under sugarcane (Rosenfeld, 1956). This may explain the limited distribution of certain nematodes that prefer coarse textured soils, such as species of *Meloidogyne* and *Paratrich-*

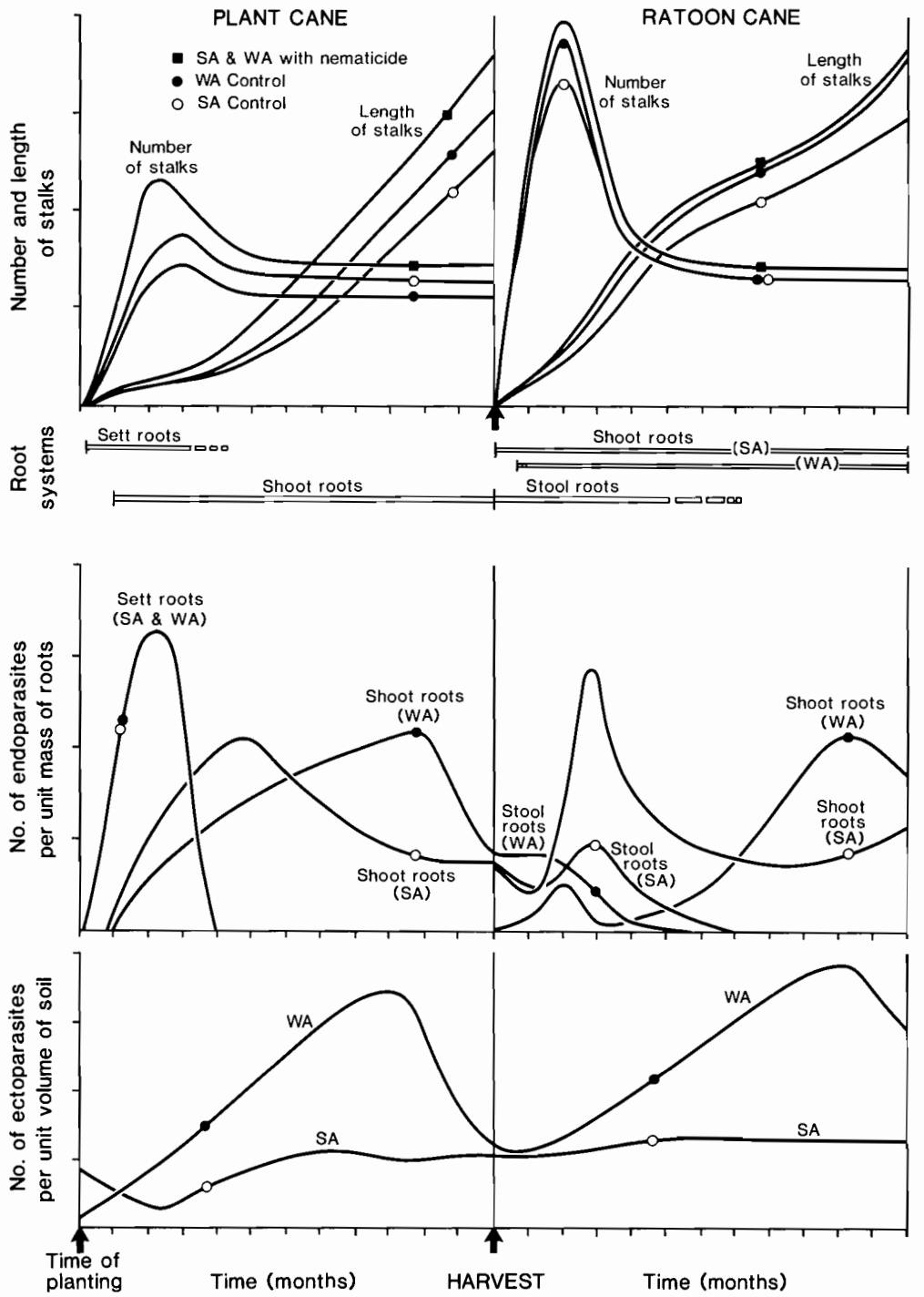

Fig. 4. Pictorial representation of the patterns of change in the numbers of nematodes in relation to the patterns of change in the development of sugarcane in South and West Africa.

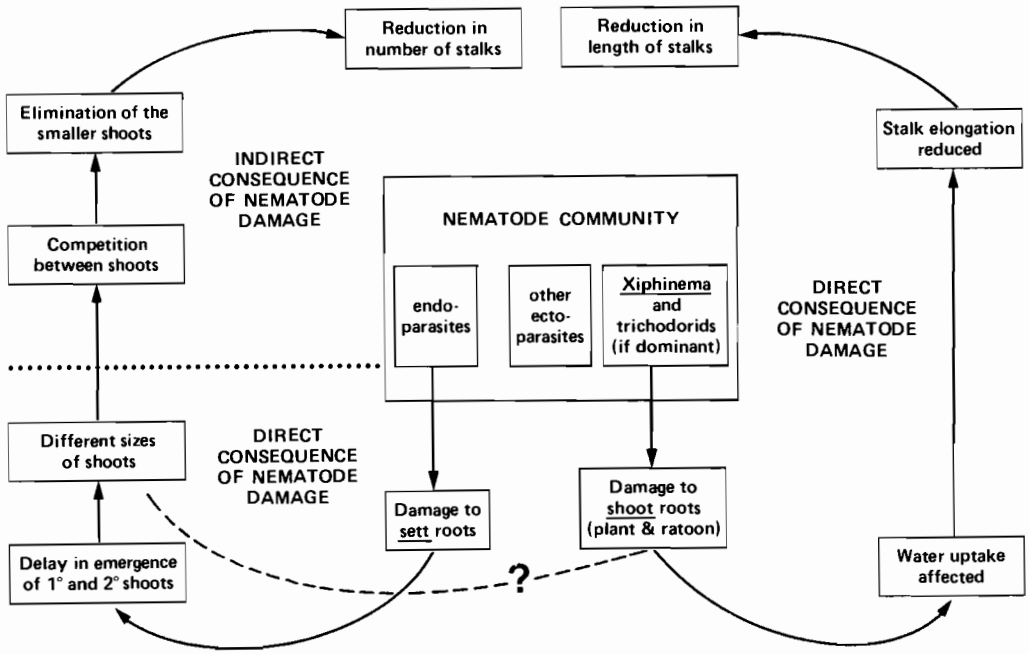

Fig. 5. Principal mechanisms of yield loss in sugarcane due to nematodes.

odorus, despite the fact that sugarcane is a good host. Thus nematodes have not been considered major pests of sugarcane throughout the world. However, locally in some countries they are a serious limiting factor and justify the use of control measures.

Cultural practices

Crop loss due to nematodes can be largely reduced by growing sugarcane on soils other than sands and loamy sands. Conventional crop rotation to reduce nematode populations is not a normal practice in sugarcane agriculture. Where rotation is practiced it is usually to enable food or cash crops to be grown, e.g. maize, tomatoes, rice, pulses, cotton and tobacco (Smith, 1978).

The problem of growing sugarcane on poor sands in some parts of South Africa was overcome by inverting and mixing the sandy topsoil with a clay subsoil (Anon., 1982). Such a procedure is expensive, though permanent and of course is limited to those areas where a suitable subsoil exists. Also in South Africa, irrigation considerably improved the yield of cane growing on a poor sand in both nematicide treated and untreated plots (Donaldson & Turner, 1988). The response to the treatment was smaller than that in plots which received only rain water. Time of planting also may influence the effect that nematodes have on sugarcane. Thus in Taiwan, judging from the greater response of spring planted sugarcane to treatment with a nematicide (mean of 33% response in 26 trials) compared with that of cane planted in autumn (mean of 16% response in 31 trials) sugarcane is more susceptible to nematodes when planted in spring (Hu *et al.*, 1968; Hu & Tsai, 1973, 1978, 1982). In Brazil, Novaretti *et al.* (1984) found that whether or not a nematicide was used the best yields were obtained from cane planted in March rather than in December, January, February or April. The second best yield from the control plots and the smallest response to treatment were from cane planted in December.

In Burkina Faso nematodes limit shoot development and tillering of plant cane but have little

effect on ratoon cane (Cadet, 1985). This natural resistance of the ratoon crop was exploited in a field trial to overcome the loss in yield of the plant crop. Plots of cane were cut back two months after planting thus converting the plant cane, prematurely, to ratoon cane (Cadet & Quénéhervé, 1988). Although the ratoon was grown for two months less than the plant crop and was subjected to the same drying off period, when no more irrigation water was supplied, the yield in tons cane and tons sugar/ha/month was increased above that of the control; but the difference was not significant (Table 4) (Cadet, unpubl.).

TABLE 4. Yield of plant cane with and without a nematicide and yield from a prematurely ratooned plant crop.

Plant crop	t cane/ha/mo	t extractable sucrose/ha/mo
Control	4.5	0.34
Prematurely ratooned	5.2	0.43
Treated with carbofuran	5.9	0.52

Filtercake, which is the sediment obtained when clarifying the juice expressed from crushed cane, is often returned to the field as a soil ameliorant and as a fertilizer. Twenty-five tons of cane produce approximately 1 ton of filtercake. Fresh filtercake contains approximately 75% water, and of the remaining solids 60% is organic matter. It also contains relatively large amounts of phosphorus.

The addition of filtercake to soil reduced the number of plant parasitic nematodes (Dick & Harris, 1975; Reyes & Beguico, 1978; Recuenco, 1980). However in Brazil, Novaretti and Nelli (1985) found that *M. javanica* and *P. zeae* were largely unaffected by the addition of 30 t filtercake /ha, although yield was increased by 23%. In Zimbabwe, treatment with approximately 50 and 100 t filtercake /ha increased yields by 85% and 130% respectively (Martin, 1967). In 21 trials on sandy soils in South Africa the yield response to treatment with 50 t filtercake/ha varied from −11 to +28 t cane /ha with a mean of 3.6 t (Moberly & Meyer, 1978). In Burkina Faso, the application of filtercake at the same rate depressed yield significantly (Cadet *et al.*, 1987*a*). But in Burkina Faso, Brazil and Zimbabwe the combined application of filtercake and a nematicide increased yield of cane more than either on its own (Martin, 1967; Novaretti & Nelli, 1985; Cadet *et al.*, 1987*a*). No such response was observed in South Africa (Moberly & Meyer, 1978).

Resistance

Sugarcane is not attacked by a single species but by a diverse community of plant parasitic nematodes. Breeding for combined resistance, even to the more important components of such a community appears extremely difficult (Luc & Reversat, 1985). Nevertheless attempts have been made to identify resistance to species of *Meloidogyne* in the cultivar collections of several countries. A number of cultivars have shown some degree of resistance (Table 2). Cultivar SP70–1143, which is resistant to *M. javanica*, is very widely grown on the sandy soils in Brazil where this species is the dominant plant parasitic nematode (G.R. Machado, pers. comm.).

Tolerance

While there is only a remote chance of finding cultivars that are resistant to a wide spectrum of plant feeding nematodes, the selection of tolerant cultivars that grow well in spite of the damage caused by nematodes appears more realistic (Matsuoka, 1980). In fact the normal selection procedures tend to select such tolerant cultivars. In Brazil, Matsuoka (1980) found that by using tolerant cultivars the damage caused by nematodes could be reduced from 48% to 15%. Similar though less spectacular data have been reported from South Africa (Moberly & Clowes, 1981). The effect on nematode populations of cultivating tolerant cultivars of sugarcane has not been studied.

Chemical control

Fumigant and non-fumigant nematicides have been used experimentally on sugarcane in many countries, particularly Australia, Brazil, Burkina Faso, India, Indonesia, Ivory Coast, Philippines, South Africa and Taiwan. Responses to treatment have in some instances been good, especially on sandy soils (Plate 12 A, B & E) (Table 5). However, due either to the relatively high cost of the chemicals and/or the erratic responses to treatment, the commercial use of nematicides is restricted to the sandy soils of a few countries, notably Australia, Burkina Faso, South Africa and Taiwan (Table 6).

TABLE 5. Response of sugarcane to treatment with nematicide.

Country	Soil type, nematicides used; (no. trials)	Control yield t cane/ha*	Response to nematicide. Mean t cane/ha (range)	Reference
Australia	sands to fine yellow podsolic; aldicarb; (17).	74.8	33.5 (8 to 113)	Bull, pers. comm.
Brazil	sandy soils to latosols, aldicarb, carbofuran; (23)	81.4	28.0 (14 to 46)	Novaretti & Nelli, 1985, Novaretti *et al.*, 1978, 1981, 1984, 1985*a*, *b*, 1986; Roccia & Lordello, 1974; Roccia *et al.*, 1975
West Africa	1–5% clay, DBCP, DD, aldicarb, carbofuran; (13)	52.5	42.5 (13 to 68)	Cadet *et al.*, 1987*b*; Cadet, unpubl.
	6–15% clay; DD, carbofuran; (7)	82.2	15.6 (0 to 46)	
India	sandy loam and unspecified; fensulfothion; (9)	52.4	22.1 (10 to 40)	Nath *et al.*, 1976*b*; Sandhu & Behar, 1974; Singh & Misra, 1978; Waraitch, 1980, 1984
Indonesia	light sandy soil; DD; (4)	111.8	26.3 (17 to 34)	Handojo *et al.*, 1975
South Africa	2–5% clay; aldicarb, carbofuran; (81)	45.8	25.3 (0 to 71)	Ringelmann, 1980; Donaldson, 1985; SASA Experiment Station, unpubl. data
	6–20% clay; aldicarb; (83)	84.8	12.2 (-8 to 67)	
Taiwan	sand; phenamiphos, turbufos thiadiazinthion; (8)	80.3	31.4 (22 to 48)	Hu & Tsai, 1978, 1982
	sandy loam; carbofuran, terbufos, thiadiazinthion; (4)	111.5	19.5 (0 to 30)	

* Age of crop varied from 10 to 23 months

Time and method of application

Plant cane

In Burkina Faso, South Africa and Taiwan the recommended practice is to apply the nematicide in the furrow at planting (Hu & Tsai, 1973; Moberly & Clowes, 1981; Cadet *et al.*, 1987*a*). In Australia, however, it is recommended that treatment be applied when the crop is at the three to five leaf

TABLE 6. Current widespread commercial use of nematicides in sugarcane.

Country	Recommended nematicides	Rate of application kg/ha	Approximate area treated, 1986 or 1987 (Approximate total area where nematodes are considered a problem)	Reference
Australia (S. Queensland)	aldicarb ethoprophos[1] phenamiphos	3.0 4.0 4.0	2 500 ha (3 600 ha)	R. M. Bull & K. J. Chandler, pers. comm.
Burkina Faso	aldicarb[2] carbofuran[3]	4.0 6.3	600 ha (600 ha)	Cadet, *et al.*, 1987*b*
South Africa	aldicarb carbofuran	2.25–3.0 2.5 –3.0	11 000 ha (>40 000 ha)	Donaldson, 1988; T. Hagermann, pers. comm.
Taiwan	oxamyl terbufos thiadiazinthion	4.0–5.0 3.0 3.0	2 500 ha (5 000 ha)	Y. S. Pan, pers. comm.

1. Also widely used to control cane grubs.
2. Not recommended, in Burkina Faso, for soils with more than 6% clay. Plant cane only.
3. Liquid formulation; recommended for sands and loamy sands. Plant cane only.

stage (R.M. Bull & K.J. Chandler, pers. comm.). This is based on data from several trials, which indicated that delaying the application of the nematicide until there was slight tillering led to greater yields than those from treatment at planting, or when tillering was well advanced (Chandler, 1978; Bull, 1981). In South Africa delaying the application of aldicarb by 8 weeks did not affect yield; but in another trial, where much higher rates were used, a 5-week delay in treatment was inferior to treatment at planting (Donaldson, 1988). In Burkina Faso, treatment cannot be delayed; when liquid carbofuran is used it is applied to the soil surface immediately after planting is completed. This is to reduce the risk of contact with the field staff who handle the cane at planting, rather than for agronomic reasons (Cadet *et al.*, 1987*a*). The results of several trials show that treatment with a nematicide at planting may not only increase the yield of the plant crop but also that of the first ratoon (Table 7). A similar residual or carry-over response was observed in the second ratoon following treatment of the first ratoon (Donaldson, 1987). Application of a nematicide to a first ratoon crop previously treated at planting increased yields still further (Table 7). The residual effect of treatment at planting may persist until the second ratoon (Chandler, 1980; Novaretti, 1982). A logical explanation for the effect of treatment of one crop carrying over to succeeding ratoons is that cane treated with nematicide develops a more extensive root system than untreated cane; after harvest the young ratoon crop is initially reliant upon the root system of the previous crop and thus benefits from its improved condition.

Ratoon cane

In Burkina Faso, despite causing considerable damage to the plant crop, nematodes have little effect on ratoon cane (Cadet, 1985). In South Africa, however, nematodes are a serious limiting factor in ratoon cane on poor sandy soils and nematicides are usually reapplied after harvest (Rau & Moberly, 1975). In a series of trials it was found that the timing of the treatment was more important for a crop ratooned in the spring or summer than for one ratooned in winter. Thus treatment with aldicarb

TABLE 7. Yield of plant and ratoon cane following application of a nematicide at planting and yield of ratoon cane following retreatment with nematicide.

Country	Nematicide (No. of trials)	Yield of plant crop, t cane/ha	Yield of first ratoon crop, t cane/ha	Residual response and response to retreatment of ratoon: mean (range) t cane/ha	Reference
Australia S. Queensland	Aldicarb & phenamiphos (6)	O.* 62.4 T. 94.4	OO. 62.4 TO. 75.6	TO. 13.2 (−2 to +27)	Bull, 1979, 1981
N. Queensland	Aldicarb (4)	O. - T. -	OO. 73.5** TO. 76.6 TT. 82.7	TO. 3.1 (−2 to +10) TT. 6.1 (−2 to +10)	Chandler, 1978, 1980.
Brazil	Carbofuran (1)	O. 73.0 T. 101.0	OO. 61.7 TO. 71.1 TT. 83.3	TO. 9.4 TT. 12.2	Novaretti, *et al.*, 1978, 1980
Burkina Faso	DBCP carbofuran oxamyl (3)	O. 50.3 T. 79.5	OO. 93.2 TO. 103.6 TT. 104.3	TO. 10.4 (+6 to +14) TT. 0.7 (−3 to +7)	Cadet, unpubl. data
Ivory Coast	DD carbofuran (1)	O. 61.4 T. 89.5	OO. 93.9 TO. 101.9 TT. 114.3	TO. 8.0 TT. 12.4	Cadet, unpubl. data
South Africa	Aldicarb (8)	O. 68.6 T. 107.1	OO. 68.0 TO. 78.4 TT. 91.0	TO. 10.4 (−6 to +21) TT. 12.6 (−6 to +45)	Moberly *et al.*, 1974; Rau & Moberly 1975
Taiwan	DD DBCP EDB (29)	O. 67.6 T. 78.5	OO. 62.1 TO. 70.2	TO. 8.1 (−2 to +20)	Hu *et al.*, 1968

* Symbols denote present and past treatment of cane crop: O = not treated; T = treated with nematicide.

** Original yield data converted from t sucrose/ha to t cane/ha in the ratio 1:7.1 (Anon, 1984*a*)

North and South Queensland data given separately as economic responses are usually obtained in the latter region but not in the former (Chandler, 1980).

6 weeks after harvest in early summer gave a significant response in yield, but treatment after 15 weeks was ineffective (Spaull & Donaldson, 1983). Treatment of cane harvested in winter could, however, be delayed for up to 5 months without affecting the response, providing that the nematicide was applied before spring. The placement of nematicides appears not to be critical in ratoon cane. (Roston, 1976, Chandler, 1980; Donaldson, 1983, 1988)

Factors affecting response to treatment with nematicides

The increase in yield of sugarcane following treatment with nematicide is generally greater in the coarse textured soils. This is well illustrated by data from Taiwan and South and West Africa (Table 5). In plant cane in West Africa this difference in response was attributed to the greater rate of invasion of the sett roots by endoparasites in the coarser textured soils. The consequent damage to these roots delayed and disrupted the normal tillering process with the result that the cane developed fewer stalks (Cadet *et al.*, 1982). In finer textured soils the endoparasites invaded the sett roots more slowly and, presumably, caused less damage during the tillering phase.

Where cane is grown under rainfed conditions as, for example, in large areas of Australia, South Africa and Taiwan, differences in the moisture holding capacity of soils of differing textures may further contribute to the differences in the response to nematicides of both plant and ratoon cane. Thus under conditions of poor rainfall, moisture stress, and therefore reduced cane growth, are more likely in coarse than in finer textured soils, particularly where the development of the root system has been limited by damage from nematodes. This is supported by the observation that the

response of cane treated with nematicide was greater under rainfed conditions than when the cane was irrigated (Donaldson & Turner, 1988). Also the response to treatment tended to be greater in field trials that experienced poor rainfall during the first 5 months of growth, than in trials that received better rainfall (Donaldson 1985). However, Chandler (1980) found that the effect of treatment with aldicarb was reduced if there was insufficient rainfall or irrigation soon after the nematicide was applied; but this was thought to be related to inadequate mobilization of the chemical. The predominance of species of *Meloidogyne* and the ease of movement of these and other nematodes in sandy soils may also explain the greater response of cane to nematicides in such soils.

Where cane growth is limited by inadequate nutrition the potential response to treatment with a nematicide may not be realized. Thus in sandy soils in North Queensland, cane did not respond to treatment with aldicarb except where low soil calcium and magnesium levels were corrected (Chandler, 1980). And in Brazil, Novaretti *et al.* (1981) found that, in soil infested with *M.incognita*, the combined application of a mineral fertilizer and carbofuran increased yields over and above the combined response from both treatments alone.

Efficacy of treatment of sugarcane with aldicarb may also be impaired in alkaline soils (Donaldson, 1985) although Cadet *et al.* (1987*a*) found that lime had no effect on the response of sugarcane to treatment with this nematicide. It has been found that carbofuran interacts adversely with certain herbicides (Novaretti & Teran, 1983; Donaldson & Turner, 1984). Summarizing data from 87 trials with aldicarb in South Africa, Donaldson (1985) reported that response to treatment increased with increasing age of the cane. However, he showed that within a given period of time, greater yields could be obtained from treated cane by harvesting several young crops than a few old crops.

Effect of nematicides on nematodes of sugarcane

In many field trials, treatment with nematicide reduced the size of nematode populations; the effect persisted for some weeks to several months and in some instances was still detectable at harvest (Holtzmann & Wismer, 1965; Chandler, 1980; Novaretti & Nelli, 1985; Cadet, 1985). Where populations recovered, numbers of nematodes in the treated plots sometimes exceeded those in the control plots (Martin, 1967; Harris, 1975). However, in some trials, although treatment improved the yield of cane this was not always reflected by a reduction in the number of nematodes (Chandler, 1980; Waraitch, 1980).

By means of principal component analysis, Cadet and Thioulouse (1989) considerably improved the precision of detecting the effect of nematicide treatment on nematode populations in cane fields.

Economics of nematode control with nematicides

On poor sandy soils the increase in yield derived from treating sugarcane with a nematicide is sometimes considerable and usually economical. Thus Bull (1981) recorded a 700% increase in yield, from 16 to 130 t cane/ha, after applying 2.6 kg aldicarb to a plant crop on deep coastal dune sand in Australia. And in several trials on the weak Recent Sands in South Africa, yields were doubled following treatment with 3.0 to 5.6 kg aldicarb/ha (Donaldson, 1985). Also in South Africa, Dick and Spaull (1982) calculated that an economic response to treatment with aldicarb was obtained in more than 3/4 of 46 trials on soils with less than 7% clay. In contrast, less than half of 22 similar trials on soils with 7–15% clay showed such a response.

Where nematodes limit the growth of sugarcane the merits of using a nematicide include benefits other than simply increasing the yield of the treated crop. The residual response of ratoon cane following treatment of the previous crop has already been mentioned (Table 7). In regions where ratoon crops are severely affected by nematodes the use of nematicides sustains yields for an extra one or perhaps more ratoon crops, and thus delays the need to replant the cane (Thompson, 1983; R. M. Bull & K. J. Chandler, pers. comm.) The improved root system of treated cane: increases resistance to drought conditions; may also permit the use of smaller quantities of fertilizer (Anon., 1984*b*); results in the more rapid development of a full leaf canopy which may reduce the cost of weed control; and more top growth provides a thicker and more effective mulch for the following

crop. Of significance, in those areas that experience frost, is that cane treated with nematicide can withstand temperatures 2 to 3°C lower than untreated cane (Winchester, 1969*b*). Yield loss from ratoon stunting disease (RSD) is most pronounced in cane subjected to moisture stress (Anon., 1981). It is therefore not surprising that treatment with a nematicide, which limits nematode activity and thus permits more normal root growth and water uptake, reduces the effect of RSD (Anon., 1977).

Summary of control measures

The only practical method of controlling nematodes, and thus increasing cane yield on sandy soils, is the use of nematicides, and in soils where the nematode fauna is dominated by one species, the use of resistant cultivars (e.g. SP70–1143 on *M. javanica* infested soils in Brazil). But crop loss caused by nematodes can be reduced by using tolerant cultivars or by growing cane on soils other than sands and loamy sands.

Methods of diagnosis

The abundance of plant parasitic nematodes associated with poorly growing cane together with marked symptoms of damage on the roots are a good indication that the nematodes are limiting growth. The supposition may be confirmed in the field by comparing the performance of cane grown in plots with and without a nematicide. The size of the plots used for assessing the effect of nematode control ranges from 50 to 170 m^2 with treatments replicated four to eight times. Sampling to determine the size and composition of the plant parasitic nematode community must be timed to take into account the dynamics of the root systems of cane, as they can have a considerable influence on the development of the nematode populations. Thus in plant cane a representative sample of sett roots is required. This can only be taken during the relatively short period after planting when the cane is dependent upon the sett roots, for example, within two months in West Africa and approximately 3 months in South Africa (Cadet & Spaull, 1985). Samples of shoot roots can be taken at any time during the subsequent growth of the crop. In ratoon cane the new roots attached to the developing shoots should be distinguished from the roots of the previous crop; these stool roots may persist for several months (Spaull & Cadet, unpubl.). Soil samples to a depth of approximately 20 cm are taken close to the row at any time during the growth of the crop.

Determination of crop loss

Crop loss in sugarcane is assessed by comparing the yield in replicated plots of cane treated with nematicide with that of untreated cane. Yield is usually measured in tons cane stalks or tons sucrose/ha. As discussed earlier, two other yield parameters, *viz*, the number of stalks per hectare and the length of stalks, when recorded at frequent intervals, provide an insight into the interaction between nematodes and sugarcane not available from a single measure of mass of cane or sucrose at harvest (Cadet & Spaull, 1985).

A recent estimate of global loss in yield of sugarcane due to nematodes was given by Sasser and Freckman (1987). Based on data provided by 65 nematologists, they reported an estimated annual loss of 15.3%, equivalent to a world loss in 1984 of more than 140 million tons of cane. A loss of 15.3% is much higher than that of a number of previous estimates for individual countries, *viz*, Australia, less than 0.2% (Anon., 1986); Peru, 3% (Carbonell, 1978); South Africa, at least 5% (Spaull, 1981*a*); USA, 6% (Feldmesser *et al.*, 1971); and Ivory Coast, 11.0%, but similar to an estimate from Burkina Fasol, 14.6% (Cadet, unpubl. data).

Methods of assessing the need for treatment with a nematicide

The criteria used to determine whether or not a nematicide is required are listed in Table 8. Test plots are used when the likely response to treatment is uncertain. If within 6 to 8 weeks the treated cane in the test plots shows a marked improvement in growth, the remainder of the field can be

treated. This system works quite well for ratoon cane where treatment can be delayed without loss of efficacy. In plant cane, where timing of treatment is more critical, the need for a nematicide can be deduced from the response to treatment in the preceding ratoon crop. In the event, as in Australia (R.M. Bull & K. J. Chandler, pers. comm.), the farmer learns from experience which fields are likely to give a good response to treatment with a nematicide (Ringelmann, 1980). In Burkina Faso, the test plots on the less sandy soils are established during the two month period between removing the old crop and replanting the field (Cadet, unpubl.).

TABLE 8. Methods for assessing the need for chemical control.

Country	Soil type	Observation	Action	Reference
Burkina Faso	sand	–	treat plant crop only	Cadet, unpubl. data
	loamy sands	–	assess likely response of plant crop to treatment with nematicide by means of test plots established between crop cycles	
South Africa	0–5% clay	cane with symptoms of nematode damage	treat subsequent crop with a nematicide	Moberly & Clowes, 1981; SA Sugar Association Experiment Station, unpubl. data
	>5% clay	cane with symptoms of nematode damage	assess likely response to nematicide by means of test plots established on existing cane	
Taiwan	Sandy	>5 *Meloidogyne* J_2 or >25 plant parasitic nematodes per 100 g soil	Apply a nematicide to subsequent crop	Y. S. Pan, pers. comm.

Conclusions and Future Prospects

With an almost static world sugar price and with increasing production costs, the financial return from growing sugarcane for the world market has declined considerably. This has not been offset by increased sales on the domestic markets or by expanded markets for the wide range of existing by-products or the development and marketing of new by-products; furthermore, existing sugar markets are being eroded by alternative sweeteners (Ahlfeld, 1986). To quote Ahlfeld (1986) in his summary of the world market for sugar in 1985/86 ". . . . the long term outlook for sugar is dim". However, sugarcane has considerable potential for the production of ethanol for use in, for example, automotive engines, as in Brazil (Reeser, 1987). And of course, unlike fossil fuels it is a renewable resource. Of necessity, increasing attention is also being given to the development of a wide range of new and existing by-products (Lator, 1986; Wang, 1986). The prospects for sugarcane, as opposed to just sugar, are consequently more promising than the existing world price of sugar would suggest. Increased productivity resulting from nematode control should not therefore be neglected.

Nematodes are primarily a problem on poor sandy soils and of little significance in the better soils, and can be a problem in plant cane but not in ratoon cane. This is generally true from the sugarcane farmer's point of view but not true when considered on a national level. Table 9 shows the estimated loss in yield due to nematodes in Burkina Faso, Ivory Coast and in South Africa. Good responses to treatment with nematicide have usually been obtained in plant and ratoon cane on soils with less than 6% clay in South Africa, and in the plant crop of cane in Burkina Faso. In the heavier soils in South Africa and in ratoon cane in Burkina Faso the response to treatment is not predictable and/or is too small to justify the widespread use of nematicides. But the projected crop loss estimates show that the loss of cane on the heavier soils in South Africa is, in total, greater

than that of cane on the weak sands, and in Burkina Faso the loss from ratoon cane is, in total, greater than that from plant cane (Table 9). In the Ivory Coast, on soils with more than 5% clay, the response to treatment is small and usually not significant;the use of nematicides is not therefore recommended although the projected total crop loss from nematodes is considerable (Table 9). Such insidious but widespread crop loss from nematodes is probably typical of many other countries where sugarcane is cultivated. Therefore future work on nematode control in sugarcane should include those situations where small or erratic crop losses occur over a wide area. It is clear that the available nematicides are not suitable for this purpose and alternative methods of control must be sought. Three lines of research appear to hold some promise: cultural control, biological control and the use of tolerant varieties.

TABLE 9. Estimated annual loss in yield of sugarcane due to nematodes in Burkina Faso, Ivory Coast and South Africa (t cane).

Type of sugarcane field	Approximate area (ha)	Loss in yield/ha per annum	Projected total loss in yield
Burkina Faso			
with plant cane	600	39.0	23 400
with ratoon cane	3 600	9.6	34 560
Ivory Coast			
(Plant and ratoon)			
with more than 5% clay	21 600	10.0	216 000
South Africa			
(Plant and ratoon)			
with 2–5% clay	30 000	13.8	414 000
with 6–20% clay	> 92 000	7.2	>662 400

More suitable cultural methods of control may be found by exploiting the interaction between nematodes and sugarcane. With increasing international attention being given to biological control, the prospects for the future are favourable. Perhaps of significance in the context of sugarcane agriculture is the large amount of bagasse and filtercake produced in the extraction of sucrose from sugarcane. These materials might be used as a cheap and readily available medium for mass production and field distribution of certain nematode antagonists, such as nematode-trapping fungi.

Nematodes restrict cane growth over a much wider area than that where the expense of chemical control is justified. The only method of control that requires no extra financial input is the use of tolerant cultivars. At present cultivars are selected according to their performance in different environments and according to their reaction to diseases. Inevitably, by choosing the best cultivars some random selection of nematode tolerance occurs. However, this quality could be considerably enhanced and stabilized if the cultivars were *specifically* selected for tolerance to nematodes.

Acknowledgements

The authors acknowledge, with thanks, the information provided by Messrs R. M. Bull, K. J. Chandler and O. W. Sturgess (Australia), Drs G. R. Machado Jr and W. R. T. Novaretti (Brazil), Dr F. V. de Agudelo (Colombia), Dr P. Quénéhervé (Ivory Coast), Dr S. F. Caceres (Mexico), Dr K.P.N. Kleynhans and Messrs T. Hagermann and J. H. Meyer (South Africa) and Dr Y. S. Pan (Taiwan).

References

Ahlfeld, H. (1986). World sugar statistics. In: *F. O,. Licht's international sugar economic yearbook and directory*. F. O. Licht, Ratzeburg, XIII + 79p.

Ahlfeld, H. (1987). World sugar statistics. In : *F. O. Licht's international sugar economic yearbook and directory*. F. O. Licht, Ratzeburg, XV + 83p.

Andrade, G. A., Rubiano, M. E., de Agudelo, F. V. (1979). Nematodos asociados con el cultivo de la cana de azucar (*Saccharum officinarum* L.) en el Valle del Cauca. *Fitopatologia Colombiana*, 8: 64–72.

Anon. (1961). Diseases. *Report of the Hawaiian Sugar Planters' Association Experiment Station*: 17–23.

Anon. (1977). Ratoon stunting disease (RSD). *Relatório Anual, Estacoes Experimentais, Planalsucar, Brasil:* 20–22.

Anon. (1981). Pathology and Nematology. *South African Sugar Association Annual Report, 1980–81;* 70.

Anon. (1982). Growing sugarcane on the Recent Sands. *South African Sugar Journal*, 66: 369–370.

Anon. (1984*a*) *Sugar industry statistics*. Australian Sugar Year Book. Brisbane, Strand Publishing Pty, Ltd.; 257–270.

Anon. (1984*b*). Recent sugarcane pest control research unveils economic benefits. *Sugar y Azucar*, 79 supplement: 50–56.

Anon. (1986). Cane pests. *86th Annual report, (Queensland) Bureau of Sugar Experiment Stations:* 24–28.

Anzalone, L. & Birchfield, W. (1977). Varietal resistance in sugarcane to *Meloidogyne incognita*. *Plant Disease Reporter*, 61: 190–191.

Apt, W. J. & Koike, H. (1962*a*). Pathogenicity of *Helicotylenchus nannus* and its relation with *Pythium graminicola* on sugarcane in Hawaii. *Phytopathology*, 52: 798–802.

Apt, W. J. & Koike, H. (1962*b*). Influence of the stubby-root nematode on growth of sugarcane in Hawaii. *Phytopathology*, 52: 963–964.

Apt, W. J. & Koike, H. (1962*c*). Pathogenicity of *Meloidogyne incognita acrita* and its relation with *Pythium graminicola* on sugarcane in Hawaii. *Phytopathology*, 52: 1180–1184.

Astudillo, G. E. & Birchfield, W. (1980). Pathology of *Hoplolaimus columbus* on sugarcane. *Phytopathology*, 70: 565.

Barnes, A. C. (1974). *The Sugar Cane*. Aylesbury, Leonard Hill Books, 572p.

Birchfield, W. (1960). A new species of *Catenaria* parasitic on nematodes of sugarcane. *Mycopathologia et Mycologia Applicata*, 13: 331–338.

Birchfield, W. (1969). Nematicides for control of plant-parasitic nematodes on sugarcane in Louisiana. *Plant Disease Reporter*, 53: 530–533.

Birchfield, W. (1984). Nematode parasites of sugarcane. In: Nickle, W. R. (Ed). *Plant and Insect Nematodes*. New York, Marcel Dekker: 571–588.

Birchfield, W. & Martin, W. J. (1956). Pathogenicity on sugarcane and host plant studies of a species of *Tylenchorhynchus*. *Phytopathology*, 46: 277–280.

Brathwaite, C. W. D. (1976). Plant-parasitic nematodes associated with sugarcane in Barbados. *Plant Disease Reporter*, 60: 294–295.

Brathwaite, C. W. D. (1980). Plant-parasitic nematodes associated with sugarcane in Trinidad. *FAO Plant Protection Bulletin*, 28: 133–136.

Bridge, J. (1986). *Plant nematode survey of Ramu Sugar Limited, Ramu Valley, Papua New Guinea*. Report, CAB International, Institute of Parasitology, St. Albans, UK., 8p.

Bull, R. M. (1979). New chemicals for nematode control in the Bundaberg district. *Proceedings of Australian Society of Sugar Cane Technologists:* 99–103.

Bull, R. M. (1981). Studies and observations on nematode control in the Bundaberg district. *Proceedings of Australian Society of Sugar Cane Technologists.*: 267–274.

Cadet, P. (1979). Traitments nématicides sur canne à sucre en Haute-Volta. *Congrès sur la lutte contre les Insectes en Milieu tropical, Marseille, 13–16 Mars 1979;* 201–217.

Cadet, P (1985). Incidence des nématodes sur les repousses de canne à sucre au Burkina Faso et en Côte d'Ivoire. *Revue de Nématologie*, 8: 277–284.

Cadet, P. (1986*a*). Evolution des nématodes ectoparasites dans la rhizosphère de la canne à sucre au Burkina Faso. *Revue d' Ecologie et de Biologie du Sol*, 23: 205–213.

Cadet, P. (1986*b*). Etude du développment des nématodes endoparasites dans la racines de la canne à sucre au Burkina Faso et en Côte d'Ivoire. *Revue d' Ecologie et de Biologie du Sol*, 23: 287–297.

Cadet, P. (1987). Etude comparative des peuplements naturels de nématodes parasites associés à la canne à sucre. *Nematologica*, 33: 97–105.

Cadet, P. & Merny, G. (1978). Premiers essais de traitments chimiques contre les nématodes parasites de la canne à sucre en Haute-Volta. *Revue de Nématologie*, 1: 53–62.

Cadet, P. & Quénéhervé, P. (1988). Etude de la résistance naturelle des repousses de canne à sucre aux nématodes phytoparasites. *Acta Oecologica, Oecologia Applicata*, 9: 127–136.

Cadet, P. & Spaull, V. W. (1985). Studies on the relationship between nematodes and sugarcane in South and West Africa: Plant Cane. *Revue de Nématologie*, 8: 131–142.

Cadet, P. & Thioulouse, J. (1989). Traitments nématicides et peuplement de nématodes parasites de la canne à sucre. 1. Repousses. *Revue de Nématologie*, 12: 35–44.

Cadet, P., Quénéhervé, P. & Hugot, R. (1987*a*). Incidence agronomique des traitments nématicides sur le rendement des cannes à sucre au Burkina Faso. *Phytoma*, 390: 47–49.

Cadet, P., Quénéhervé, P. & Merny, G. (1982). Pathogenic action of nematodes on irrigated sugar-cane. *Revue de Nématologie*, 5: 205–209.

Cadet, P., Quénéhervé, P. & Saunier, P (1987*b*). Incidence des formulations liquides de nematicides sur le rendement des cannes à sucre en Afrique de l'Ouest. *Phytoma*, 392: 56–59.

Carbonell, E. E. (1978). The nematodes, pests of sugarcane in Peru. *Proceedings of the international Society of Sugar Cane Technologists*, 16: 545–551.

Chandler, K. J. (1978). Non-volatile nematocides: An initial assessment in North Queensland sugar cane fields. *Proceedings of Queensland Society of Sugar Cane Technologists*, 45: 85–91.

Chandler, K. J. (1980). Continued experiments with non-volatile nematicides in North Queensland sugar cane fields. *Proceedings of Australian Society of Sugar Cane Technologists:* 75–82.

Chu, H. T. & Hsu, S. C. (1965). [Studies on the nematode-trapping fungi in Taiwan sugarcane soils] *Report of Taiwan Sugar Experiment Station*, 37: 81–88.

Cooke, D. A. & Draycott, A. P. (1971). The effects of soil fumigation and nitrogen fertilizers on nematodes and sugarbeet in sandy soils. *Annals of applied Biology*, 69: 253–264.

Costilla, M. A. (1973). E1 nematode *Pratylenchus zeae* Graham en cana de azucar. *Revista Industrial y Agricola de Tucuman*, 50: 39–43.

Daniels, J. & Roach, B. T. (1987). Taxonomy and evolution. In: Heinz, D. J. (Ed.). *Developments in Crop Sciences 11. Sugarcane improvement through breeding*. Amsterdam, Elsevier: 7–84.

Von Decker, H., Rodriguez Fuentes, M-E. & Casamayor Garcia, R. (1970). Untersuchungen über die Phytonematodenfauna unterschiedlich lang genutzter Zuckerrohr – Monokulturen in Cuba. *Wissenschaftliche Zeitschrift der Universität Rostock*, 19: 561–570.

Dick, J. & Harris, R. H. G. (1975). Nematodes and sugarcane. *South African Sugar Journal*, 59: 397–410.

Dick, J. & Spaull, V. W. (1982). Nematode pests of sugarcane. In: Keetch, D. P., Heyns, J. (Eds). *Nematology in southern Africa*, Science Bulletin No. 400, Department of Agriculture and Fisheries, Republic of South Africa: 47–57.

Donaldson, R. A. (1983). The effect of placement on the efficacy of granular nematicides. *Proceedings of the South African Sugar Technologists' Association*, 57: 120–122.

Donaldson, R. A. (1985). The effects of soil pH, clay content, rainfall and age at harvest on the yield response of sugarcane to Temik. *Proceedings of the South African Sugar Technologists' Association*, 59: 164–167.

Donaldson, R. A. (1987). Some aspects related to the use of nematicides on sugarcane in South Africa. *Proceedings of the South African Sugar Technologists' Association*, 61: 117–120.

Donaldson, R. A. (1988). Nematicides for Sugarcane. *South African Sugar Journal*, 72: 57–61, 92–97.

Donaldson, R. A. & Turner, P. E. T. (1984), The interaction of herbicides and nematicides on plant cane grown in weak sandy soils. *Proceedings of the South African Sugar Technologists' Association*, 58: 137–142.

Donaldson, R. A. & Turner, P. E. T. (1988). A preliminary report of the effect of soil moisture level on responses to Temik and Curaterr. *Proceedings of the South African Sugar Technologists' Association*, 62: 164–168.

Estioko, R. V. & Reyes, T. T. (1984). Population dynamics of plant-parasitic nematodes associated with sugarcane in Negros Occidental in relation to soil type and weather pattern. *Proceedings of the Philippine Sugar Technologists' Association*, 31: 235–252.

Fargette, M. (1987). Use of the esterase phenotype in the taxonomy of the genus *Meloidogyne*. 2. Esterase phenotypes observed in West African populations and their characterization. *Revue de Nématologie*, 10: 45–56.

Feldmesser, J., Edwards, D. I., Epps, J. M., Heald, C. M., Jenkins, W. R., Jensen, H. J., Lear, B., McBeth, C. W., Nigh, E. L. & Perry, V. G. (1971). *Estimated crop losses due to plant-parasitic nematodes in the United States*. Special publication No. 1, Society of Nematologists, 7p.

Gargantiel, F. T. & Davide, R. G. (1973). Survey and pathogenicity tests of plant-parasitic nematodes associated with sugarcane in Negros Occidental. *Philippine Phytopathology*, 9: 59–66.

Gomes Carneiro, R. M. D., Lordello, L. G. E., Gomes Carneiro, R. & Monteiro, A. R. (1980). Flutuacao populacional de quatro espécies de nematoides parasitos de cana-de-acucar (*Saccharum officinarum* L.) em relacâo à pluviosidade e umidade do solo. *Trabalhos apresentados à IV Reuniao de Nématologia, Sociedade Brasileira de Nématologia, Piracicaba, SP, Brazil: 127–141.*

Gotoh, A. (1965). [The plant-parasitic nematodes found mainly in sugarcane fields in the Satsunan Islands, South Kyushu]. *Proceedings of the Association of Plant Protection, Kyushu*, 11: 105–110.

Gupta, J. C. & Atwal, A. S. (1971). Biology and ecology of *Hoplolaimus indicus* (Hoplolaiminae: Nematoda). II. The influence of various environmental factors and host plants on the reproductive potential. *Nematologica*, 17: 277–284.

Handojo, H., Siswojo & Legowo, L. (1975). The influence of soil fumigation with DD at the sugar factory Ngadirejo during the years 1971–1974. *Berita Balai Penyelidikan Perusalhaan Perkebunan, Gula*, 1: 5–17.

Handojo, H., Siswojo & Legowo, L (1980). Nematodes and nematicide trials in sugarcane in Java. *Proceedings of the international Society of Sugar Cane Technologists*, 17: 1416–1425.

Harper, R. S. (1975). Pests, diseases and weeds of crops in Indonesia. *World Crops*, 27: 134–137.

Harris, R. H. G. (1974). The effects on sugarcane of plant-parasitic nematodes in non-sterile monospecific cultures. *Proceedings of the international Society of Sugar Cane Technologists*, 15: 327–337.

Harris, R. H. G. (1975). Studies on nematode populations in sugarcane soil profiles. *Proceedings of the South African Sugar Technologists' Association*, 49: 164–170.

Holtzmann, O. V. (1964). Nematodes and Sugarcane. In: Hughes, C. G., Abott, E. V. and Wismer, C. A. (Eds). *Sugarcane diseases of the World*, Vol II., Amsterdam, Elsevier: 317–341.

Holtzmann, O. V. & Santo, G. S. (1971). Effect of temperature on the interrelationship of *Pratylenchus zeae* and *Phythium graminicola* on sugarcane. *Phytopathology*, 61: 1321.

Holtzmann, O. V. & Wismer, C. A. (1965). Effectiveness of DD and DBCP against lesion and root-knot nematodes on sugarcane in Hawaii. *Proceedings of the international Society of Sugar Cane Technologists'*, 12: 1413–1419.

Hu, C. H. (1963). [A preliminary report of the effects of root knot nematodes, *Meloidogyne* spp. on the growth of sugarcane and its interplanting crops]. *Report of Taiwan Sugar Experiment Station*, 31: 121–136.

Hu, C. H. & Chu, H. T. (1964). [The nematode investigation in sugarcane fields of Taiwan (II)]. *Report of Taiwan Sugar Experiment Station*, 33: 63–82.

Hu, C. H. & Tsai, T. K. (1973). [Effects of Terracur P and Thimet on parasitic nematodes and yield increase of sugarcane]. *Report of Taiwan Sugar Research Institute*, 60: 61–75.

Hu, C. H. & Tsai, T. K. (1975). [The nematode investigation in sugarcane fields of Taiwan (III)]. *Report of Taiwan Sugar Research Institute*, 70: 13–25.

Hu, C. H. & Tsai, T. K. (1978). [Control of parasitic nematodes with Counter, Furadan and Temik and its effect on sugarcane yield]. *Report of Taiwan Sugar Research Institute*, 81: 25–34.

Hu, C. H. & Tsai, T. K. (1982). [Control of parasitic nematodes with Vydate, Nemacur and Geofos and its effect on sugarcane yield]. *Report of Taiwan Sugar Research Institute*, 95: 9–23.

Hu, C. H. & Tsai, T. K. (1983). [Resistance of sugarcane varieties and interplanting crops to root-knot nematodes]. *Report of Taiwan Sugar Research Institute*, 100: 45–63.

Hu, C. H., Tsai, T. K. & Chu, H. T. (1968). The nematode investigation in sugarcane fields of Taiwan and

effects of soil fumigation. *Proceedings of the international Society of Sugar Cane Technologists*, 13: 1262–1269.

Humbert, R. P. (1968). *The growing of sugarcane*. Amsterdam, Elsevier Publishing Co., 779p.

Interiana Munoz, J. D. (1971). Identification of nematodes found in lands of the Escuela Nacional de Agricultura in El Salvador and pathogenicity of ring nematodes *Criconemoides* spp. on rice (*Oryza sativa* L.) under greenhouse conditions. *Nematropica*, 1: 2–3.

Jensen, H. J., Martin, J. P., Wismer, C. A. & Koike, H. (1959). Nematodes associated with varietal yield decline of sugarcane in Hawaii. *Plant Disease Reporter*, 43: 253–260.

Khan, S. A. (1963). Occurrence and pathogenicity of *Pratylenchus zeae* on sugarcane in Louisiana. *Proceedings of the international Society of Sugar Cane Technologists*, 11: 711–717.

Khurana, S. M. P. & Singh, S. (1971). Interrelationship of a fungus, *Curvularia lunata* with root-knot nematode, *Meloidogyne javanica* in sugarcane seedling blight. *Annals of the Phytopathological Society of Japan*, 37: 313–315.

Kirby, M F. & Kirby, M. E. (1977). Plant-parasitic nematodes associated with sugarcane in Fiji. *Fiji agricultural Journal*, 39: 13–24.

Koike, H. & Roman, J. (1970). Pathogenicity of *Pratylenchus brachyurus* and *Pythium graminicola* to sugarcane. *Phytopathology*, 60: 1562–1565.

Lainer Gonzalez, F. (1979). Nematodos fitoparasitos asociados con la cana de azucar en varias zonas de Costa Rica. *Nematropica*, 9: 32–35.

Lator, T. (1986). Energy and By-products from sugarcane. *Proceedings of the Inter-American Sugarcane Seminars, Miami, Florida, Sept, 1986*, 341p.

Luc, M. (1968). Nematological problems in the former French African tropical territories and Madagascar. In: Smart, Jr, G. C. & Perry, V. G. (Eds). *Tropical Nematology*. Gainesville, USA, University of Florida Press: 93–112.

Luc, M. & Reversat, G. (1985). Possibilités et limites des solutions génétiques aux affections provoquées par les nématodes sur les cultures tropicales. *Comptes rendus des Séances de l' Académie d'Agriculture de France*, 71: 781–791.

Madamba, C. P., Espina, J. N. & Empig, L. T. (1974). Screening sugarcane varieties for resistance to root-knot nematode *Meloidogyne* spp. *Sugarcane Pathologists' Newsletter*, 11/12: 27–31.

Martin, G. C. (1962). Population levels of nematodes in roots, and soil around the root zones of tea, sugarcane, tobacco and wheat grown in the Federation of Rhodesia and Nyasaland. *Rhodesia agricultural Journal*, 59: 28–35.

Martin, G. C. (1967). Plant parasitic nematodes associated with sugarcane production in Rhodesia. *FAO Plant Protection Bulletin*, 15: 45–58.

Matsuoka, S. (1980). Como e quando controlar doencas e nematoides da Cana-de-acucar. *Saccharum. stab*, 3: 12–22.

Meredith, J. A. & Castro, R. C. L. (1978),. Nematodos fitoparasitos asociados al cultivo de la cana de azucar en los estados Aragua, Portuguesa y Yaracuy, Venezuela. *Nematropica*, 8: 17.

Moberly, P. K. & Clowes, M. St. J. (1981). Trials with nematicides registered for use on sugarcane in South Africa. *Proceedings of the South African Sugar Technologists' Association*, 55: 92–98.

Moberly, P. K. & Meyer, J. A. (1978). Filtercake – a field and glasshouse evaluation. *Proceedings of the South African Sugar Technologists' Association*, 52: 131–135.

Moberly, P. K., Harris, R. H. G. & Millard, E. (1974). An investigation into the problem of poor sugarcane growth on some sandy soils of the Natal Sugar belt. *Proceedings of the international Society of Sugar Cane Technologists*, 15: 923–931.

Nath, R. P., Singh, R. K. & Haider, M. G. (1976*a*). Combined effect of *Fusarium moniliforme* and *Hoplolaimus indicus* on sugarcane plants. *Sugarcane Pathologists' Newsletter*, 17: 24–25.

Nath, R. P., Akhter, S. W., Haider, M. G. & Bhide, V. S. (1975). Effect of *Hoplolaimus indicus* Sher, 1963 on sugarcane seedlings. *Indian Journal of Nematology*, 4: 241–242.

Nath, R. P., Singh, R. K., Haider, M. G. & Ashraf, H. M. (1976*b*). Effect of some nematicides on sugarcane in a nematode infested field. *Sugarcane Pathologists' Newsletter*, 17: 23–24.

Novaretti, W. R. T. (1981). *Efeitos de diferentes niveis de populacoes iniciais de* Meloidogyne javanica *em duas variedades de cana-de-asucar* (Saccharum *spp.*) *cultivadas no estado de Sao Paulo.* Dissertacao, Mestre em Entomologia, Escola Superior de Agricultura "Luis de Queiros", Universidade de Sao Paulo, 100p.

Novaretti, W. R. T. (1982). Control of root-knot nematodes on sugarcane in Brazil. *Proceedings of the Research and planning Conference on root-knot Nematodes,* Meloidogyne *spp, October 25–29, 1982,* University *of Brasilia, Brasilia, International* Meloidogyne *Project*: 111–123.

Novaretti, W. R. T. & Nelli, E. J. (1985). Use of nematicide and filtercake for control of nematodes attacking sugarcane in Sao Paulo state. *Nematologia Brasileira,* 9: 175–184.

Novaretti, W. R. T. & Nunes, D. Jr. (1980). Comportamento de clones SP e variedades comerciais de cana-de-acucar em relacao ao nematoide *Meloidogyne javanica.* Resultados preliminares. *Sociedade Brasileira de Nematologia,* 4: 47–58.

Novaretti, W. R. T. & Teran, F. O. (1983). Controle de nematoides parasitos de cana-de-acucar. Reuniao Tecnica Agronomica. In: *Pragas da cultura de cana-de-acucar,* (Sept 1983), Centro de Technologia Copersucar: 16–24.

Novaretti, W. R. T., Carderan, J. O. & Totino, L. C. (1985*a*). Efeito fitotoxico do EDB em cana-de-acucar. *Nematologia Brasileira,* 9: 153–160.

Novaretti, W. R. T., Nelli, E. J. & Carderan, J. O. (1985*b*). Teste de novos nematicidas em cana-de-acucar. *Nematologia Brasileira,* 9: 123–133.

Novaretti, W. R. T., Dinardo, L. L., Totino, L. C. & Strabelli, J. (1986). Efeito da aplicacao conjunta do fungo *Paecilomyces lilacinus* e do nematicida Furadan 5G no controle de nematoides em cana-de-acucar. *Nematologia Brasileira,* 10: 133–144.

Novaretti, W. R. T., Lordello, L. G. E., Nelli, E. J. & Carderan, J. O. (1980). Viabilidade economica do nematicida "carbofurano" na cultura de cana-de-acucar – cana de segundo corte. *Sociedada Brasileira de Nematologia,* 4: 179–196.

Novaretti, W. R. T., Lordello, L. G. E., Nelli, E. J. & Wenig Filho, G. (1978). Viabilidade economica do nematicida 'carbofurano' na cultura da cana-de-acucar. *Sociedade Brasileira de Nematologia,* 3: 117–131.

Novaretti, W. R. T., Nelli, E. J., Dinardo, L. L. & Carderan, J. O. (1984). Influencia da epoca de plantio da cana-de-acucar no controle quimico de nematoides. *Nematologia Brasileira,* 8: 219–232.

Novaretti, W. R. T., Roccia, A. O., Lordello, L. G. E. & Monteiro, A. R. (1974). Contribuicao ao estudo dos nematoides que parasitam a cana-de-acucar em S. Paulo.*Sociedade Brasileira de Nematologia,* 1: 27–32.

Novaretti, W. R. T., Coleti, J. T., Lorenzetti, J. M., Gasparini, C. T. & Teodoro Neto, O. (1981). Influencia do ataque de nematodies na produtividade da cana-de-acucar e seus efeitos na absorcao de nutrients. *Saccharum – stab,* 4: 49–55.

Onapitan, J. A., & Amosu, J. O. (1982). Pathogenicity and histopathology of *Pratylenchus brachyurus* and *Helicotylenchus pseudorobustus* on sugarcane. *Nematropica,* 12: 51–60.

O'Relly, J. P. & Milian, J. R. P. (1978). Nematodes parasitising sugarcane in Cuba. *Proceedings of the international Society of Sugar Cane Technologists,* 16: 497–507.

Oteifa, B. A., Rushdi, M. & Salem, A. (1963). Vertical distribution of some nematodes associated with sugarcane. *Bulletin of Science and Technology, Assiut University,* 6: 263–270.

Parsons, H. N. (1970). Preliminary investigations on the incidence and control of plant nematodes in a new sugarcane estate in Nigeria. *Tropical Agriculture, Trinidad,* 47: 103–113.

Pinochet, J, (1987). Management of plant parasitic nematodes in central America: The Panama experience. In: Veetch, J. A. and Dickson, D. W. (Eds). *Vistas on Nematology.* Hyattsville, Maryland, USA, Society of Nematologists: 105–113.

Rao, V. R. & Swarup, G. (1975). Pathogenicity of the spiral nematode, *Helicotylenchus dihystera,* to sugarcane. *Indian Journal of Nematology,* 4: 160–166.

Rau, S. & Moberly, P. K. (1975). Nematicide application to ratoon crops of sugarcane grown in some sandy soils of the Natal sugarbelt. *Proceedings of the South African Sugar Technologists',* 49: 171–173.

Razak, A. R. (1982). Nematodes associated with sugarcane in Malaysia. *Proceedings of the international Conference on plant protection in the tropics. 1–4 March 1982, Kuala Lumpur, Malaysia*: 165–171.

Recuenco, J. D. (1980). Control of nematodes attacking sugarcane with nematocides and organic amendments. *Sugarcane Pathologists' Newsletter*, 24: 32–34.

Reeser, L. G. (1987). Food and energy from crops: An international perspective. *Sugar y Azucar*, 82: 14–15 & 18.

Reyes, T. T. & Beguico, E. D. (1978). Nematodes in sugarcane. *NSDB Technology Journal*, 3: 25–35.

Riess, C. M. (1971). Investigation sobre nematodes en suelos caneros de Mexico. *V Congreso Nacional de la Ciencia del Suelo, Agosto, 1971, Guadalajara, Mexico*, 8p.

Ringelmann, E. H . (1980). The evaluation of nematicides on Mount Elias farm at Fawn Leas. *Proceedings of the South African Sugar Technologists' Association*, 54: 158–160.

Roccia, A. O. & Lordello, L. G. E. (1974). Ensaio de controle quimico de nematoides em cultura de cana-de-acucar. *Sociedade Brasileira de Nematologia*, 1: 74–80.

Roccia, A. O., Lordello, L. G. E. & Lordello, R. R. A. (1975). Ensaios de controle de nematoides em cana-de-acucar com aldicarb. *Revista de Agricultura, Piracicaba*, 50: 175–181.

Roman, J. (1961). Pathogenicity of five isolates of root-knot nematodes (*Meloidogyne* spp.) to sugarcane roots. *Journal of Agriculture, Puerto Rico*, 45: 55–84.

Roman, J. (1967) Preliminary investigations on the nematodes associated with sugarcane in Puerto Rico. *Proceedings of the international Society of Sugar Cane Technologists'*, 12: 1401–1407.

Roman, J. (1968). Nematode problems of sugarcane in Puerto Rico. In: Smart, G. C. Jr. & Perry, V. G. (Eds). *Tropical Nematology*, Gainesville, USA, University of Florida Press: 61–67.

Roman, J. & Grullon, L. (1975). Nematodes associated with sugarcane in the Dominican Republic. *Journal of Agriculture, Puerto Rico*, 59: 138–140.

Rosenfeld, A. H. (1956). *Sugar Cane around the World*. University of Chicago Press, 562p.

Rostron, H. (1976). Rate, time and methods of Temik application in ratoon sugarcane. *Proceedings of the South African Sugar Technologists' Association*, 50: 29–33.

Salawu, E. O. (1986). Reaction of sugarcane varieties to a root-knot nematode, *Meloidogyne incognita*. *Pakistan Journal of Nematology*, 4: 19–26.

Sandhu, S. S. & Behar, D. S. (1974). Chemical control of nematodes on sugarcane in the Punjab. *Proceedings of the international Society of Sugar Cane Technologists*, 15: 338–342.

Santo, G. S. & Holtzmann, O. V. (1970). Interrelationships of *Pratylenchus zeae* and *Pythium graminicola* on sugarcane. *Phytopathology*, 50: 1537.

Sasser, J. N. (1979). Economic importance of *Meloidogyne* in tropical countries. In: Lamberti, F. & Taylor, C. E. (Eds). *Root-knot nematodes* (Meloidogyne *species*) *systematics, biology and control*. London, Academic Press: 359–373.

Sasser, J. N. & Freckman, D. W. (1987). A world perspective on nematology: The role of the Society. In: Veetch, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*, Hyattsville, USA, Society of Nematologists: 7–14.

Singh, K. (1967). The incidence and chemical control of nematodes associated with sugarcane in India. *Proceedings of the international symposium on plant pathology. Indian Phytopathology*, 589–596.

Singh, K. & Misra, S. R. (1974). Incidence and distribution of nematodes associated with sugarcane in Uttar Pradesh. *Indian Journal of Nematology*, 4: 182–188.

Singh, K. & Misra, S. R. (1976). Pathogenicity and histopathology of *Hoplolaimus indicus* on sugarcane. *Nematologica*, 22: 433–436.

Singh, K. & Misra, S. R. (1978). Seasonal fluctuations in the populations of nematodes associated with sugarcane and their control. *Proceedings of the international Society of Sugar Cane Technologists'*, 16: 633–642.

Smith, D. (1978). *Cane Sugar World*. New York, Palmer publications, 240p.

Spaull, V. W. (1981*a*). Nematodes associated with sugarcane in South Africa. *Phytophylactica*, 13: 175–179.

Spaull, V. W. (1981*b*). *Bacillus penetrans* in South African plant-parasitic nematodes. *Nematologica*, 27: 244–245.

Spaull, V. W. (1984). Observations on *Bacillus penetrans* infecting *Meloidogyne* in sugarcane fields in South Africa. *Revue de Nématologie*, 7: 277–282.

Spaull, V. W. & Donaldson, R. A. (1983). Relationship between time of nematicide application, numbers of

nematodes and response to treatment in ratoon sugarcane. *Proceedings of the South African Sugar Technologists' Association*, 57: 123–127.

Sreenivasan, T. V., Ahloowalia, B. S. & Heinz, D. J. (1987). Cytogenetics. In: Heinz, D. J. (Ed). *Developments in crop sciences II. Sugarcane improvement through breeding*. Amsterdam, Elsevier: 211–253.

Tarte, R., Cerrud, D., Rodriguez, I. & Osorio, J. M. (1977). Presencia y parasitismo de *Pratylenchus zeae* en cana de azucar en Panama con indicaciones sobre la susceptibilidad relativa de algunos cultivares. *Turrialba*, 27: 259–265.

Thompson, G. D. (1983). *The Weak Sand Project*. Mount Edgecombe Research Report No. 1 Mount Edgecombe, South Africa, SASA Experiment Station, 143p.

Valle-Lamboy, S. & Ayala, A. (1980). Pathogenicity of *Meloidogyne incognita* and *Pratylenchus zeae*, and their association with *Pythium graminicola* on roots of sugarcane in Puerto Rico. *Journal of Agriculture. Puerto Rico*, 64: 338–347.

van den Berg, E. & Spaull, V. W. (1981). *Rotylenchulus* species found associated with sugarcane in South Africa with a description of *R. sacchari* sp.n. (Nematoda: Rotylenchulinae). *Phytophylactica*, 13: 43–47.

Wang, L. H. (1986). Recent progress in research and development of by-products utilization at Taiwan Sugar Research Institute. *Taiwan Sugar Research Institute Annual Report*, 1985–86: 37–45.

Waraitch, K. S. (1980). Effect of some nematicides on sugarcane in the Punjab. *Sugarcane Pathologists' Newsletter*, 24: 29–31.

Waraitch, K. S. (1984). Effect of systemic nematicides on yield of sugarcane. *Tropical Pest Management*, 30: 108–109.

Williams, J. R. (1963). Investigations in Mauritius on the soil inhabiting nematodes associated with sugarcane. *Proceedings of the international Society of Sugar Cane Technologists'*, 11: 717–722.

Williams, J. R. (1967). Observations on parasitic Protozoa in plant-parasitic and free living nematodes. *Nematologica*, 13: 336–342.

Williams, J. R. (1969). Nematodes attacking sugarcane. In: Peachey, J. E. (Ed). *Nematodes of Tropical Crops*. Farnham Royal, Commonwealth Agricultural Bureau: 184–203.

Williams, J. R. & Luc, M. (1977). The species of *Xiphinema* Cobb, 1913 (Nematoda: Longidoridae) in the sugarcane fields of Mauritius. *Occasional Paper Mauritius Sugar Industry Research Institute*, 30: 19p.

Wilson, G. (1969). Insecticides for the control of soil-inhabiting pests of sugarcane. In: Williams, J. R., Metcalfe, J. R., Mungomery, R. W. & Mathes, R. (Eds). *Pests of sugarcane*. Amsterdam, Elsevier: 259–282.

Winchester, J. A. (1969*a*). Sugarcane nematodes of the world. *Proceedings of the international Society of Sugar Cane Technologists*, 13: 1276–1283.

Winchester, J. A. (1969*b*). Sugar-cane nematode control. In: Peachey, J. E. (Ed). *Nematodes of Tropical Crops*. Farnham Royal, Commonwealth Agricultural Bureau: 204–209.

Winfield, A. L. & Cooke, D. A. (1975). The *ecology of Trichodorus*. In: Lamberti, F., Taylor, C. E. & Seinhorst, J. W. (Eds). *Nematode Vectors of plant viruses*. London & New York, Plenum Press: 309–341.

Wolff Schoemaker, R. L. P. (1968). Population studies of plant-parasitic nematodes around sugarcane roots in Nyanza Province, Kenya. *Nematologica*, 14: 295–299.

Chapter 15

Nematode Parasites of Tobacco

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Tobacco (*Nicotiana tabacum* L.) is a high value crop that is in wide demand throughout the world for the production of cigarettes, cigars and other tobacco products, and is the most widely grown commercial non-food crop in the world (Akehurst, 1981). The total world production in 1987 was estimated to be about 6.5 million metric tonnes, of which almost one third was produced in China, followed by the United States, India and Brazil (Table 1). The sale of cured leaf and manufactured products is a major source of income for many countries and many governments rely heavily on taxes levied on sales to consumers. Although production has increased by about 30% during the last 16 years, the increasing concern about the effects of smoking on health clouds the future for the crop (Milne, 1972; Anon, 1987).

Tobacco originated as a natural hybrid in Central America and has been under cultivation for many centuries. By the time explorers from Europe came to the Americas, tobacco cultivation was widespread in North, Central and South America and since then has spread all over the world (Akehurst, 1981).

Cultivation techniques

As tobacco seed is very small and the germinating seedling delicate, it is normal practice to produce seedlings in seedbeds or nurseries. The seedlings are then transplanted into the field when they are strong enough. The production of strong seedlings is essential for growing a good crop in the field.

Tobacco does not need a highly fertile soil, but it should be deep and well drained. Much of the flue-cured crop is grown in sandy soils, where nematode problems may develop rapidly, whereas air and fire-cured tobaccos are often grown on heavier soils. In some parts of the world where paddy rice is grown, or where low-lying areas are flooded by tropical rain, tobacco may be planted after the water has receded and grown without further water. Oriental tobacco, having developed in an area of winter rainfall, is very drought resistant and does not require much extra water during its growth in the field.

Nematodes of Tobacco

Throughout the world, plant parasitic nematodes are found wherever tobacco is grown, but the severity of the problem depends on climate and soil type. A large number of tobacco producing countries are close to, or within, the inter-tropical zone. The dominant nematodes there are *Meloidogyne* spp., of which the most important are *M. arenaria, M. incognita* and *M. javanica. M. hapla* and

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

TABLE 1. Estimated tobacco production of selected countries (after Anonymous, 1987).

Country	Hectares Harvested (Thousands)	Production (metric tonnes)
China	1 183.2	2 094 700
United States	243.5	558 074
India	390.0	447 730
Brazil	272.0	410 000
U.S.S.R.	193.5	381 000
Indonesia	307.0	178 383
Turkey	190.0	175 000
Italy	78.4	149 400
Zimbabwe	72.3	138 526
Bulgaria	105.0	138 150
Greece	89.8	134 450
Burma	70.0	115 080
Japan	43.6	105 780
Poland	50.2	97 800
Philippines	57.9	83 231
Korea, Republic of	34.6	78 710
Pakistan	41.1	73 310
Malawi	79.4	66 713
Yugoslavia	62.0	66 000
Thailand	61.2	62 921
Canada	26.5	60 680
Bangladesh	54.0	51 545
Cuba	55.0	50 000
Korea, North	37.0	46 000
Mexico	30.5	38 730
Colombia	24.5	38 366
Romania	35.0	36 000
South Africa	26.2	33 185
Spain	22.0	37 800
Others	420.0	520 551
Total	4 355.7	6 467 815

other *Meloidogyne* spp., species of *Pratylenchus, Tylenchorhynchus*, and *Globodera, Ditylenchus dipsaci* and *Aphelenchoides ritzemabosi* may cause yield losses in certain restricted areas. Although other nematodes, such as the spiral nematodes, (*Helicotylenchus, Rotylenchus, Scutellonema*), *Rotylenchulus* species, *Tetylenchus* and *Criconemella* species, have been found in tobacco fields, they are not normally associated with losses. Some species of *Xiphinema, Longidorus, Trichodorus*, and *Paratrichodorus* are reported to transmit viruses to tobacco.

Meloidogyne

Tisdale (1922), in Florida, was one of the first people to report on the damage that *Meloidogyne* spp. or root-knot nematodes can do to tobacco. They were also recognized as serious pests in Southern Africa in the late 1920's (Jack, 1927; Naudé, 1929), and have by now been recorded, usually as pests of great importance, in most of the tobacco growing countries of the tropical and subtropical zone.

Meloidogyne incognita and *M. javanica* are the most widely distributed of the important root-knot species (Table 2). Their relative importance is largely dependent on the climate, since *M. javanica* has a greater tolerance to drought and high temperature than has *M. incognita* (Daulton

TABLE 2. Importance of *Meloidogyne* species in some tobacco growing countries.

Country	*Meloidogyne*			
	arenaria	*hapla*	*incognita*	*javanica*
AFRICA				
Malagasy			1	2
Malawi				3
Nigeria			2	
South Africa	1	1	3	3
Zimbabwe			1	3
AMERICA				
Argentina			1	1
Brazil	1		3	3
Canada		1		
Chile			2	2
Colombia			1	1
Cuba			3	
Guatamala			3	
Mexico	2		3	3
Paraguay			3	3
U.S.A.	2	1	3	3
ASIA & OCEANIA				
Australia		1	2	2
Bangladesh			2	1
China			2	1
India			3	3
Japan			2	2
Korea			1	
Malaysia			2	2
Pakistan			3	3
Philippines	1		3	2
Thailand	1		2	3
Vietnam			3	3
EUROPE				
Albania			2	
Bulgaria			2	2
France	1		2	
Germany			2	2
Greece			2	2
Hungary	1	1	2	2
Italy			3	3
Spain			3	3
Yugoslavia		1	2	2
MEDITERRANEAN COUNTRIES				
Iraq	1		2	3
Morocco			2	2
Syria			3	3
Turkey			3	3

KEY

1. Minor importance 2. Moderately important or locally important 3. Very important

Adapted from: Survey of Pests and Diseases of Tobacco and Chemicals Used. CORESTA: Agronomy and Phytopathology groups, 1987.

& Nusbaum, 1961, 1962; Taylor *et al.*, 1982). *M. arenaria* and *M. hapla* are the next most widely distributed, with *M. hapla* confined to the cooler parts of the world. *M. javanica* was found in 65% of fields surveyed in Florida and *M. incognita* in 33% , whereas *M. arenaria* was rarely found (Rich & Garcia, 1985). Although *M. incognita* is the predominant species in North Carolina, *M. arenaria* has increased dramatically recently, as it has also in South Carolina (Fortnum *et al.*, 1984; Schmitt & Barker, 1988). *M. javanica* and *M. hapla* are also found in North Carolina. In South Africa, Milne (1961) reported that 73% of females identified were *M. javanica* and 4% *M. incognita*; however, in a later survey *M. javanica* was reported in 62% of populations and *M. incognita* in 72%, of which 40% were mixed (van Niekerk, 1985). Martin (1955, 1962) reported that 99% of infestations in Zimbabwe were by *M. javanica* and subsequent work has confirmed this. In Brazil *M. javanica* was identified in 50% of cases and *M. incognita* in 20% and both together in 25% of samples (Sudo & Espindola, 1987). In the Philippines, Madamba (1981) reported *M. incognita* in 64% of fields and *M. javanica* in 29%. In Sri Lanka both *M. javanica* and *M. incognita* are found. By contrast root-knot nematodes are rare in Canada, with *M. hapla* occurring more than the others. *M. incognita grahami, M. microcephala, M. mayaguensis, M. cruciani, M. enterolobii, M. ethiopica, M. platani, M. thamesi* and *Meloidogyne* sp are also reported to reproduce on tobacco, but their importance is very restricted (Cliff & Hirschmann, 1984; Jepson, 1987; Rammah 1988; Rammah & Hirschmann, 1988).

Symptoms of damage

The characteristic symptoms of root-knot nematode attack are the root galls formed as a reaction to the invasion and feeding by the nematode (Plate 13 C–D). These can range from small individual galls to severe distortion and restriction of root development. The size and magnitude of the galls can be a guide to the species involved. Galls induced by *M. hapla* are usually little and affect only a small part of the root system. *M. arenaria* causes bead-like galls to form which may involve a large proportion of the root system. *M. incognita* and *M. javanica* cause large galls, which may affect 90% or more of the root, with the latter usually causing the more extensive gall formation (Plate 13 D). Root decay often develops in roots galled by *M. javanica, M. incognita* and *M. arenaria* (Fig. 1), whereas decay is usually less severe in roots infested by *M. hapla*.

The above-ground symptoms of a severe attack are stunting of growth, associated with premature wilting, typically in the afternoon, on hot days (Fig 2, Plate 13 A). There may also be signs of nitrogen and potassium deficiency and scorching of the leaf tips and margins. These symptoms are often seen in a patchy distribution in the field, unless the infestation is uniformly severe. Weeds, which are usually largely controlled by healthy tobacco plants, are able to grow successfully and compete for soil moisture and nutrients. Sucker development is also much suppressed on plants heavily parasitized by nematodes.

Pathotypes

All four pathotypes of *M. incognita* have been recorded on tobacco, but by far the commonest is race 1 (Taylor *et al.*, 1982). Race 1 is the commonest in North Carolina, although races 2 and 4, which can attack the *M. incognita*-resistant tobaccos, and race 3 are also found. All four pathotypes have been reported in Brazil, and races 1, 2 and 3 in India. In Zimbabwe, races 1 and 3 have been recorded on tobacco, of which the commonest is race 3, while in South Africa races 2 and 4 have been identified with race 4 the commonest (van Wyk, 1985). Race 2 of *M. arenaria* is the commoner pathotype, when this species is recorded (Taylor *et al.*, 1982).

Survival and dissemination

All the root-knot nematodes that attack tobacco have a wide host range and can survive between tobacco crops on many weeds and other crops, especially if tobacco is frequently grown in the same field. The nematodes can also be spread by using water contaminated with eggs and juveniles to irrigate fields or seedbeds. Although bore-hole or mains water would be clean, river or dam water

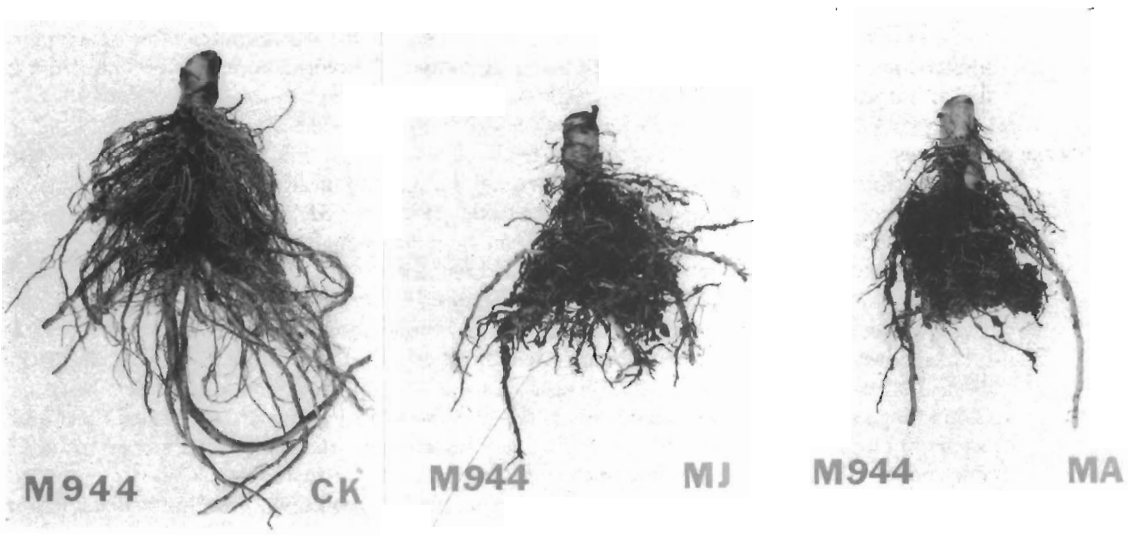

Fig. 1. Uninfested susceptible McNair-944 root (Left), infested with *Meloidogyne javanica* (Middle) and with *M. arenaria* (Right).

Fig. 2. Field Damage to young tobacco by *Meloidogyne arenaria* in South Carolina, USA.

could become contaminated if infested soil was washed into the water source after heavy rain. Root-knot nematodes can also be spread by using improperly prepared compost or dung from animals fed on infected root crops (Hopkins, 1927; Martin, 1968).

Disease complexes

The development of certain fungal and bacterial disease organisms in tobacco roots is encouraged by the successful invasion of root-knot nematodes (Plate 13 E). The galls, in particular the giant cells, provide a favoured site for the organism's development which can overcome the resistance that the plant might have in the absence of the nematode.

Tyler (1933) suggested that Blackshank (*Phytophthora parasitica* var. *nicotianae*), which can be a very serious disease in America, was increased by root-knot nematode invasion, and invasion also breaks down the resistance of cultivars bred for Blackshank resistance (Sasser *et al.*, 1955). The disease is reported in Malawi, where losses of 40 to 60% are reported, and in South Africa, Java, China, Japan and Iraq. Blackshank is primarily a disease of warm growing conditions and rarely occurs at temperatures below 20°C. Control may be obtained by using cultivars resistant to Blackshank and root-knot nematodes, and multi-purpose soil fumigants.

Fusarium wilt (*F. oxysporum* var. *nicotianae*) is also associated with root-knot nematode damage (Porter & Powell, 1967). The disease has been reported from U.S.A., South Africa, Zimbabwe, Chile, Mexico, Iraq and Malawi, where it is now regarded as a serious problem on most of the burley estates and many of the smallholder farms. Control is again dependent on effective nematode control and resistant cultivars.

Granville wilt, caused by the bacterium *Pseudomonas solanacearum*, is also encouraged by root-knot damage and can be largely controlled by the effective use of nematicides and wilt-resistant cultivars (Lucas, 1975). Granville wilt can be a serious problem in some parts of America. It also has been reported in Malawi, Malagasy and Zimbabwe, but does not seem to have spread much from its original areas in these countries.

Batten and Powell (1971) in America, showed that when *M. incognita* inoculation preceded that of the sore-shin fungus *Rhizoctonia solani* by 10–20 days, the stem damage caused by the fungus was increased; a similar effect is also reported from Iraq. In Zimbabwe, Hartill (1968) reported that *M. javanica* invasion had no consistent effect on the stem damage, although galling did increase the root invasion by the fungus (Shepherd, 1976).

Plants heavily infested with root-knot nematodes are more severly affected by the "brown spot" leaf disease caused by *Alternaria alternata* in the United States, Zimbabwe and Malawi, where it can be a very serious disease of flue-cured tobacco. It has been suggested that the successful invasion of the gall by *Fusarium* may encourage the development of *Alternaria* in the leaf (Powell & Batten, 1969). Many other soil fungi that do not normally cause disease on their own can invade galled roots and enhance the damage caused by root-knot nematodes by increasing root necrosis (Powell *et al.*, 1971).

Eisenback (1983) showed in greenhouse trials that prior infection with *M. arenaria* or *M. hapla* reduced the resistance of NC 95 to *M. incognita*. This effect, which could be of importance with the increase of *M. arenaria* in tobacco areas in America, has not yet been confirmed in natural field infestations. Similar work, in Zimbabwe, has not shown any reduction in *M. javanica* resistance (Way, 1985).

Economic importance

Root-knot nematodes are always pests of economic importance in tobacco culture, wherever the climate favours them (Nusbaum, 1960; Daulton, 1964; Barker *et al.*, 1981; Rich *et al.*, 1982). They are of limited importance in the cooler areas, such as Canada, where mainly *M. hapla* occurs, or France, where *M. incognita* and *M. arenaria* have been found on tobacco.

Actual yield losses can be estimated by using regressions based on initial or mid-season estimates of nematode populations, and root-gall or root-necrosis indices (Barker *et al.*, 1981) (Figs. 4–6).

The relative aggressiveness of the four common root-knot species is reflected in the percent loss in yield for each ten-fold increase in initial population: *M. hapla*, 3%; *M. incognita*, 8–9%; *M. arenaria*, 16–17% and *M. javanica*, 19%. Although of less economic importance, yield losses occur with *M. incognita* races 1 and 3 on resistant cultivars, such as Speight G28, where a 3% loss for each ten-fold increase of race 3 has been reported (Barker *et al.*, 1981). The hypersensitive reaction of the resistant cultivars to these nematodes is apparently responsible for the associated stunting, especially with high inoculum levels (Sosa-Moss *et al.*, 1983) (Fig. 3).

Daulton (1963) estimated that losses from root-knot nematodes, almost entirely *M. javanica*, in Zimbabwe, were from eight to eleven million kilogrammes annually, despite widespread fumigation of seedbeds and fields. He stated that field fumigation could cause increases of 55–1800 kg/ha of cured leaf, while the cost of EDB fumigation was covered by the value of 40 kg of tobacco. Subsequent experiments have confirmed these estimates and indicated that, under conditions of severe infestation, even greater yield increases can be expected from fumigation (Nusbaum, 1960; Rich *et al.*, 1982).

In America losses to tobacco from root-knot nematodes have been estimated to range from 1% to 14% annually (Powell *et al.*, 1986; Sasser & Freckman, 1987), though it is likely that an earlier estimate of 5% is more realistic. Root-knot nematodes are estimated to cause yield losses of 50 to 60% in some parts of Turkey. In Iraq more than 40% of the tobacco is reported to be infested, with infestation levels going up to 100% in some fields, while in India 25% loss is reported from field infestation and a 50% loss if the infestation started in the seedbed.

The threshold damage levels for these important nematodes are low. The Nematode Advisory Service of the North Carolina Department of Agriculture recommends that, if as few as 10–200 juveniles/pint of soil are found in a soil sample collected at the end of the season before tobacco is planted, a resistant cultivar should be used. It implies that, if a resistant cultivar is not available, as when *M. javanica* or *M. arenaria* are present, a nematicide should be used; while if the number of juveniles is above 200 a reliable nematicide is essential (Powell *et al.*, 1986). In Zimbabwe no threshold levels have been published, because it has been found that whenever any juveniles have been detected, an economic yield response to nematicides can be expected.

Pratylenchus

The migratory endoparasitic root-lesion nematodes, *Pratylenchus* species, while less important in the tropical and subtropical regions than the root-knot nematodes, are responsible for significant yield losses in some tobacco growing areas (Table 3). Lucas (1975) and Shepherd (1982) have reported on the species occurring in America and southern Africa. *P. pratensis* is reported from Hungary and *P. penetrans* from Iraq. In parts of Canada *P. penetrans, P. crenatus* and *P. neglectus* are often found in tobacco fields (Mountain, 1954; Kimpinski *et al.*, 1976). *P. penetrans* has also been reported from New Zealand (Canter-Visscher, 1969), and *P. zeae* from Trinidad (Singh, 1974).

The symptoms of *Pratylenchus* attack are brown lesions which may encircle the root and the cortex may fall off. *P. pratensis* was first associated with the "brown-root rot" disease of tobacco in 1931 (Lehman, 1931; Mountain 1954).

P. brachyurus can enhance the development of Blackshank by wounding the roots and providing entry sites for the fungus (Inagaki & Powell, 1969) and Milne (1972) reported that *P. hexincisus* is associated with the development of "Black root-rot" (*Thielaviopsis basicola*) in the black turf soils of South Africa, when they are wet at planting time. When certain lesion nematodes occur in large numbers, they can cause yield losses. They often have a wide host range and, because they can overwinter in plant roots and through their ability to withstand desiccation, they can remain viable from tobacco crop to tobacco crop. In greenhouse trials, *P. brachyurus* invaded tobacco roots and reproduced causing a reduction in yield, while *P. zeae* did not reproduce and had no effect (Southards, 1965; Shepherd, 1982). Microplot experiments with *P. brachyurus* and *P. scribneri* in North Carolina failed to demonstrate that low to moderate numbers had any significant effect on yield

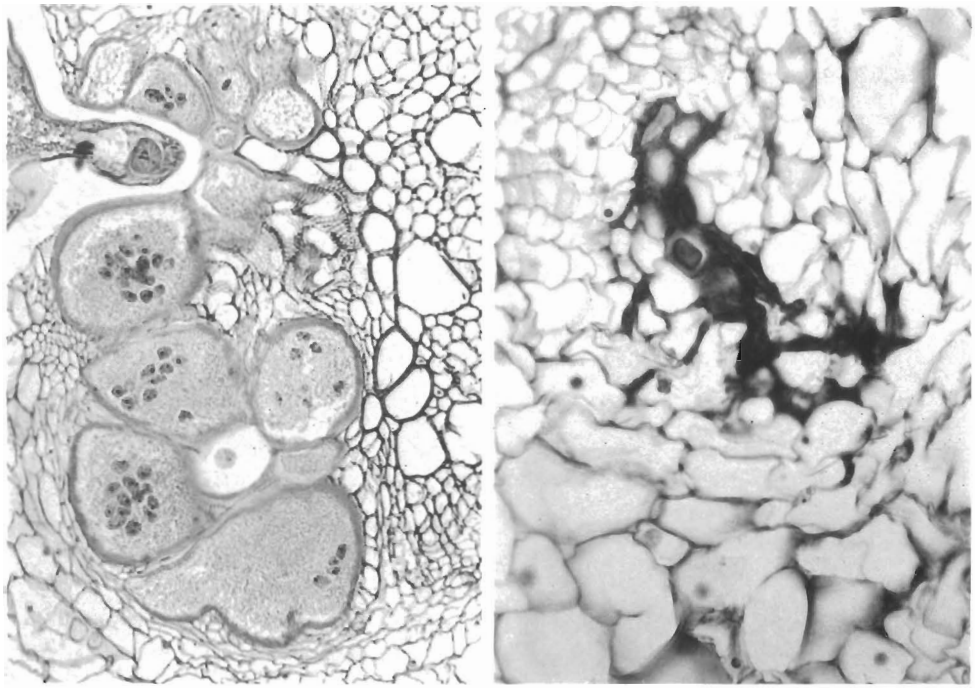

Fig. 3. Susceptible McNair-944 root sections 14 days after inoculation with *Meloidogyne incognita* juveniles (Left) and *M. incognita* (race 1 and 3) resistant Speight G-28 root section, 35 days after inoculation (Right) (Sosa-Moss *et al.*, 1983).

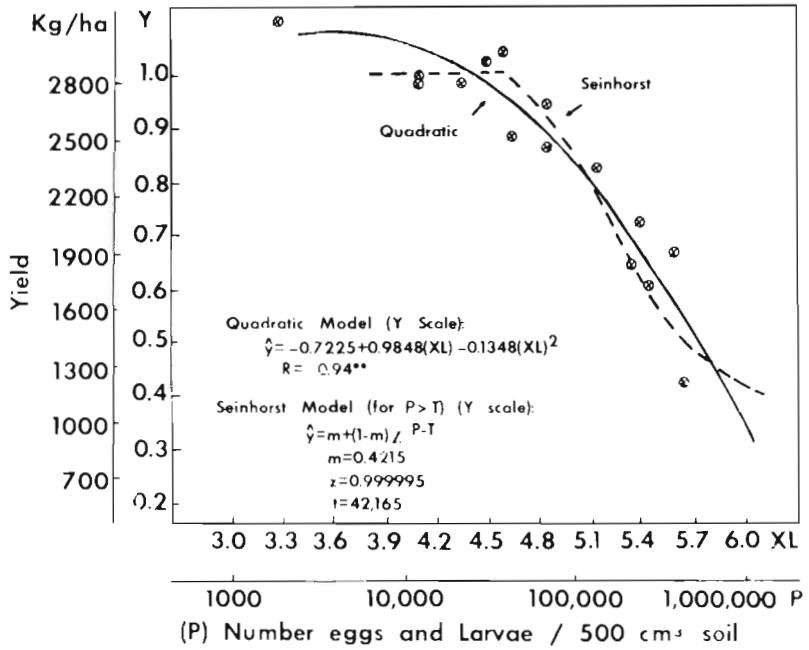

Fig. 4. Relationship of midseason counts of *Meloidogyne* juveniles and eggs/500 cm^3 soil and yield in sandy soil in North Carolina, USA (Barker *et al.*, 1981).

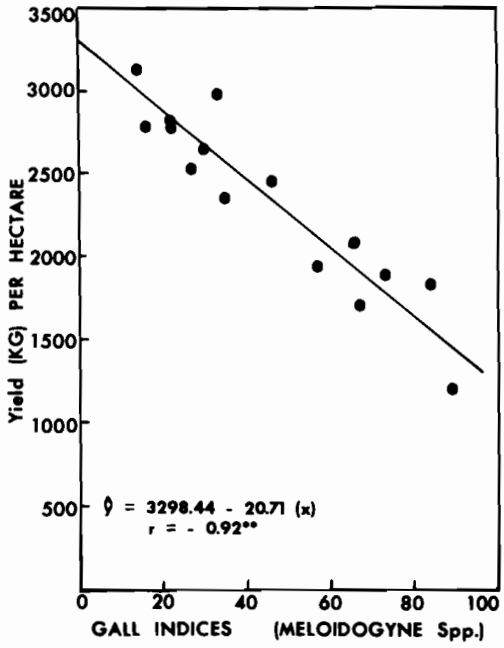

Fig. 5. Regresson of root-galling vs. tobacco yields in sandy soil in North Carolina, USA.

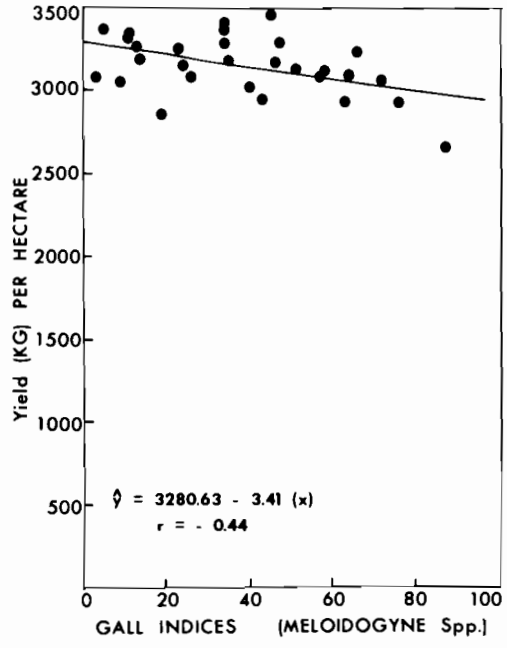

Fig. 6. Regression of root-galling vs. tobacco yields in a heavy fine texture soil in North Carolina, USA.

TABLE 3. Importance of certain plant-parasitic nematodes in some tobacco growing countries.

Country	*Aphelenchoides*	*Ditylenchus*	*Globodera*	*Pratylenchus*
AFRICA				
Malagasy			1	1
S. Africa				2
Zimbabwe				1
AMERICA				
Brazil	2			2
Canada				2
Chile	1	1		2
Colombia			1	
Mexico				1
Paraguay		1		2
U.S.A.			2	1
ASIA & OCEANIA				
Australia				1
China	1	1	2	2
India				1
Korea		1	1	1
Malaysia				2
Pakistan	1	1	2	1
Thailand				1
Vietnam				3
EUROPE				
Albania		1		
France	2	2	2	
Germany	1	2		2
Greece			1	
Hungary		1		1
Italy		2	2	2
Yugoslavia		2	2	1
MEDITERRANEAN COUNTRIES				
Iraq				1
Morocco			2	
Turkey		1		1

KEY
1. Minor importance
2. Moderately important or locally important
3. Very important

Adapted from: Survey of Pests and Diseases of Tobacco and Chemicals Used. CORESTA: Agronomy and Phytopathology Groups, 1987.

(Barker, unpubl.). However, severely stunted plants infected with these two species, and recently *P. alleni*, are found in North Carolina. But, when tobacco was grown each season for 3 years, the numbers of *P. neglectus* dropped which suggests that tobacco was not a good host (Mountain, 1954). Also the widespread use of *M. incognita*-resistant tobaccos in North America, which often exhibit some resistance to *Pratylenchus* species, may have contributed to the decline in importance of these nematodes in America (Graham, 1965).

Thus, damage caused by these nematodes is slight when compared with the root-knot nematodes, and when nematicides are used their slower reproduction rate, one egg per day for about 30 days, means that they cannot recover quickly (Lucas, 1975).

Globodera

The tobacco cyst nematode, *Globodera tabacum*, has been important in shade-grown tobacco in Connecticut since 1951 (Lownsbery & Lownsbery, 1954). This nematode has a narrow host range, only including tobacco and certain members of the Solanaceae. A sub-species, *G. tabacum solanacearum*, originally described as *Heterodera solanacearum* (Miller & Grey, 1972), is known to attack flue-cured tobacco, predisposing it to Granville wilt, but it only occurs in 10 to 15 counties in Virginia (Komm *et al.*, 1983). Another species, *G. virginiae* (*G. tabacum virginiae* according to some authorities), occurs in Virginia and North Carolina, and reproduces slowly on burley tobacco, but does not attack flue-cured cultivars (Miller & Grey, 1968; Miller, 1977). Tobacco cyst nematodes are reported from many parts of the world, but not yet from Africa, except in Morocco (Table 3).

Infected plants have small root systems with visible cysts attached to them. The plants can be severely stunted with dark-green leaves, in a patchy distribution in a field and are subject to premature wilting (Plate 13 G). The eggs are retained within the female body that hardens to become a cyst and can survive for years in the soil until stimulated to hatch by the root exudates of a host and are difficult to kill with nematicides.

Yield losses of infested tobacco can be very high. In 1982 some Virginia farmers recorded a complete crop failure and the average loss over 339 affected hectares was 15% (Komm *et al.*, 1983). Nematicide trials indicate that yield losses of 35% can be expected (Osborne, 1967). These nematodes are spreading, especially in Virginia, and could become a serious problem in the future.

Ditylenchus dipsaci

Ditylenchus dipsaci, the stem and bulb nematode, is reported from many countries, but only causes yield loss in tobacco in Holland, France, Germany and Switzerland (Lucas, 1975; Valloton & Corbaz, 1976) (Table 3). Invasion by the nematode of the lower parts of the stem causes "stem break", which is very rarely found in subtropical or tropical countries. The nematode can remain dormant in a cryptobiotic stage for many years and withstand freezing. "Stem break" is usually associated with cool, damp weather and heavy soils and is only of localized importance, but it has been reported to cause losses of up to 54% in parts of northeast France (Lucas, 1975).

Aphelenchoides ritzemabosi

Aphelenchoides species are reported in five countries (Table 3), but it is only in France that *A. ritzemabosi* has been described as the cause of "checkered leaf disease" or "la maladie en damiers" in a localized area near the Atlantic end of the Pyrénées (Delon *et al.*, 1981). The symptoms of polygonal leaf blotches bounded by the veins are similar to those caused by this nematode in chrysanthemums.

Other Nematodes

Many other nematodes have been reported to parasitize tobacco, but it is doubtful if any are of much importance.

Species of *Tylenchorhynchus*, the stunt nematode, are reported to damage the roots of tobacco plants in Canada, U.S.A. and India (Lucas, 1975; Krishna & Prasad, 1985). In North Carolina, *T. claytoni* was shown to reproduce on tobacco, but to have no effect on growth (Barker, unpubl.). *T. capitatus* is also reported from tobacco fields in New Zealand (Wouts, 1966). Stunt nematodes are

reported to increase the incidence of *Fusarium* wilt, but not to encourage Granville wilt (Milne, 1972).

The spiral nematodes are frequently reported from tobacco soil and, though Shepherd (1982) reported that *Scutellonema brachyurum* can reduce growth, they are of little importance. *Rotylenchulus reniformis* is reported to limit the growth of bidi tobacco in greenhouse trials in India (Patel *et al.*, 1986), and has been found in Trinidad (Singh, 1974), also recently in tobacco fields in eastern North Carolina. Shepherd (1977) reported that *R. parvus* did not parasitize tobacco.

Paratrichodorus and *Trichodorus* species are vectors of the "tobacco rattle" virus, which is reported to cause yield losses in tobacco in parts of Holland and Germany (Lucas, 1975).

P. lobatus is also reported to cause stunting of tobacco in Australia (Meagher, 1969). *Xiphinema* and *Longidorus* species are widespread and are also virus vectors. *X. americanum* is a relatively efficient vector of the "tobacco ringspot" virus, which is reported in many countries and has localized importance (Lucas, 1975). *L. elongatus* is also reported to damage tobacco in Canada (Marks & Elliot, 1973).

Control

The extent to which nematode control measures are taken in the various countries growing tobacco varies greatly. In some places, such as France or China, losses due to nematode damage are slight or are of localized importance only, and little attention is paid to control measures. Such countries are usually those where tobacco is grown under cool conditions, often on heavier soil types and where the root-knot nematode is not widely distributed.

In U.S.A., Australia, parts of central and southern Africa and other places where the root-knot nematode is widely distributed, the entire tobacco growing cycle is centred around nematode control. The basic strategies being to reduce the initial nematode populations in the soil and in the plant, and to reduce the subsequent rate of nematode increase. However, there are still many countries where, for various reasons, nematodes do cause economic yield losses and little attention is paid to nematode control, except maybe at the most basic level.

Cultural control

Some of the earliest control measures practised were the adaptation of cultivation methods to reduce the nematode population and its effect on the tobacco crop, and the use of non-susceptible crops in rotation with tobacco. As suggested by Atkinson (1889), the early and efficient destruction of tobacco roots after harvest by deep ploughing or by burning is an effective way of reducing damage to subsequent crops by nematodes and other pests (Daulton, 1955; Powell *et al.*, 1986). In Zimbabwe much of the crop is planted on ridges, before the rains start, in fields that were ploughed at the end of the preceding season. Jack (1920) reported that root-knot nematode damage was much less when tobacco was planted into soil that had dried out, and Collins (1938) advocated planting into hillocks made from the top 50 mm of soil, which would give the seedling 200 mm of nematode-free soil in which to start growing. He realized that the most important time to protect the plant is in the early stages of its growth. The recommendations of Collins (1938) were investigated and found correct (Jack, 1945, 1946; Daulton, 1952; Ferris 1969). Ferris (1969) showed that in an early ploughed sandy soil the top 50 mm, from which the ridge is made, often exceeded 36°C and had soil moisture levels of less than one percent, the conditions under which root-knot nematode eggs and juveniles are killed (Daulton & Nusbaum, 1961; Ferrris, 1969). Early planting, by taking advantage of the reduced nematode damage and reduced risk of aphid infestation, is an effective way of increasing yield in areas with a climate similar to Zimbabwe (Table 4). In places such as Malawi, India, Chile and Turkey where much of the crop is grown by peasant farmers, who may find nematicides and non-

TABLE 4. Impact of planting date on tobacco yield, Zimbabwe, 1953–1954.

Planting date	Yield (kg/ha)
8/11	1 380
19/11	1 344
3/12	1 030
17/12	461
31/12	231
14/1	166

productive rotations too expensive, early deep ploughing, early planting and destruction of tobacco roots are recommended as methods of protecting the crop.

Naudé (1929) recommended a period of bare fallow between tobacco crops, but this practice is not to be recommended in most of the inter-tropical areas as it can lead to severe erosion. In addition, Martin (1967) demonstrated that *M. javanica* could still be recovered from a bare fallow after four years. Allowing the land to revert to a natural weed cover would reduce the risk of erosion, but does not provide effective nematode control as many weeds are nematode hosts (Smee, 1928; Jack, 1944, 1945; Martin, 1969). Post cropping management will reduce root-knot densities in the soil (Barker *et al.*, 1981) (Fig. 7).

The choice of crops to grow in a rotation with tobacco depends on the most important nematode species present. In southern Africa the main nematode pest of tobacco is *M. javanica,* but in many other parts of the world it may be *M. incognita*, *M. arenaria* or one of the *Globodera* species. In cooler parts *Pratylenchus* species or *D. dipsaci* may severely limit yield. The choice of rotation crops is made more difficult when mixtures of root-knot nematode species are present, as in U.S.A., South Africa, Turkey, Brazil, Philippines, Mexico, Hungary, Iraq, Thailand and Greece. In many places,

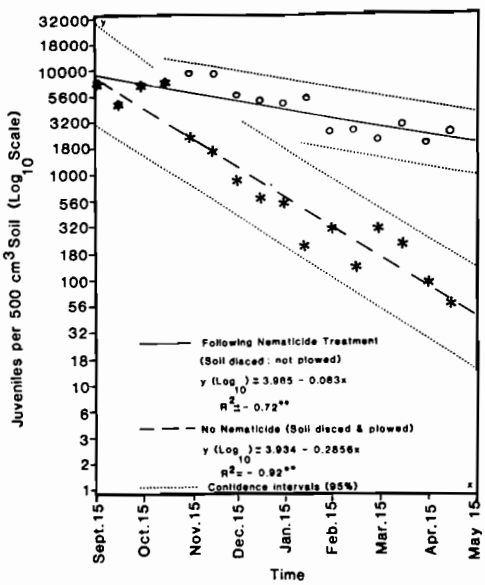

Fig. 7. Effect of post cropping management on decline of *M. incognita* population (Barker *et al.*, 1981).

particularly in peasant agriculture, vegetable crops, many of which are highly susceptible, are grown and the damage to the subsequent tobacco may be severe.

In places where *M. javanica* is the main problem, crops such as cotton and groundnuts can be grown (Table 5), but where *M. incognita* or *M. arenaria* is the dominant nematode, these crops may not be satisfactory. In North Carolina, where *M. incognita* has been the dominant nematode for many years, three-year rotations with fescue, small grains or other non-hosts are very effective (Powell *et al.*, 1986). The sunnhemps, *Crotalaria juncea, C. spectabilis* and *C. intermedia* , also *C. fulva* and *C. grahamiana* can be used to suppress root-knot nematodes (Table 5) (Daulton, 1955; de Guiran, 1970). The toxins produced by some *Crotalaria* spp. have resulted in prohibition of their use in some countries. Also, the increased nitrogen status of the soil after a legume is not always desirable for flue-cured tobacco. Maize, although lightly attacked, is often grown in tobacco rotations, as it is an important food crop and, provided that it is grown for two years or more, it lowers the *M. javanica* population to a level at which it can be easily controlled by nematicides (Rangeley, 1917). Norse (1972) reported on a cultivar that was apparently resistant to *M. javanica*, but most cultivars are susceptible in varying degrees to all the common species of *Meloidogyne*, except *M. hapla*. Many of the cereal crops, in particular oats, are fairly resistant. Cereals are grown in India, Bangladesh, China, Chile, Turkey and America in rotation with tobacco.

TABLE 5. Root damage by *Meloidogyne javanica* to tobacco after five years of various crops, Zimbabwe, 1960–1961.

Crop	Root-knot index (0–100)
Maize	18
Groundnuts	2
Cotton	3
Soyabeans	32
Sunnhemp (*Crotalaria juncea*)	19
Sunnhemp (*Crotalaria speciabilis*)	1
Tobacco	66

Pasture grasses that are resistant to root-knot nematodes are useful rotation crops, as they protect the soil from erosion better than row crops and, if sown densely enough, will smother weeds which might be nematode hosts. As stated earlier Fescue (*Festuca pratensis*) is recommended in North Carolina as a particularly useful grass (Powell *et al.*, 1986). In southern and central Africa the Ermelo and Umgeni strains of Weeping Lovegrass (*Eragrostis curvula*), Katambora Rhodes grass (*Chloris gayana*) and Sabi Panic grass (*Panicum maximum)* are recommended (Daulton, 1964; Shepherd, 1968, 1978) (Table 6). To obtain the maximum benefit from grasses such as these, it is necessary to grow them for three or four years before planting tobacco (Table 7). Other grasses, such as some of the *Paspalum* species and *Digitaria decumbens* are resistant to *M. javanica* and some of the other root-knot nematodes, but do not fit well into a tobacco rotation (Shepherd, 1982).

TABLE 6. The effects of three years of grass on the yield and *Meloidogyne javanica* damage to tobacco grown in unfumigated soil in Zimbabwe (after Daulton, 1964).

Grass	Yield (kg/ha)	Root-knot index (0–100)
Eragrostis curvula cv Ermelo	1817	31
Chloris gayana cv Giant	1530	63
Chloris gayana cv Katambora	1966	33
Setaria sphacelata cv Kazungula	1342	80
Panicum maximum cv Sabi	1605	50

TABLE 7. The effect of length of *Eragrostis curvula* cv Ermelo ley on yield and *Meloidogyne javanica* infestation on tobacco in Zimbabwe (after Daulton, 1964).

Rotation	Yield (kg/ha)		Root-knot index (0–100)	
	Not fumigated	Fumigated	Not fumigated	Fumigated
Continuous tobacco	486	1571	93	37
1 year grass ley	712	1599	73	21
2 year grass ley	1190	1900	58	18
3 year grass ley	1416	2050	34	11
4 year grass ley	1597	2101	14	7

Most *Pratylenchus* species have a wide host range and this can cause problems in selecting rotation crops. Fortunately, tobacco is not a good host to many species and, depending on the dominant *Pratylenchus* species present, suitable crops can be found. The cyst nematodes and *Ditylenchus dipsaci* have very limited host ranges which facilitate their control by rotation, but their effective survival mechanisms may require the use of non-host crops for a long time.

Physical control

Many of the early attempts to control nematode pests of tobacco, particularly in seedbeds or nurseries, relied on heating the soil either by burning grass and brushwood on the surface or by steam confined under a cover. Even though burning was recommended in Zimbabwe (Jack, 1920) and in North Carolina, it was realized that heat penetration was not always enough to kill nematodes at depths below 150 mm (Smee, 1928). However, peasant farmers in Malawi, Zimbabwe and India often use burning or rabbing – as it is called in India – as their only method of seedbed control. Burning can be used to control weeds, when a non-herbicidal nematicide is used.

Steaming can kill weeds, nematodes, insects and fungal pathogens (Anon, 1913, 1953; Milne, 1965), but by upsetting the balance of soil bacteria, it can lead to an increase in soil ammonium and to manganese toxicity. Effective penetration is usually about 300 mm, but being slow and expensive, the method is only suitable for seedbeds.

Solarization, the heating by the sun of soil covered with clear polythene, is an attractively cheap method of killing nematodes in seedbeds. Although the method appears to be simple, it is very time consuming, as the soil has to be covered for 6 weeks or more, and the results are not always successful (Stapleton & De Vay, 1986).

Some degree of nematode control can be obtained in places where the tobacco fields are flooded naturally or when tobacco is grown after paddy rice (de Guiran, 1970). Jack (1945) found that it needed at least 75 days to reduce the root-knot populations by flooding and that some nematodes survived for up to 105 days.

Growers in some countries, such as India, who have to use seedlings heavily galled by *Meloidogyne* species have been advised to cut off as much of the galled root as possible before planting (Patel *et al.*, 1983). Although this practice is of limited value, it is better than doing nothing and has some value if the field is treated with a nematicide.

Control by resistance

In the U.S.A. many tobacco cultivars have been bred with resistance to *M. incognita* races 1 and 3 (Clayton *et al.*, 1958), and these cultivars can be grown in any part of the world which has a problem with these races of *M. incognita*, and where the type of tobacco produced by these cultivars is acceptable. These cultivars are grown in Chile, Mexico and the Philippines where they are also breeding their own cultivars with resistance to *M. incognita*, and also in Brazil. The gene for this source of resistance apparently came from *N. tomentosa* (Slana & Stavely, 1981). Other sources of resistance to *M. incognita* race 3 are available from a *N. repanda* x *N. tabacum* cross

(Gwynn *et al.*, 1986) and for races 1 and 4 from selections of *N. otophora* (Arcia & Wernsman, 1983).

In Zimbabwe, where *M. javanica* is the most important nematode, attempts to breed resistance into commercial cultivars started in 1941 (Mackenzie & Ternouth, 1986). Sources of resistance to *M. javanica* have been found in *N. repanda*, some strains of *N. longiflora* and some locally grown primitive tobacco types. These lines were later crossed to *M. incognita*-resistant tobacco obtained from America. Recently, hybrids between local susceptible cultivars and the advanced resistant breeding lines have been tested and found to have a high level of resistance to *M. javanica* and to produce good quality tobacco (Ternouth *et al.*, 1986). However, when grown in fields with a high nematode population, the resistant cultivars, although producing better yields than the susceptible cultivars and having much less root galling, do benefit from the extra protection provided by nematicides (Ternouth *et al.*, 1986) (Table 8). These cultivars are not yet ready for general use, but are in the final stages before release. Other sources of resistance to *M. javanica* have been reported by Slana (1978) and Kadotani *et al.*, (1985). Cultivars with tolerance can be effective in fields with low moderate infections (Plate 13 B).

TABLE 8. Effects of two nematicides on *Meloidogyne javanica* resistant hybrids in a heavily infested site, Zimbabwe, 1985–86 (after Ternouth *et al.*, 1986).

Nematicide	Rate/ha	Yield, kg/ha			Root-knot index (0–100)		
		K51E (suscept.)	RK3 (resistant)	RK5	K51E (suscept.)	RK3 (resistant)	RK5
Untreated		946	2363	2999	90	4	9
EDB 41% m/m	22.5 l	2693	3761	3868	50	<1	1
	45.0 l	4120	3968	4374	42	<1	<1
Aldicarb	1.5 kg	2067	2957	3386	75	1	3
	3.0 kg	2075	3220	3598	66	<1	3

The resistance to *M. javanica* and *M. incognita* can break down at temperatures between 30°C and 35°C (Fukudome & Kamigana, 1982; Rufty *et al.*, 1983). In Zimbawe (J. I. Way, unpubl.) it was found that the amount of invasion and gall damage by *M. javanica* in both susceptible and resistant cultivars increased as the soil temperature was raised from 25°C to 30°C and fell as the temperature increased to 35°C. The effect on the resistant cultivars was always much less than on the susceptible ones. An Indian strain of *M. javanica* is reported to parasitize the Japanese *M. javanica* resistant cultivars (Shah *et al.*, 1985). *M. incognita* races 2 and 4, also, *M. javanica, M. arenaria* and *M. grahami* can break the resistance of the *M. incognita* races 1 and 3 resistant tobaccos (Eisenback, 1983) (Plate 13C). In Zimbabwe some of the *M. javanica* resistant breeding lines were susceptible to *M. arenaria* and *M. incognita* race 3 (Shepherd & Coombs, 1981).

The biochemical basis for resistance to *Meloidogyne* in tobacco is not known, though as a hypersensitive reaction is usually found in the nematode-infested resistant plants, a phytoalexin may be involved.

No cultivars with resistance specific to *Pratylenchus* have been developed. Nevertheless, several *M. incognita* resistant cultivars have some resistance (Graham, 1965; Southards & Nusbaum, 1967), and some burley cultivars have resistance to *P. penetrans* (Olthof, 1968). Sources of resistance to the tobacco cyst nematode have also been established and breeding lines are being developed (Baalawy & Fox, 1971; Gwynn *et al.*, 1986). There has been no attempt to breed resistance to other nematode parasites of tobacco.

Chemical control

Although many nematicides are under close scrutiny because they are believed to be a health hazard, they still continue to be an important tool in tobacco production. The fumigant nematicides are particularly important in seedbed management as they are more effective than the non-fumigants. Methyl bromide is widely used as it can give excellent control of most nematodes, weeds and other soil-borne pathogens (Martin, 1950; Daulton, 1956; Lucas, 1975) (Table 9), however, it sometimes fails to kill some nematodes, such as *Paratrichodorus*, especially at lower soil levels. In many countries the less expensive fumigants, such as EDB and 1,3-D (1,3-dichloropropene) are recommended (Daulton, 1950; Patel *et al.*, 1983). These fumigants can provide very good nematode control, but it is necessary to burn brushwood, or something similar, on the seedbeds to obtain weed control. The mixture of 1,3-D and MITC (methyl isothiocyanate) can also give good nematode control with reasonable weed control (Table 9). In Zimbabwe, metham-sodium and dazomet, both of which break down to form MITC, have been extensively tested but have not proved reliable enough to be recommended for seedbed use, although they are used in other countries.

TABLE 9. Impact of seedbed fumigation on the incidence of weeds, seedling number and root-knot infestation of tobacco seedlings, Zimbabwe, 1967.

Material	Rate	Spacing	Weeds per m^2	Tobacco seedlings /m^2	Root-knot index (0–100)
Untreated	–	–	1281	517	43
Methyl bromide	50 g/m^2	–	32	624	0
EDB 41% m/m	5 ml	35×35 cm	1216	624	0
DD/MITC	3 ml	30×30 cm	129	613	0

In the field EDB, DD and 1,3-D have been the cheapest and most successful nematicides (Martin, 1949, 1951; van der Linde *et al.*, 1951), however, in many countries their use has been restricted or eliminated (Powell *et al.*, 1986). In Zimbabwe, as in many other countries where the highly aggressive *M. javanica* predominates, the fumigants are still widely used, as they give better control and higher yields than non-fumigant nematicides (Tables 8 & 10). Chloropicrin, recommended 55 years ago (Plate 13 E) (Tyler, 1933), can be used, either on its own or in combination with 1,3-D, when nematodes are found in association with soil-borne diseases, such as Blackshank (Powell *et al.*, 1986). In America, carbon disulphide which was recommended by Atkinson (1889) is again being studied, as EDB can no longer be used.

TABLE 10. Effects of nematicides on tobacco yield and root-knot nematode damage with a high *Meloidogyne javanica* population, Zimbabwe, 1985–86.

Material	Rate		Yield	Root-knot index
	per plant	per ha	kg/ha	(0–100)
Untreated	–	–	1264	88
EDB 41% m/m	3 ml	45 l	3244	32
1,3-D 92% m/m	4 ml	60 l	2958	35
Aldicarb	–	3 kg	2459	58

The non-fumigant nematicides aldicarb, fenamiphos, ethoprophos and oxamyl are used in America (Powell *et al.*, 1986), although they are rarely as effective as the fumigants (Plate 13 G,H). The use of aldicarb is restricted in some states because it has been found in the ground water and has contaminated some wells. Aldicarb is also used in Zimbabwe, Malawi and South Africa, but is not recommended for use when there is a high root-knot nematode population. Fenamiphos is also

recommended in Malawi as a pre-planting nematicide. Oxamyl, applied as a spray about 3–5 weeks after planting is used in Malawi, South Africa and Zimbabwe, as a supplement to fumigation, thus extending the period of control. This can be beneficial if there is a large nematode population or where there are poor growing conditions early in the season. Fenamiphos can be used in the same way in Zimbabwe. Chemical control recommendations in Australia are similar to those in southern Africa.

Where tobacco is grown on small plots of land by peasant farmers, nematicides are not often used, even when they are recommended. Dazomet, 1,3-D and 1,3-D + MITC are recommended in Turkey and used to some extent; in Spain the big estates use 1,3-D in the fields and in Brazil aldicarb and 1,3-D are used in some areas. In Chile and India, aldicarb, fenamiphos and carbofuran are used by some growers. Fenamiphos is recommended in Mexico and aldicarb and carbofuran have been tested there. Greece also uses aldicarb and carbofuran. Aldicarb and terbufos are also recommended in Hungary. Methyl bromide is used as a seedbed fumigant in the Philippines, and EDB, 1,3-D, carbofuran and oxamyl are recommended for use in the fields, but are not widely used. Methyl bromide is also used in Chile and Hungary, and to a small extent in Iraq. Nematicides are rarely used in the field in Albania, but in some places metham-sodium is used in the seedbeds. Where "stem break" and "checkered leaf disease" occur in France, fumigants, organophosphate and carbamate nematicides are used. Tobacco cyst nematodes can be controlled by the conventional nematicides, but are also reported to be temporarily controlled by benomyl application (Miller, 1969). Root-knot nematodes are equally effectively controlled by DD, 1,3-D and EDB, but *Pratylenchus* species are reported to be controlled better by the chlorinated fumigants (Nusbaum, 1955). Carbofuran has been found to be relatively ineffective against root-knot nematodes in Zimbabwe, but to give good control of *Pratylenchus* . Similar differential efficiencies have been found with other non-fumigant nematicides (Barker *et al.*, 1981; Nordmeyer & Dickson, 1985).

The halogenated fumigants, in addition to being phytotoxic, may increase total nitrogen and alkaloids and lower reducing sugars in the leaf (Elliot *et al.*, 1972) and also interfere with the normal nitrification processes in the soil (Elliot & Mountain, 1963; Tillet, 1964). This would not normally be a problem in the field as the situation would have returned to normal during the two to three weeks before the seedlings are planted. The fumigants may suppress yield if used when there is no nematode or a slight problem (Nusbaum, 1960). Some non-fumigants, by contrast, can enhance growth and yield of tobacco under similar conditions (Barker & Powell, 1988).

There is no doubt that great care must be exercised in the handling of all nematicides and that the intelligent use of protective clothing must be encouraged if nematicides are to continue to be safely used. Also, the cured tobacco must be analysed to ensure that residue levels of all nematicides are kept below acceptable levels and application rates only recommended that will not lead to unacceptable residue levels or environmental pollution.

Biological control

All over the world more attention is being devoted to manipulating natural methods of reducing nematode populations, with the hope that such methods, which may be less damaging to man and the environment, can, at least partially, replace chemical control methods. Work with *Paecilomyces lilacinus* and *Pasteuria penetrans* has shown that these microorganisms can suppress root-galling and reduce stunting of tobacco by *M. incognita* (Dube & Smart, 1987). Other fungi can parasitize eggs of *Meloidogyne* and *Globodera* and may become useful control agents (Stirling & Mankau, 1978).

Plants with toxic root exudates, such as the *Tagetes* species, can be used to reduce nematode populations in small areas (Daulton & Curtis, 1964), but unless they are sown as a dense ground cover to suppress weeds, much of the benefit can be lost. Such control measures are difficult to handle on a large scale. Unfortunately, the activity of α-terthienyl is light dependent and this reduces the nematicidal effect at lower soil depths (Bakker *et al.*, 1979). Plant extracts, plant waste and other organic materials can be incorporated into the soil and will reduce nematode populations (Singh *et al.*, 1985; Culbreath *et al.*, 1986). These soil amendments probably operate through the

breakdown of the organic matter releasing toxic substances (Sayre *et al.*, 1965) and also by encouraging the development of antagonistic or parasitic fungi.

Summary of control measures

There is no doubt that the most effective method of controlling nematodes, in particular the root-knot nematode, is by combining all possible methods. This combined approach was advocated originally by Atkinson in 1889 and again by Tyler in 1933.

It is essential that the seedbed area should be free from all nematode pests, because if infested seedlings are transplanted into the field, then any control measures used there are valueless. Fumigation with methyl bromide, which kills nematodes, weed seeds, soil insects and soil fungi, is a very effective way to protect the seedlings. If the seedbed area is not to be used every year, a nematode-resistant crop should be planted in it. Fumigation with 1,3-D or burning brushwood is a cheaper alternative which, if carried out properly, is very effective. In the field, tobacco should not be grown often on the same site; a break of a couple of years, preferably three or four, of nematode resistant crops, in particular a grass, will lower the nematode population throughout the whole field, thereby making any chemical control measure more effective (Daulton, 1964) (Table 7).

Resistant cultivars are at present only available for *M. incognita* races 1 and 3, and where these nematodes are the dominant ones, such cultivars are very valuable. In many situations the use of good rotations and a resistant cultivar may be enough, but often the addition of a nematicide will help to realize the full yield potential of the tobacco. If the nematode population is high, a fumigant will give better control than an organophosphate or carbamate nematicide, and will also be cheaper. Multi-purpose fumigants, such as 1,3-D + chloropicrin, should be used in fields with a history of root-knot and wilt or other root diseases (Powell *et al*, 1986). However the choice may be limited by administrative restrictions on the sale of nematicides.

Methods of diagnosis

The meaningful selection of appropriate control measures can be greatly assisted by assessment of the initial nematode population by simple methods or by a nematode advisory service, where available (Barker & Imbraiani, 1984; Barker, 1985).

Advisory services are available in some of the tobacco growing areas of America and Europe, but are not usually found in most other tobacco growing areas. Bioassays offer a very reliable method of detecting root-knot nematodes, as well as *Globodera* and *Ditylenchus* species, and of estimating their population size (Barker, 1985). The characteristic galling of root-knot nematodes and the cysts of *Globodera* make their field assessment relatively easy. These methods of monitoring root-knot nematodes were suggested as early as 1933 (Tyler, 1933), but were largely ignored until recently. The collecting of soil samples, their extraction and the interpretation of the numbers of nematodes recovered does not give reliable information unless very carefully and timely carried out, but a simple bioassy of the soil using susceptible indicator plants can give very useful information. It is often found that a study of the cropping systems practised over the preceding few years can give a better idea what advice to give a grower than the taking of soil samples. In Zimbabwe it has often been said of soil samples that:- "If you find any root-knot nematode juveniles, you have a problem; if you don't, you may have a problem".

Conclusions and Future Prospects

Tobacco is a high value crop and throughout most of its growing areas is liable to severe losses in yield from nematode attack, in particular by root-knot nematodes. Nematode control measures are essential to ensure maximum production and in those places where tobacco is grown on a large scale under sound financial conditions, a wide range of control measures are used. Unfortunately, many of the better and cheaper nematicides, in particular EDB and other fumigants, are being withdrawn

as they are considered too dangerous for various reasons. Cultivars with a high level of resistance to *M. incognita* are already available and when successful cultivars resistant to *M. javanica* are ready, this will be a major advance. Biological control measures using antagonistic fungi or *Pasteuria penetrans* are attractive, but at present not enough is known about them to know whether they can be made commercially viable.

The use of cropping systems analysis may enable the problems to be better identified and so lead to the development of better rotations and other control measures (Noe, 1986). Advanced plant breeding techniques and "genetic engineering" offer the promise of new cultivars incorporating multiple resistance to nematodes, disease organisms and insects and also tolerance to presently phytotoxic chemicals.

With increasing concern over the use of toxic chemicals, the future of nematode control in tobacco growing lies in breeding resistant cultivars, the intelligent use of cultural and cropping techniques and the use of minimal amounts of chemicals, possibly backed by biological agents, when necessary.

Acknowledgements

We would like to acknowledge, with gratitude, the assistance given to us by: Y. Arinc, J.D. Arnett Jr., J. Bridge, T. Bwalo, R. Delon, N. Gnanapragasam, B. Janos, A. Kapidani, I. Rinen, H. Rodriguez, C. Sosa-Moss, Z. Stephan, R. Stewart and G. Swarup.

References

Akehurst, B. C. (1981). *Tobacco,* 2nd Edition. London, New York, Longman, 764 p.

Anonymous. (1913). *Handbook of tobacco culture for planters in Southern Rhodesia.* Department of Agriculture of Southern Rhodesia, Salisbury, 115 p.

Anonymous. (1953). How to grow quality tobacco seedlings in Southern Rhodesia. *Bulletin of the Tobacco Research Board of Southern Rhodesia, No.2.*

Anonymous. (1987). World tobacco situation. *USDA Foreign Agriculture Service. Circular series, FT 12–87 (December, 1987).*

Arcia, M. A. & Wernsman, E. A. (1983). Reaccion de algunas introducciones de *Nicotiana otophora* a dos razas del nematodo nodulador *Meloidogyne incognita. Nematropica,* 13:221–227.

Atkinson, G. F. (1889). Nematode root-galls. *Alabama Agricultural Experimental Station. Bulletin 9:*1–54.

Baalawy, H. A. & Fox, J. A. (1971). Resistance to Osborne's cyst nematode in selected *Nicotiana* species. *Journal of Nematology,* 3:395–398.

Bakker, J., Gommers, F. J., Nieuwenhuis, I. & Wynberg, H. (1979). Photoactivation of the nematicidal compound α-terthienyl from the roots of marigolds *Tagetes* species. A possible singlet oxygen role. *Journal of Biological Chemistry,* 254:1841–1844.

Barker, K. R. (1985). Nematode extraction and bioassays. In: Barker, K. R., Carter, C. C. & Sasser, J. N. (Eds.). *An Advanced Treatise on Meloidogyne.* Raleigh, N.C. U.S.A. Department of Plant Pathology and the United States Agency for International Development: 19–35.

Barker, K. R. & Imbriani, J. L. (1984). Nematode advisory programs – status and prospects. *Plant Disease,* 68:735–741.

Barker, K. R. & Powell, N. T. (1988). Influence of aldicarb on the growth and yield of tobacco. *Journal of Nematology,* 20:432–438.

Barker, K. R., Todd, F. A., Shane, W. W. & Nelson, L. A. (1981). Interrelationships of *Meloidogyne* species with flue-cured tobacco. *Journal of Nematology,* 13:67–79.

Batten, C. K. & Powell, N. T. (1971). *Rhizoctonia – Meloidogyne* disease complex in flue-cured tobacco. *Journal of Nematology,* 3:164–169.

Canter -Visscher, T. W. (1969). The association of root-lesion nematodes with reduced growth of tobacco in the Nelson district. *New Zealand Journal of Agricultural Research,* 12:423–426.

Clayton, E. E., Graham, T. W. Tood, F. A., Gaines, J. G. & Clark, F. A. (1958). Resistance to the root-knot disease of tobacco. *Tobacco Science,* 2:53–63.

Cliff, G. M. & Hirschmann, H. (1984). *Meloidogyne microcephala* n.sp. (Meloidogynidae), a root-knot nematode from Thailand. *Journal of Nematology,* 16:183–193.

Collins, A. D. (1938). Eelworm in tobacco. *Rhodesia Agricultural Journal,* 35:448–451.

Culbreath, A. K., Rodriguez-Kabana, R. & Morgan-Jones, G. (1986). Chitin and *Paecilomyces lilacinus* for control of *Meloidogyne arenaria. Nematropica,* 16:153–166.

Daulton, R. A. C. (1950). Fumigant control of nematodes in seedbeds. *Rhodesian Tobacco Journal,* 2:39–41.

Daulton, R. A. C. (1952). *The depth distribution of root-knot nematode in Trelawney sandveld soil.* Report of Tobacco Research Board of Southern Rhodesia, 1951–1952.

Daulton, R. A. C. (1955). Progress report on eelworm control experiments. *Rhodesian Tobacco.* 11:21–24.

Daulton, R. A. C. (1956). Seedbed fumigation and eelworm control. *Rhodesian Tobacco Journal,* 8:74–76.

Daulton, R. A. C. (1963). Controlling *M. javanica* in Southern Rhodesia. *Rhodesia Agricultural Journal,* 60:150–152.

Daulton, R. A. C. (1964). Effect of soil fumigants on tobacco in Southern Rhodesia. *Biokemia,* 5:10–15.

Daulton, R. A. C. & Curtis, R. F. (1964). Effects of *Tagetes* spp. on *Meloidogyne javanica* in Southern Rhodesia. *Nematologica,* 9:357–362.

Daulton, R. A. C. & Nusbaum, C. J. (1961). The effect of soil temperature on the survival of the root-knot nematodes *Meloidogyne javanica* and *M. hapla. Nematologica,* 6:280–294.

Daulton, R. A. C. & Nusbaum, C. J. (1962). The effect of soil moisture and relative humidity on the root-knot nematode *Meloidogyne javanica. Nematologica,* 8:157–168.

Delon, R., Schlitz, P. & Mazières, M. (1981). "La maladie en damiers", une nouvelle affection du tabac provoquée par un nematode foliaire, *Aphelenchoides ritzemabosi* (Schwartz) Steiner. *Annales du Tabac,* 17. Section 2:73–84.

Dube, B. & Smart, Jr. G. C. (1987). Biological control of *Meloidogyne incognita* by *Paecilomyces lilacinus* and *Pasteuria penetrans. Journal of Nematology,* 9:222–227.

Eisenback, J. D. (1983). Loss of resistance in tobacco cultivar 'NC95' by infection of *Meloidogyne arenaria* or *M. hapla. Journal of Nematology,* 15:478 (abstr.).

Elliot, J. M., Marks, C. F. & Tu, C. M. (1972). Effects of nematicides on *Pratylenchus penetrans* soil microflora and flue-cured tobacco. *Canadian Journal of Plant Science,* 52:1–11.

Elliot, J. M. & Mountain, W. B. (1963). The influence of spring and fall application of nematicides on *Pratylenchus penetrans* and quality of flue-cured tobacco grown with various forms of nitrogen. *Canadian Journal of Soil Science,* 43:18–26.

Ferris, H. (1969). The vertical distribution of the root-knot nematode (*Meloidogyne javanica*) in Rhodesian sandy soil. *Rhodesian Journal of Agricultural Research,* 7:15–24.

Fortnum, B. A., Krausz, J. P. & Conrad, N. G. (1984). Increasing incidence of *Meloidogyne arenaria* in flue-cured tobacco in South Carolina. *Plant Disease,* 68:244–245.

Fukodome, N. & Kamigana, K. (1982). (Resistance of tobacco to *Meloidogyne javanica.* II. Effect of soil temperature on the manifestations of resistance.) *Japanese Journal of Nematology,* 11:13–18.

Golden, A. M. & Slana, L. J. (1978). *Meloidogyne grahami* n.sp. (Meloidogynidae), a root-knot nematode on resistant tobacco in South Carolina. *Journal of Nematology,* 10:355–361.

Graham, T. W. (1965). Tobacco varieties used to show differential response to root-lesion and root-knot nematodes. *Plant Disease Reporter,* 49:822–826.

de Guiran, G. (1970). Le problème *Meloidogyne* sur tabac à Madagascar. *Cahiers ORSTOM, Série Biologie,* No. 11:187–208.

Gwynn, G. R., Barker, K. R., Reilly, J. J., Komn, D. A., Burk, L. G. & Reed, S. M. (1986). Genetic resistance to tobacco mosaic virus, cyst nematodes, root-knot nematodes and wildfire from *Nicotiana repanda* incorporated into *N. tabacum. Plant Disease,* 70:958–962.

Hartill, W. F. T. (1968). The influence of soil conditions on the development of *Rhizoctonia solani* Kuhn, on tobacco. *Rhodesian Journal of Agricultural Research,* 6:77–79.

Hopkins, J. C. F. (1927). The care of tobacco seedbeds. *Rhodesia Agricultural Journal,* 24:736–739, 847–857.

Inagaki, H. & Powell, N. T. (1969). Influence of the root-lesion nematode on Blackshank symptom development in flue-cured tobacco. *Phytopathology,* 59:1350–1355.

Jack, R. W. (1920). Tobacco pests of Rhodesia, Part 2. *Rhodesia Agricultural Journal,* 17:28–33.

Jack, R. W. (1927). Root gallworm or rootknot eelworm (*Heterodera radicicola*). *Rhodesia Agricultural Journal,* 24:957–964.

Jack, R. W. (1944). *Rootknot nematode research.* Report of the Trelawney Tobacco Research Station, 1943, 27–39.

Jack, R. W. (1945). *Rootknot nematode.* Report of the Trelawney Tobacco Research Station, 1944:40–59.

Jack, R. W. (1946). *Rootknot nematode.* Report of the Trelawney Tobacco Research Station, 1945:39–79.

Jepson, S. B. (1987). *Identification of root-knot nematodes (Meloidogyne species).* Wallingford, United Kingdom, C.A.B. International, 256 p.

Kadotani, N., Hokaguchi, N. & Fukudome, N. (1985). Genetic studies on resistance of Okinawa native tobacco lines to *Meloidogyne javanica. Bulletin Kagoshima Tobacco Experimental Station.* N° 26:1–17. [In: CORESTA information Bulletin 1985, abstract 8250.]

Kimpinski, J., Lelacheur, K. E., Marks, C. F., Thompson, L. S. & Willis, C. B. (1976). Nematodes in tobacco in the Maritime Provinces of Canada. *Canadian Journal of Plant Science,* 56:357–364.

Komm, D. A., Reilly, J. J, & Elliott, A. P. (1983). Epidemiology of a tobacco cyst nematode (*Globodera solanacearum*) in Virginia. *Plant Disease,* 67:1249–1251.

Krishna, M. & Prasad, K. S. K. (1985). *Tylenchorhynchus annulatus,* a potential pest in Virginia flue-cured tobacco. *Indian Journal of Nematology,* 15:257–258.

Lehman, S. G. (1931). Research in botany. A new tobacco root disease. *North Carolina Agricultural Experimental Station Annual Report.* 54:73–76.

Lownsbery, B. F. & Lownsbery, J. W. (1954). *Heterodera tabacum* new species, a parasite of solanaceous plants in Connecticut. *Proceedings of the Helminthological Society of Washington,* 21:42–47.

Lucas, G. B. (1975). *Diseases of tobacco, 3rd edition.* Raleigh, N. Carolina, Biological Consulting Agencies. 621 p.

Mackenzie, J. & Ternouth, R. A. F. (1986). Review on breeding for resistance to root knot, *Meloidogyne javanica* in flue-cured tobacco in Zimbabwe. *CORESTA Information Bulletin, 1986 Symposium, Taormina, Italy,* abstract P 05.

Madamba, C. P. (1981). Distribution and identification of *Meloidogyne* spp. in the Philippines and five other Asian countries. *Philippines Agriculturist,* 64:21–39.

Marks, C. F. & Elliot, J. M. (1973). Damage to flue-cured tobacco by the needle nematode *Longidorus elongatus. Canadian Journal of Plant Science,* 53:689–692.

Martin, G. C. (1949). Soil pests in lands. *Rhodesian Tobacco Journal,* 1:48–53.

Martin, G. C. (1950). Eelworm and weed control combined in seedbeds. *Rhodesian Tobacco Journal,* 2:35, 37, 39.

Martin, G. C. (1951). Ethylene dibromide proves itself in eelworm campaign. *Rhodesian Tobacco Journal,* 3:70–78, 107.

Martin, G. C. (1955). Plant and soil nematodes of the Federation of Rhodesia and Nyasaland. Preliminary investigations. Nematodes catalogued under hosts or associated plants. *Rhodesia Agricultural Journal,* 52:346–361.

Martin, G. C. (1962). Population levels of nematodes in roots and soil around root zones of tea, sugarcane, tobacco and wheat grown in the Federation of Rhodesia and Nyasaland. *Rhodesia Agricultural Journal.* 59:28–35.

Martin, G. C. (1967). Longevity of *Meloidogyne javanica* under conditions of bare fallow in Rhodesia. *Rhodesia Agricultural Journal,* 64:112–114.

Martin, G. C. (1968). Survival and infectivity of eggs and larvae of *Meloidogyne arenaria* after ingestion by a bovine. *Plant Disease Reporter,* 52:100–103.

Martin, G. C. (1969). Plants infected with root-knot nematodes (*Meloidogyne* spp.) in Rhodesia, Malawi and Zambia. *Rhodesia Agricultural Journal, Technical Bulletin No. 8.*

Meagher, J. W. (1969). Nematodes as a factor in citrus production in Australia. *Proceedings of the First International Citrus Symposium,* 2:999–1006.

Miller, L. I. (1977). Pathogenicity of *Globodera virginiae* to Kentucky 16 burley tobacco. *Proceedings of the American Phytopathology Society,* 4:217 (abstr.).

Miller, L. I. & Gray, B. J. (1968). Horsenettle cyst nematode, *Heterodera virginiae* n. sp., a parasite of solanaceous plants. *Nematologica,* 14:535–543.

Miller, L. I. & Gray, B. J. (1972). *Heterodera solanacearum* n. sp., a parasite of solanaceous plants. *Nematologica,* 18:404–413.

Miller, P. M. (1969). Suppression by benomyl and thiabendazole of root invasion by *Heterodera tabacum. Plant Disease Reporter,* 53:963–966.

Milne, D. L. (1961). A preliminary survey of nematodes present in South African tobacco soils. *South African Journal of Agricultural Science,* 4:217–223.

Milne, D. L. (1965). Tobacco eelworm, *Leaflet of the Department of Agricultural Technical Services, Republic of South Africa,* No. 24. Pretoria, Government Printer.

Milne, D. L. (1972). Nematodes of tobacco. In: Webster, J.M. (Ed.). *Economic Nematology.* London, Academic Press: 159–186.

Mountain, W. B. (1954). Studies of nematodes in relation to brown root rot of tobacco in Ontario. *Canadian Journal of Botany,* 32:737–759.

Naudés, T. J. (1929). Insect pests of cotton and tobacco in South Africa. *Pan-African Agricultural and Veterinary Conference. Agricultural Section.* Paper No. 52:255–256.

Noe, J. P. (1986). *Cropping systems analysis for limiting losses due to plant-parasitic nematodes: guide to research methodology. Cooperative Publication.* Plant Pathology Department, North Carolina State University and the United States Agency for International Development, Raleigh, N.C.

Nordmeyer, D. & Dickson, D. W. (1985). Management of *Meloidogyne javanica, M. arenaria* and *M. incognita,* on flue-cured tobacco with organophosphate, carbamate and avermectin nematicides. *Plant Disease,* 69:67–69.

Norse, D. (1972). Nematode populations in a maize-groundnut-tobacco rotation and the resistance of maize varieties to *Meloidogyne javanica. Tropical Agriculture,* 49:355–360.

Nusbaum, C. J. (1955). Variable effects of nematicides on parasitic nematode populations in row-fumigated tobacco. *Phytopathology,* 45: 349 (abstr.).

Nusbaum, C. J. (1960). Soil fumigation for nematode control in flue-cured tobacco. *Down to Earth,* 16:15–17.

Olthof, Th. H. A. (1968). Races of *Pratylenchus penetrans,* and their effect on black root rot resistance of tobacco. *Nematologica,* 14:482–488.

Osborne, W. W. (1967). *Fungicide-Nematicide Tests,* 23:138.

Patel, D. J., Desai, M. V. & Patel, D. B. (1986). Inoculum potential of reniform nematode (*Rotylenchulus reniformis*)on tobacco. *Tobacco Research,* 12:38–42. In: *CORESTA Information Bulletin. 1987,* abstract 1708.

Patel, G. J., Shah, H. M., Patel, D. J. & Voland, G. B. (1983). Effect of removal of knotted root portion on the establishment and yield of bidi tobacco. *Tobacco Research,* 9:99–100.

Porter, D. M. & Powell, N. T. (1967). Influence of certain *Meloidogyne* species on Fusarium wilt development in flue-cured tobacco. *Phytopathology,* 57:282–285.

Powell, N. T. & Batten, C. K. (1969). Complexes in tobacco involving *Meloidogyne incognita, Fusarium oxysporum, F. sp. nicotianae* and *Alternaria tenuis. Phytopathology,* 59:1044 (abstr.).

Powell, N. T., Melendez, P. L. & Batten, C. K. (1971). Disease complexes in tobacco involving *Meloidogyne incognita* and certain soil fungi. *Phytopathology,* 61:1332–1337.

Powell, N. T., Porter, D. & Wood, K. (1986). Disease control practices. In: *Tobacco Information 1986,* North Carolina Agricultural Extension Service: 59–92.

Rammah, A. (1988). *Morphological and taxonomic studies in certain populations of the root-knot nematodes Meloidogyne arenaria* and *M. javanica.* Ph.D. Thesis, North Carolina State University, Raleigh, U.S.A.

Rammah, A. & Hirschmann, H. (1988). *Meloidogyne mayaguensis* n. sp. (*Meloidogynidae*), a root-knot nematode from Puerto Rico. *Journal of Nematololgy,* 20:58–69.

Rangeley, H. (1917). Eelworm. *Rhodesia Agricultural Journal,* 14:406.

Rich, J. R., Arens, M. L. & Johnson, J. T. (1982). Nature and extent of Javanese root-knot nematode damage to flue-cured tobacco in Florida. *Florida Agricultural Experiment Stations, Bulletin 826.*

Rich, J. R. & Garcia, M. R. (1985). Nature of the root-knot disease in Florida tobacco. *Plant Disease,* 69:972–974.

Rufty, R. C., Powell, N. T. & Gooding, Jr. G. V. (1983). Relationship between resistance to *Meloidogyne incognita* and a necrotic response to infection by a strain of potato virus Y in tobacco. *Phytopathology*, 73:1418–1423.

Sasser, J. N. & Freckman, D. W. (1987). A world perspective on nematology: The role of the Society. In: Veech, J. A. & Dickson, D. W. (Eds.). *Vistas on Nematology.* Society of Nematologists Inc., Hyattsville, Maryland, U.S.A.

Sasser, J. N., Lucas, G. B. & Powers, H. R. (1955). The relationship of root-knot nematodes to blackshank resistance in tobacco. *Phytopathology*, 45:459–461.

Sayre, R. M., Patrick, Z. A. & Thorpe, H. J. (1965). Identification of a selective nematicidal component in extracts of plant residues decomposing in soil. *Nematologica,* 11:263–268.

Schmitt, D. P. & Barker, K. R. (1988). Incidence of plant-parasitic nematodes in the coastal plains of North Carolina. *Plant Disease,* 72:107–110.

Shah, H. M., Patel, D. J. & Jaisani, B. G. (1985). Reactions of two Japanese tobacco varieties 'Okinawa–6' and 'Okinawa–12' to *Meloidogyne javanica* under Gujarat conditions. *Indian Journal of Nematology.* 15:108.

Shepherd, J. A. (1968). A nematode survey of tobacco soils in Rhodesia and Zambia, and the effects of grass-tobacco rotations on nematode populations. *Rhodesian Journal of Agricultural Research,* 6:19–26.

Shepherd, J. A. (1976). *The inter-relationship of the soil fungus,* Rhizoctonia solani, *Kühn, and certain nematode parasites of* Nicotiana tabacum *L.* M. Phil. Thesis, University of London, U.K.

Shepherd, J. A. (1977). Hosts of non-gall forming nematodes associated with tobacco in Rhodesia. *Rhodesian Journal of Agricultural Research,* 15; 95–97.

Shepherd, J. A. (1978). TRB tests new lovegrass strain, and recommends it. *Rhodesian Tobacco Today,* 1:15.

Shepherd, J. A. (1982). Nematode pests of tobacco. In: Keetch, D. P. & Heyns, J. (Eds.). *Nematology in Southern Africa.* Science Bulletin, Department of Agriculture and Fisheries, Republic of South Africa. No. 400:58–68.

Shepherd, J. A. & Coombs, R. F. (1981). The effect of four *Meloidogyne* species (Nematoda: Meloidogynidae) on breeding lines of *Nicotiana* resistant to *Meloidogyne javanica. Zimbabwe Journal of Agricultural Research,* 19:123–125.

Singh, N. D. (1974). Preliminary investigations on the parasitic nematodes associated with tobacco in Trinidad. *Nematropica,* 4:11–16.

Singh, S. P., Veena Pant, Khan, A. M. & Saxena, S. K. (1985). Changes in the phenolic contents, related rhizosphere mycoflora and nematode population in tomato inoculated with *Meloidogyne incognita* as a result of soil amendment with organic matter. *Indian Journal of Nematology,* 15:197–201.

Slana, L. J. (1978). Studies on resistance to *Meloidogyne* in *Nicotiana* species. *Dissertation Abstracts International,* 40B (4) : 1450–1451.

Slana, L. J. & Stavely, J. R. (1981). Indentification of the chromosome carrying the factor for resistance to *Meloidogyne incognita* in tobacco. *Journal of Nematology,* 13:61–66.

Smee, C. L. (1928). Root gallworm in tobacco seedbeds in Nyasaland (*Heterodera radicicola,* Greef). *Bulletin of the Nyasaland Department of Agriculture, Entomology Series No. 3.* 22p.

Sosa-Moss, C., Barker, K. R. & Daykin, M. E. (1983). Histopathology of selected cultivars of tobacco infected with *Meloidogyne* species. *Journal of Nematology,* 15:392–397.

Southards, C. J. (1965). *Host-parasite relations of the lesions nematodes,*Pratylenchus brachyurus, P. zeae *and* P. scribneri, *and flue-cured tobacco.* Ph.D. thesis, North Carolina State University, Raleigh, U.S.A., 101 p.

Southards, C. J. & Nusbaum, C. J. (1967). Genetic variability of tobacco response to *Pratylenchus brachyurus*. *Phytopathology*, 57:18–21.

Stapleton, J. J. & De Vay, J. E. (1986). Soil solarization: a non-chemical approach for management of plant pathogens and pests. *Crop Protection*, 5:190–198.

Stirling, G. R. & Mankau, R. (1978). Parasitism of *Meloidogyne* eggs by a new fungal parasite. *Journal of Nematology*, 10:236–240.

Sudo, S. & Espindola, E. E. (1987). Survey of root-knot nematode species in tobacco plants grown in the South of Brazil. *CORESTA meeting; Agronomy and Phytopathology groups, 15 p. CORESTA Information Bulletin, 1987,* abstract 2086.

Taylor, A. L., Sasser, J. N. & Nelson, L. A. (1982). *Relationship of climate and soil characteristics to geographical distribution of Meloidogyne species in agricultural soils.* International Meloidogyne Project, Raleigh, North Carolina, U.S.A. 65 p.

Ternouth, R. A. F., Mackenzie, J. & Shepherd, J. A. (1986). Introduction of *Meloidogyne javanica* resistance into flue-cured tobacco in Zimbabwe. *CORESTA Information Bulletin, 1986 Symposium, Taormina, Italy*, abstract P 06.

Tillet, E. R. (1964). The effects of different fumigants on the mineralization of soil nitrogen. *Rhodesian Journal of Agricultural Research,* 2:13–16.

Tisdale, W. B. (1922). Tobacco disease in Gadsden county in 1922. *University of Florida Agricultural Experimental Station, Bulletin 166.*

Tyler, J. (1933). The root-knot nematode. *California Agricultural Experimental Station, Circular 330:* 1–33.

Valloton, R. & Corbaz, R. (1976). Etude de la verse parasitaire du tabac causée par le nématode *Ditylenchus dipsaci* (Kühn) Filipjev, en Suisse romande avec recherches sur les moyens du lutte chimique. *Annales du Tabac, SEITA, Section 2,* 13; 49–68. In: *CORESTA Information Bulletin, 1977,* abstract 7833.

van der Linde, W. J., Smith, A. J. & Angelopulo, V. (1951). The control of eelworm. *Farming in South Africa,* 24:243–248.

van Neikerk, D. R. M. (1985). A survey of rootknot nematodes (*Meloidogyne* spp.) in South Africa. *Phytophylactica,* 17:112 (abstr.).

van Wyk, R. J. (1985). The occurence of root-knot nematodes, *Meloidogyne* spp. in the tobacco-producing areas of South Africa. *Phytophylactica,* 17:165–166.

Way, J. I. (1985). Testing the resistance of tobacco lines to *Meloidogyne javanica* in the presence of other root-knot nematode species. *Phytophylactica,* 17:112 (abstr.).

Wouts, W. M. (1966). The indentity of New Zealand populations of *Tylenchorhynchus capitatus* Allen, 1955, with a description of an intersex. *New Zealand Journal of Science,* 9:878–881

Chapter 16

Nematode Parasites of Pineapple

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The cultivated pineapple *Ananas comosus* L. (Merr.) (Bromeliaceae) is a monocotyledonous perennial herb that probably originated in South America (Plate 14A) (Collins, 1968). Five major groups of vegetative clones are grown, with "Cayenne" (typically "Smooth Cayenne") the most common in commercial production areas of the world (Table 1). Clones from other groups are often cultivated in small-scale production areas for local consumption. In South America the fruits of some wild species [e.g. *Ananas monstrosus* and *Bromelia karatas* ("pinuella")] are eaten while others (*Ananas lucidus* = *erectifolius*) are used as fibre crops (Py *et al.*, 1984).

More than 60% of world pineapple production is in Asia. Thailand and the Philippines concentrate on the canned commodity and are the largest producers and exporters in Asia. About 20% of world production is in Mexico, Central and South America, and the Caribbean. Africa produces about 10% and the largest export is from the Ivory Coast, South Africa, and Kenya. The main producers in the Pacific are Australia (Queensland) and Hawaii (Py *et al.*, 1984).

Cultivation techniques

Cultivation techniques vary widely. However, large plantations throughout the world generally use similar cultural practices, and nematode diseases have been studied primarily in these intensive production systems.

Pineapple has retained epiphytic characteristics such as the ability to absorb water and minerals through the leaves, and a fragile root system (Py *et al.*, 1984). The fruit is a multiple berry with 100–200 berry-like fruitlets arranged around a central core continuous with the peduncle (Collins, 1968).

Cultivated pineapple is self-sterile and is vegetatively propagated from crowns, slips, suckers, or stumps (Dalldorf, 1977; Evans *et al.*, 1988). Crowns are removed at harvest from fruits intended for canning and are commonly used as planting material (seed) for Smooth Cayenne in Hawaii and South Africa. Slips originate axially and are borne on the fruit stalk, becoming visible when the fruit is approximately half developed. The number of slips developing on a plant varies with the clone and the climate (Evans *et al.*, 1988). Slips are used as seed in South Africa. Suckers begin growing at floral differentiation, originating from axillary buds on the stem. They may be removed from the plant after fruit harvest and used as seed (as in the Ivory Coast or South Africa) or left on the plant to produce a ratoon crop as is common in South Africa and Hawaii (Anon., 1982; Dalldorf, 1977).

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Stumps are suckers that have borne a fruit and are used in South Africa for "Queen" plantings (Dalldorf, 1977).

Pineapple is planted throughout the year in most growing areas. Planting density varies from 15 000–120 000 plants per hectare in single to triple-row beds, depending on the clone, ecological conditions, and production system. Seed is typically planted in two-row beds (rows 40–60 cm apart, beds 120–140 cm centre-to-centre) with densities of 50 000–75 000 plants per hectare (Evans *et al.*, 1988; Guyot *et al.*, 1974; Lacoeuilhe & Guyot, 1979; Anon., 1982; Py *et al.*, 1984). Beds may be covered with black plastic mulch before planting to retain fumigant and moisture, increase soil temperature, and control weeds. Plastic mulch is commonly used in Hawaii. A soil fumigant is usually injected (usually 1,3-D) for nematode control during soil preparation (Ivory Coast) or as the mulch is being laid (Hawaii) (see Control Measures).

Pineapple is essentially a xerophyte and has stomata and trichomes adapted for reducing water loss, a growth habit allowing collection of rainfall, and a crassulacean acid metabolism. It can be successfully grown in areas with as little as 600 mm annual rainfall. The adventitious root system is not extensive and penetrates the soil to a depth of 5–60 cm and extends 40–80 cm horizontally from the base of the plant (Guérout, 1975) (Plate 14B); consequently, supplemental irrigation can greatly improve plant growth and yield. Although pineapple can survive poor growing conditions, high levels of nitrogen, potassium and some microelements such as iron are required for profitable yield. Preplant fertilizers are placed in the bed during soil preparation, helping to maintain pH in the optimum range of 4.5–5.5, whereas post-plant fertilizers are applied by foliar sprays or through drip irrigation.

Ethylene or other growth regulators are used to force flowering ("forcing") 6–18 months after planting. The time of forcing depends on the climate, the seed, and the intended use of the fruit (canning or fresh market) (Anon., 1982; Py *et al.*, 1984). Fruits are ready for harvest approximately 5–9 months after forcing. If nematode problems are not severe and soil conditions are adequate a second ratoon crop can be harvested.

Nematodes of Pineapple

More than one hundred species of plant-parasitic nematodes have been reported in association with pineapple root systems. Most are of limited or unknown pathogenicity. The most important species of plant-parasitic nematodes in pineapple production are the root-knot nematodes, *Meloidogyne javanica*, and *M. incognita*, the reniform nematode, *Rotylenchulus reniformis* and the root-lesion nematode *Pratylenchus brachyurus*.

Meloidogyne

The root-knot nematode, *M. javanica*, is a severe pathogen of pineapple, and was the basic nematode disease problem in Hawaiian pineapple from 1920 until the 1950s when reniform nematode became the primary challenge. It is the most important pineapple nematode in Australia, being widespread in south-east Queensland, and is significant in Mexico, South Africa, Zimbabwe, Thailand, and some areas of the Philippines. *M. javanica* is now significant on a limited acreage in Hawaii (Rohrbach & Apt, 1986).

M. incognita has been reported from several pineapple growing areas, but does not cause serious damage except in some areas of Puerto Rico and Mexico (Ayala *et al.*, 1969; Garcia & Adam, 1972). In the Ivory Coast, *M. incognita* caused damage when some plantations were first established, but its importance has decreased relative to *P. brachyurus* (see Guérout, 1965).

Symptoms of damage

Second-stage juveniles infect primary root tips. Root growth is retarded within 24 hours of nematode penetration, and usually a terminal club-shaped gall is produced as the nematode develops (Godfrey

TABLE 1. The five groups of *Ananas comosus* cultivars (after Py *et al.*, 1984).

Usual name	CAYENNE	SPANISH	QUEEN	PERNAMBUCO	MORDILONA
Synonyms	none	none	none	ABACAXI	MAIPURE PEROLERA
Main production zones	All	Caribbean Mexico Malaysia Canaria	S. Africa Australia Reunion	Brazil Venezuela West Africa (2)	Colombia Ecuador Peru
Leaves:	Broad and short Spineless except near tip	Narrow and long Usually spiny	Narrow and short Hook-shaped spines	Narrow and long Spiny	Broad and long Inermous (piping)
Fruit:					
Size	Large	Smaller (1)	Smaller (1)	Smaller (1)	Large
shape	Cylindrical	Globular	Conical-cylindr.	Pyramidal	Cylindrical
colour	Orange-yellow	Reddish-yellow	Bright-yellow	Greenish-yellow	Bright reddish-yellow
Uses	Local consumption Fresh and canning exports	Local consumption Fresh exports	Local consumption Fresh exports	Local consumption	Local consumption Fresh exports.

(1) Compared to CAYENNE
(2) "Bush pineapple" only cultivated in small gardens at family scale.

& Oliveira, 1932) (Plate 14C). Large galls are not formed, but small, non-terminal fusiform galls may form and cause brooming of the root system (Godfrey 1936). Second-generation juveniles infect lateral roots, causing a reduction of the total root length of the plant, decreased nitrogen absorption and plant growth rate, and reduced yield (Magistad & Oliveira, 1934; Godfrey & Hagan, 1937). Severe infections result in a stunted root system, poor anchorage, and plants susceptible to moisture and nutrient stress.

Nematode parasitism should be suspected if symptoms of stress are evident in the foliage despite satisfactory climatic and agronomic conditions. In some cases careful observation of the roots may permit diagnosis of nematode infection, but nematode sampling is usually required to diagnose the nematode species involved.

Biology and life cycle

Second-stage juveniles penetrate roots in the meristematic region of the root tip and become sedentary after 2–3 days (Godfrey & Oliveira, 1932). Development through subsequent moults leads to vermiform adult males and saccate, sedentary females. Reproduction is by mitotic parthenogenesis and female nematodes produce eggs contained in a gelatinous matrix (see Chapter 1).

Pathotypes and races/biotypes

Distinct host races of *M. javanica* have not been characterized, but there exist atypical populations that are able to reproduce on cotton, peanut or pepper (Jepson, 1987). This variation suggests that races exist.

Survival and dissemination

Eggs in egg masses survive up to approximately 2 hours at a relative humidity (RH) of 50%, increasing to 8 hours at a RH of 90% (Godfrey & Hoshino, 1933). Eggs contained in galled tissue can tolerate 20 days exposure to 90% RH. Exposure to ultra-violet radiation was lethal to eggs, eggs in egg masses, and juvenile stages of the nematode (Godfrey & Hoshino, 1933).

Juveniles of *M. javanica* may survive in desiccated soil without a host for 20–24 weeks, although soil moisture influences survival (Godfrey *et al.*, 1933; Towson & Apt, 1983). The time required to reduce soil populations of *M. javanica* juveniles 50% in Hawaiian soils was 2.7, 4.9, 110, 10 and 2.6 days at soil moistures of −0.16, −0.30, −1.1, −15 and −92 bars, respectively (Towson & Apt, 1983). *M. javanica* can survive, although at low levels, as long as 2 years in fallow field soil (Godfrey, 1936).

The nematode survives a wide range of temperatures; however, 127 minutes at 40°C is lethal to juveniles, while 4.5 days at 40°C is lethal to eggs (Hoshino & Godfrey, 1933). Bare pineapple soils may reach 40°C at a depth of 0.6 cm during the summer, and if covered with mulch paper, temperatures greater than 40°C may extend to a depth of 7.5 cm (Hagan, 1933).

The spread of root-knot infestation between root-systems of adjacent plants is quite slow. Godfrey (1936) observed that up to 7 months were required for an infestation to move 30 cm within a row. The root-knot nematodes may be disseminated over long distances in soil adhering to workers shoes, implements, and equipment that is moved from field to field. In South Africa, the nematode is spread by planting infested stumps, so seed material from infested areas is destroyed (Dalldorf, 1977).

Environmental factors affecting parasitism

The minimum temperature for infection by *M. javanica* is approximately 13°C (Godfrey, 1936). *M. javanica* is capable of surviving a wide range of pH levels, and can successfully infect pineapple roots at soil pH of 4.0–8.5, the range of pH at which pineapple is usually grown (Godfrey & Hagan, 1933).

Other hosts

M. javanica has a host range of more than 770 plants, including many economically important crops such as potato, tomato, grape, pineapple, and tobacco.

Disease complexes

Galls of *M. javanica* are subject to secondary invasion by various fungi that cause blackening and drying of the nematode galls, and death of the nematodes within the gall (Godfrey, 1936; Keetch, 1982).

Economic importance and damage threshold

Godfrey (1936), working in Hawaii, suggested that plants could become well established when the population density of root-knot nematodes was less than approximately 6 juveniles per cm^3 of soil. He did not directly relate the initial population density to yield, so his estimate can not actually be considered a damage threshold. Under South African conditions a single juvenile of *M. javanica* in a root or soil sample is interpreted as a potential problem (Keetch, 1982).

Rotylenchulus reniformis

The reniform nematode, *Rotylenchulus reniformis*, occurs in the tropics and subtropics throughout the world. It is the major nematode problem of pineapple in Hawaii and the Philippines (Davide, 1988). Reniform nematode is also important in the Caribbean (e.g. Puerto Rico), some areas of Thailand, in North Queensland, Australia, and in Oxaca, Mexico. In South Africa, *Rotylenchulus parvus* is more frequently observed but is of no economic importance (Keetch, 1982).

Symptoms of damage

In Hawaii, leaves of infected plants are less erect than those of healthy plants, are reddish in colour, and show poor growth. The foliar symptoms are similar to those caused by nutrient or moisture stress. Heavy infestations may result in plant collapse and death (Plate 14D).

In contrast to root-knot nematode infections, primary roots of pineapple infected with *R. reniformis* continue to elongate and provide good anchorage for the plant. However, reniform nematode infection inhibits secondary root formation and root systems are poorly developed (Plate 14E). Improper management of reniform populations typically leads to ratoon crop failures in Hawaii.

Biology and life cycle

The reniform nematode has a unique life cycle. Egg hatch is stimulated by root exudates of certain host plants (Kahn, 1985), and second-stage juveniles leave the egg and move into the soil. Once in the soil they undergo three moults without feeding, yielding adult males and "pre-adult" females. Females enter the root system, initiate a feeding site, become sedentary, and develop into swollen, mature egg-producing females (Linford & Oliveira, 1940; Bird 1984). Although amphimixis appears to be the rule, some populations from Japan are reported as parthenogenetic (Nakasono, 1977, 1983). As far as is known, males do not feed.

Pathotypes and races/biotypes

Distinct races of the reniform nematode are not known, although on the basis of host range and reproductive strategy the existence of races has been suggested (Dasgupta & Seshadri, 1971; Heald, 1978; Nakasono, 1983). There are differences in temperature optima and reproductive behaviour among populations of reniform nematode (Nakasono, 1977, 1983). For example, exposure to low temperatures (15°C) resulted in decreased reproduction in populations from Puerto Rico compared to populations from Louisiana and Texas (Heald & Inserra, 1988).

Survival and dissemination

The reniform nematode tolerates extreme temperatures, and survives extended periods without a host. Reniform nematode populations from Louisiana, Texas, and Puerto Rico survived for 6 months without a host at temperatures of −5, −1, 4, and 25°C (Heald & Inserra, 1988). Although the reniform nematode is able to survive low soil moisture, soil moistures greater than 7% increase nematode survival at 25°C, but decrease nematode survival at temperatures below freezing (Heald & Inserra, 1988).

Populations of *R. reniformis* can survive for 2 years in fallow soil. Apparently, the nematode survives fallow periods in the egg stage or as anhydrobiotic juvenile stages, depending on soil moisture (Apt, 1976; Tsai & Apt, 1979).

Environmental factors affecting parasitism

The optimum temperature for development is 25–29.5°C, and reproduction is limited by temperatures above 36°C (Rebois, 1973; Heald & Inserra, 1988). Soil temperatures in pineapple growing regions are extremely favourable to the development of the reniform nematode.

The reniform nematode did not become a significant agronomic problem in Hawaii until the mid–1950s. The tendency of the pineapple industry to use shorter and shorter fallow periods contributed to the increasing problem with reniform nematode (Rohrbach & Apt, 1986). In addition the pH of pineapple soils steadily decreased from 1930–1950 due to the application of ammonium sulfate fertilizers. The pH in some fields in Hawaii was as low as 3.2 by 1950. The optimal pH for reproduction of the reniform nematode in Hawaiian soils is approximately 4.8–5.2 (Rohrbach & Apt, 1986).

Another factor contributing to the reniform nematode problem was soil fumigation. Fumigation with D-D (1,2-dichloropropane, 1,3-dichloropropene mixture), EDB (ethylene dibromide), and DBCP (dibromochloropropane) began in the late 1940s. These soil fumigants undoubtedly suppressed populations of nematode antagonists in the soil (Rohrbach & Apt, 1986). The above mentioned agricultural practices combined with intensive monoculture created a soil environment suitable for the reniform nematode. Consequently, in 35–40 years *R. reniformis* went from an initial limited occurrence to becoming a major limiting factor in Hawaiian pineapple culture.

Other hosts

The reniform nematode has an extensive host range, including many weed species commonly found in pineapple and sugarcane growing areas (Linford & Yap, 1940; Birchfield & Brister, 1962).

Economic importance and damage threshold

The reniform nematode is a strong pathogen of pineapple, and in Hawaii heavy infestations combined with moisture stress can result in complete ratoon failures (Plate 14D). Current research in Hawaii deals with quantifying the damage threshold for *R. reniformis* in pineapple.

Pratylenchus

The root-lesion nematode, *Pratylenchus brachyurus*, was originally described from pineapple roots in Hawaii (Godfrey, 1929). It is prevalent, and of economic importance, throughout the equatorial tropics, such as the Ivory Coast, Uganda, Hluhluwe in Northern Natal (South Africa) and Brazil (Guérout, 1975; Zem & Reinhardt, 1978; Bafokuzara, 1982; Keetch, 1982). Although present, it is of limited importance in higher latitudes, such as the Caribbean, Hawaii, Australia, or the Cape Province in South Africa (Guérout, 1975; Keetch, 1982; Rohrbach & Apt, 1986; Stirling, pers. comm).

Pratylenchus zeae is observed in some production areas, but there is no information on its pathogenicity to pineapple.

Symptoms of damage

Black lesions caused by *P. brachyurus* develop in the roots at the point of nematode infection, and the developing necrosis may extend progressively over the whole surface of the root as the nematodes feed and move through the root. Lesions are surounded by dead and discoloured epidermal cells and may extend throughout the parenchyma (Godfrey, 1929; Keetch, 1982). In the later stages of infection the parenchyma is destroyed and the cortex separates from the central cylinder (Guérout, 1975). Secondary roots and root hairs are also destroyed by this nematode, leading to a root system composed of poorly developed primary roots. The damage to parenchyma tissue is not generally visible in the field as pineapple roots are rapidly and heavily suberized.

Infection by *P. brachyurus* decreases plant growth rate, delays leaf emergence, and reduces leaf weights 35–40% (Guérout, 1975; Lacoeuilhe & Guérout, 1976; Sarah, 1986). Leaves turn yellow and then red, lose turgidity, and their tips wither (Py *et al.*, 1984). Foliar symptoms result from deficient water and mineral supply to the plant and are especially noticeable if fertilizers are applied as granules to the soil before planting, as fertilizer absorption is suppressed by nematode damage. Foliar application of fertilizer decreases nematode influence on plant growth because leaves absorb nutrients and this compensates for decreased root function (Lacoeuilhe & Guérout, 1976).

Biology and life cycle

P. brachyurus is a migratory endoparasite. Males are rare, and reproduction is by mitotic parthenogenesis (Roman & Triantaphyllou, 1969). The life cycle may be completed within the roots. Thus, large populations can develop quickly and cause the rapid destruction of the cortical parenchyma (Guérout, 1975).

Survival and dissemination

Under laboratory conditions, populations of *P. brachyurus* from the Ivory Coast survive from 20 to 22 months in fallow soil (Feldmesser in Wallace, 1963), as long as viable root fragments are present in the soil (Guérout, 1975). If root fragments are absent from the soil, survival without a host is limited to approximately 7 months. After 35 days at 44°C only 25–50% of an original South African population survived (Keetch, 1977).

In the Ivory Coast, *P. brachyurus* is sometimes disseminated when infected suckers are used as seed. Generally, the suckers used as seed are uninfested.

Environmental factors affecting parasitism

The optimum temperature for *P. brachyurus* development is 25–30°C (Olowe & Corbett, 1976). This temperature range encompasses the yearly average soil temperatures in the Ivory Cost. Although nematode movement is inhibited by soil temperatures above 40°C (Endo, 1959; Olowe & Corbett, 1976), many Ivorian plantations are located on sandy soils which are very favourable to the movement of *P. brachyurus* when temperatures are adequate.

The soil temperatures in the Ivory Coast are relatively constant, and the root-lesion nematode responds primarily to changes in soil moisture. If pineapple is planted during the dry season, the nematode populations in the roots will remain at low levels, increasing several weeks after the return of regular rainfalls (Fig. 1). When planted during the rainy season, nematode population densities in the roots increase rapidly after approximately 3 months (Fig. 2). If soil moisture remains favourable, root population densities remain relatively stable until forcing and then decline. Approximately 20 mm of rainfall per 10 days is required in the Ivory Coast to maintain high root populations of *P. brachyurus* (Sarah, unpubl.).

Population densities of *P. brachyurus* in roots are higher in acid soils and remain low if pH exceeds 5–5.5 (Table 2). Most Ivorian soils are very acid, which may contribute to the prevalence of the nematode in that country. In the Ivory Coast *P. brachyurus* competitively displaces *Meloidogyne* spp., as the rapid destruction of root tissue by the root-lesion nematode seems to prevent the establishment of the root-knot nematode (Guérout, 1965).

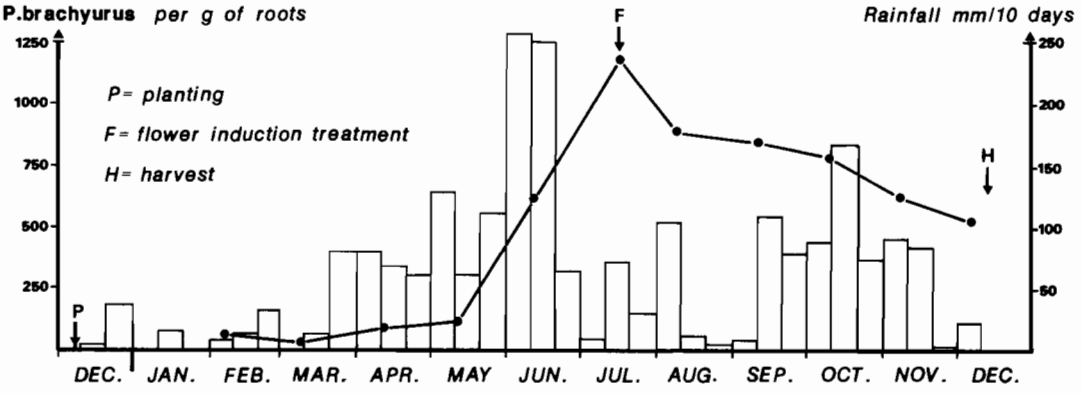

Fig. 1 Populations of *Pratylenchus brachyurus* in the roots of pineapple cv Smooth Cayenne related to rainfall, planted December just before the main dry season, Ivory Coast.

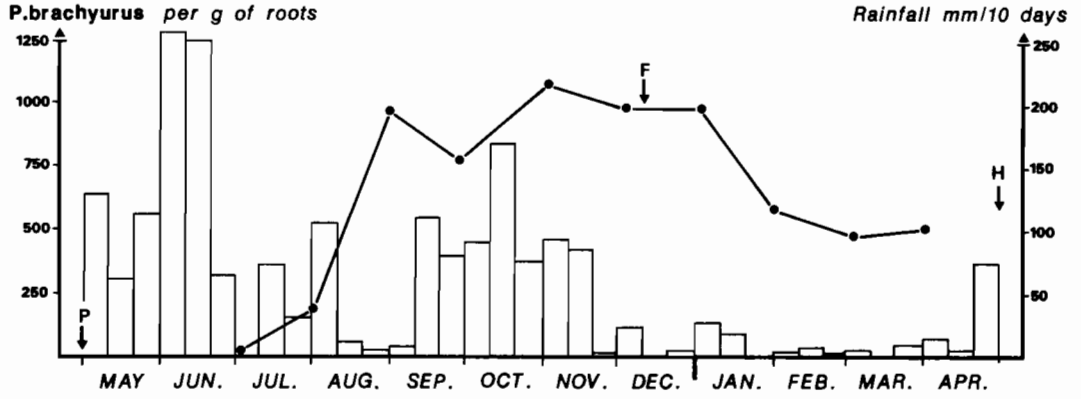

Fig. 2 Populations of *Pratylenchus brachyurus* in the roots of pineapple cv Smooth Cayenne related to rainfall, planted July at the end of the main rainy season, Ivory Coast.

TABLE 2. Influence of soil pH on *P. brachyurus* root infestation levels, and on the vegetative and fruit growth in the Ivory Coast (Sarah & Osseni, unpubl.).

	pH				
	3.9	4.2	4.6	5.1	6.2
Average number of *P. brachyurus*/g of roots during the vegetative growth	1060	880	390	280	140
"D" leaf weight at forcing (g)	43.8	48.6	58.4	57.6	57.8
Fruit weight (g)	637	721	769	858	973

Other hosts

The root-lesion nematode has a very wide host range that includes 100 recorded host species, many of them grasses found in the natural savannahs of the Ivory Coast (Luc & de Guiran, 1960). Maize and cassava are very sensitive to root-lesion nematode, and these plants cannot be used as rotation crops with pineapple in the Ivory Coast (Anon., 1987).

Disease complexes

P. brachyurus may infect galls caused by *M. javanica* and cause the rapid breakdown of the gall and death of the root tip (Godfrey, 1929). In the Ivory Coast, Guérout (1975) demonstrated an interaction between *P. brachyurus* and pytheaceous fungi. The fungus-nematode combination results in plant damage greater than that caused by the nematode alone.

Economic importance and damage threshold

In South Africa, inoculation with 200 *P. brachyurus* decreased plant growth by 25% after 10 months. This compares with a decrease of 10% caused by similar inoculation with *M. javanica* (Keetch, 1982). The damage caused by *P. brachyurus* can be severe, and in the Ivory Coast yield losses may reach 30% for the plant crop and 80% for the first ratoon crop (Lacoeuilhe & Guérout, 1976; Sarah, 1986). The damage threshold is partially determined by the planting date because climatic conditions, including soil moisture and temperature, influence nematode population growth rate and the capacity of the plant to tolerate infection. For example, dry conditions combined with *P. brachyurus* infection cause a drastic reduction in sucker development in the Ivory Coast (Sarah, 1987*a*). The linear relationship between initial population density of *P. brachyurus* and average fruit weight for pineapple planted just before the rainy season in the Ivory Coast (Fig. 3) suggests that the damage threshold is very low in that environment (Sarah, 1986).

Control measures

The primary emphasis of nematode control in pineapple is on protection of the young, growing root system. Reduction of nematode inoculum in the soil prior to planting, or reduction of population growth rate once plants are established in the field is the goal of management. Preplant control of nematode populations is most important, as damage to the developing roots of the young plant results in poor plant growth (Godfrey, 1936). Preplant strategies to suppress nematode inoculum include application of nematicides, rotations with non-host crops, fallowing, and soil amendments. Post-plant management options are currently limited to nematicide application.

Cultural practices

Growers usually specialize in pineapple production and the crop is grown in long-term monoculture. Some fields in the Ivory Coast have been producing continuous pineapple for 30 years, while fields in Hawaii have produced pineapple for over 70 years. Pineapple is essentially a perennial, and crop cycles can be very long, e.g. 8 years in South Africa. Fields are typically left fallow during the period between pineapple crops (the intercycle). The duration of the intercycle is dictated by economics and pest control considerations. Long crop cycles can be considered to include a long intercycle while short crop cycles usually have a short intercycle. The success of the intercycle in reducing nematode populations is also influenced by the type of fallow (e.g. clean vs. "natural" fallowing), soil moisture conditions, and the host range of the nematode species involved.

Clean fallow

Weed-free fallow can be used to decrease nematode populations. Keeping a field free of weeds is difficult, as seeds can remain viable for years and even small seedlings have a root system capable of supporting significant numbers of nematodes. Fields can be kept near weed free by application of herbicides, or through periodic cultivation (the added benefit of cultivation is that it brings deeper soils layers to the surface, exposing eggs and juveniles to ultra-violet radiation and desiccation). Weeds such as nightshade and pigweed (*Amaranthus* spp.) growing during a 1 year fallow period supported high populations of root-knot and reniform nematodes in Hawaii (Apt, unpubl.). Although nematode populations decline during a clean fallow, it is virtually impossible to eradicate nematode populations. Even after fallow periods as long as two years, residual inoculum is still present, though difficult to detect (Godfrey, 1936; Guérout, 1975).

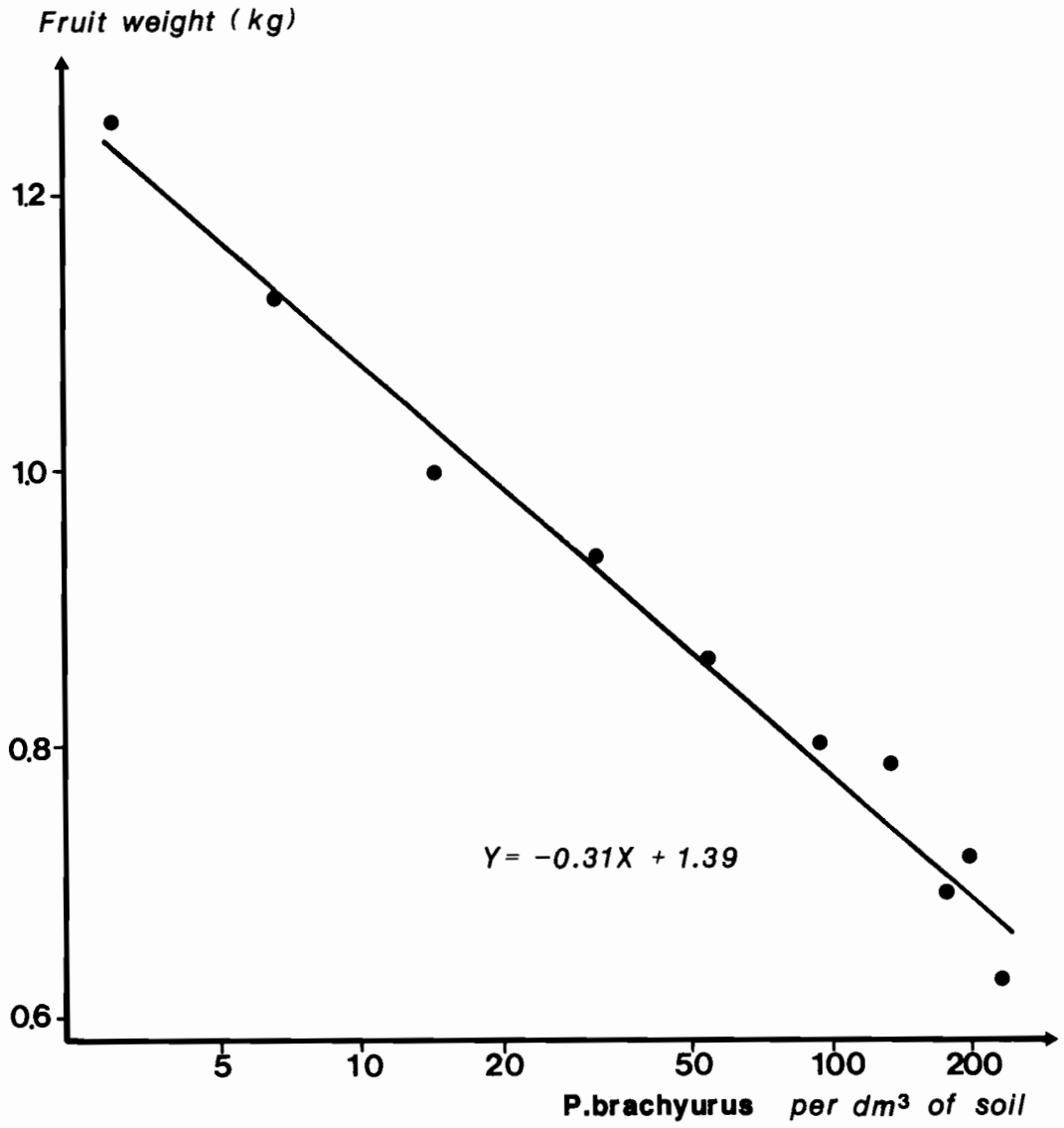

Fig. 3 Relationship between fruit weight and soil populations of *Pratylenchus brachyrus* before planting (Sarah, 1986).

Some nematode species have life-history strategies that include cryptobiotic capacities, such as dauer stages that allow survival despite environmental extremes. The success of fallowing will depend, to a degree, on the nematode species involved.

The pineapple industry in Hawaii currently uses a 6–12 month clean fallow period between plant cycles. Fallow periods hasten the decline of reniform nematode populations in soil but moisture plays a role in determining the extent of population decline. *R. reniformis* can survive for as long as 1.5 years in desiccated, fallow soils (Apt, 1976; Tsai & Apt, 1979). In the Ivory Coast six weeks fallow can reduce populations of *P. brachyurus* by half (Guérout, 1975).

Clean fallow can be a problem on large plantations as it is energy intensive and may not be economically justifiable. In addition, erosion, one of the most important problems facing modern

agriculture, may be increased considerably by fallow. The absence of a cover crop may reduce soil fertility by slowing the addition of organic matter and decreasing retention of soluble nutrients in the soil. Fallow may decrease the population densities of beneficial micro-organisms, such as endomycorrhizae, as has been observed in the Ivory Coast (Sarah, 1987*b*).

Crop rotation

Because of some of the problems associated with clean fallow, planting non-host cover crops may be desirable. Cover crops may suppress plant-parasitic nematode populations, decrease erosion, maintain or enhance soil fertility, and provide a niche for nematode-antagonistic fauna. Some plants may produce allelochemicals as root exudates that are actively toxic or inhibitory to nematodes. Research in Hawaii and Japan has shown that French marigold (*Tagetes patula*) (Nakasono, 1973), Rhodes grass (*Chloris gayana*) and sunn hemp (*Crotalaria juncea*) reduce soil populations of *R. reniformis* faster than clean fallow (Caswell *et al.*, unpubl.). *C. gayana* and *Desmodium unicatum* have been successful as rotation crops to reduce nematode populations (mixed Hoplolaiminae genera and *Meloidogyne* spp.) in the Cape Province (Keetch & Dalldorf, 1980). Pangola grass (*Digitaria decumbens*) has potential as a rotation crop for pineapple as it apparently stimulates eclosion of *M. incognita*, and toxins produced by the roots affect juvenile survival (Ayala *et al.*, 1967; Haroon & Smart, 1983*a*). Plantings of *D. decumbens* eliminate populations of *M. incognita* after one year, and *Criconemella* spp. and *Helicotylenchus* spp. after 18 months. *D. decumbens* is a poor host for *M. javanica* (Haroon & Smart, 1983*b*), but *P. brachyurus* remained abundant even after 3 years of *D. decumbens* growth (Ayala *et al.*, 1967).

Many plant species have been tested for their ability to suppress nematode populations in the Ivory Coast. The legumes *Crotalaria usaramoensis, Stylosanthes gracilis* and *Flemingia congesta* reduced populations of *P. brachyurus* after 18 months of growth, increased the nitrogen content of the soil and the subsequent pineapple crop, and increased the fruit weights of the subsequent pineapple crop by 25–30% (Guérout, 1969). When grown for 6 months, the grass *Panicum maximum* increased pineapple yields better than did 6 months of *Chromolaena odorata* (Asteraceae), even though the latter showed the superior reduction of the nematode population (Anon., 1987). This demonstrates that the cover crop that gives the best nematode population reduction will not necessarily result in the best yield of the subsequent pineapple crop.

Sugarcane is frequently grown in areas where pineapple is produced. Sugarcane is generally considered a non-host for *R. reniformis*, so planting pineapple into sugarcane soils may decrease problems with the nematode, provided that weed hosts are not present. This strategy is being used in Hawaii where possible, with poor success. Sugarcane is a host for *P. brachyurus* in Hawaii, Brazil, and Venezuela.

Organic improvements and soil amendments

The addition of organic matter to pineapple soils is beneficial, as the decline of soil organic matter is faster in pineapple soils than under other crops (Py *et al.*, 1984). The addition of organic matter may have direct and indirect effects on nematode populations. For example, adding cassava residues or extracts of Neem (*Azadirachta indica*) leaves to soil reduces populations of *P. brachyurus* by 75 and 72% respectively, in Nigeria (Egunjobi & Larinde, 1975). These are not common amendments to pineapple soils however. Linford (1937) found that adding organic matter to soil increased the activity of nematode-trapping fungi (see Biological control, below). Working in Hawaii, Klemmer and Nakano (unpubl.) found that incorporating pineapple plant residues into the field (rather than burning them) significantly increased the numbers of nematode antagonists present in the soil. These antagonists reduced reniform nematode populations, but not as effectively as did soil fumigation. Furthermore, the surviving nematode populations rapidly increased during the next crop cycle, with resulting crop damage the equivalent of untreated control plots. Much of the observed beneficial effect of organic matter incorporation is probably due to its stimulatory effect on predators and parasites of nematodes.

Resistance and tolerance

There has been very little research addressing nematode resistance in pineapple. Collins and Hagan (1932) assessed the tolerance of several pineapple clones to *M. javanica* infection by determining the influence of the nematode on root growth. They found that Cayenne was very intolerant of nematode infection, while Wild Brazil and an F1 hybrid from Wild Brazil x Cayenne were much more tolerant, if not immune to damage from nematode infection as measured by shoot weight and root length (Collins & Hagan, 1932; Hagan & Collins, 1935). They did not assess nematode reproduction in these clones. *Ananas ananasoides* and three other selections are resistant to *M. incognita* (Ayala, 1961, 1968; Ayala *et al.*, 1969). *A. ananasoides*, cv Venezolana, and two other clonal selections are resistant to *R. reniformis*. Unfortunately, *A. ananasoides* has undesirable agronomic characteristics and has been found to be an excellent host for *P. brachyurus* in the Ivory Coast (Py *et al.*, 1984).

Different clones, cultivars, species, and genera have been tested for resistance to *P. brachyurus* in the Ivory Coast with negative results (Anon., 1987). However, *Ananas nannus* is still being investigated. The group "Queen" and *Ananas bracteatus* are extremely susceptible to *P. brachyurus*.

Nematicides

Chemical nematicides are the primary means of managing plant parasitic nematodes in pineapple, regardless of the nematode species involved. Preplant or at-plant soil treatments are necessary to protect the root system of the young pineapple plant if nematode populations are present. Such treatments can be applied as preplant fumigation, at-plant incorporation of granular nematicides, or preplant nematicide application via drip irrigation (Rohrbach & Apt, 1986; Apt & Caswell, 1988).

An effective nematode management strategy must be based on the cycle length and the number of ratoons desired. Research in Hawaii has shown that protecting the root system for a minimum of 6 months is necessary, and 8–12 months of control is preferred, if ratoon crops are to be harvested.

Preplant fumigation with 1,3-dichloropropene at a rate of 224–336/ l/ha is used in Hawaii and South Africa (Rohrbach & Apt, 1986). In Hawaii, the plastic mulch laid over the beds helps to retain the fumigant. If the fumigation is successful, it is usually sufficient to protect the plant crop and subsequent ratoons. Ethylene dibromide is still registered for use as a preplant fumigant in Australia and is widely used there, although its use will probably be phased out (Stirling, pers. comm.)

Postplant non-fumigant nematicides are sometimes necessary in Hawaii if preplant fumigation is unsuccessful. Postplant treatments without successful fumigation may not give adequate nematode control (Plates 14F & 14G). In the Ivory Coast postplant applications are imperative for a successful plant crop.

The systemic properties of some of the non-fumigant nematicides allows for foliar application during any point in the plant growth cycle. As early as 1966, Apt (unpubl.) conducted extensive studies with foliar applications of fenamiphos. He obtained control of reniform nematode with foliar applications of fenamiphos at rates of 600–2400 ppm (Zeck, 1971). Apt is credited with being the first individual to design a pineapple nematode management programme based on the systemic properties of foliar-applied fenamiphos (Zeck, 1971). Carbofuran and fenamiphos have proved effective as foliar sprays in the Ivory Coast, although carbofuran may be phytotoxic. Carbofuran has not been effective in foliar applications in Hawaii. In the Ivory Coast foliar application of oxamyl may be as effective as fenamiphos if applied at twice the rate of fenamiphos (Sarah, 1987*a*); however, such a rate is currently not economical. Foliar applications just after planting may be effective and help minimize worker exposure to the nematicide (Keetch, 1982).

Dipping suckers in 1500 ppm solutions of fenamiphos or carbofuran (1500 ppm) provides control of *P. brachyurus* in the Ivory Coast, but it is not as effective as preplant fumigation (Guérout, 1975). In South Africa, dipping crowns in solutions of oxamyl at 2400–4800 ppm, or solutions of fenamiphos at 300 ppm provides a good protection against *Helicotylenchus multicinctus* and *M. incognita*, but is not as effective as soil fumigation (Milne, 1974).

Postplant application of non-fumigant nematicides requires good soil moisture conditions to promote movement in the soil, absorption by the plant, and assure that the nematode target is physiologically active (Sarah, 1980). In the Ivory Coast, one to three (Anon., 1982) successive postplant treatments may be applied, provided successive applications are at least 60 days apart (to avoid overdose) and the last application is at least 8 weeks prior to forcing (to avoid disturbing the inflorescence) (Sarah, 1981*b*). Postplant applications of fenamiphos or oxamyl is an optimal treatment in South Africa (Milne *et al.*, 1977*a*; Keetch & Webster, 1977).

In the Ivory Coast, two nematicide applications are used after plant crop harvest; one immediately following harvest and one at 2–4 months after harvest to improve sucker production and decrease nematode reproduction. In Hawaii however, nematicidal treatments applied after the plant crop harvest have no influence on subsequent plant growth or ratoon yield (Apt, unpubl.).

Application of non-volatile nematicides through drip irrigation systems has been the subject of recent research in Hawaii (Apt & Caswell, 1988). Oxamyl and fenamiphos are registered for use in the United States as foliar sprays or through drip irrigation systems. Oxamyl can be applied as a postplant nematicide through drip irrigation or as foliar sprays, with the maximum total application limited to 53.8 kg a.i./ha for the plant crop and 26.9 kg a.i./ha for ratoon crops. The application rate for fenamiphos is 0.56–3.36 kg a.i./ha at 1–3 month intervals to within 30 days of harvest. The total application of fenamiphos cannot exceed 44.7 kg a.i./ha for the plant crop and 22.5 kg a.i./ha for the ratoon crop (Rohrbach & Apt, 1986; Apt & Caswell, 1988). Oxamyl and fenamiphos are most effective when applied to soils having optimal moisture levels.

Under some conditions the non-fumigant nematicides may have phytotoxic side-effects, including heart and leaf burns (ethoprophos and fenamiphos), disturbance of growth (isazophos) and flowering (fenamiphos and carbofuran), and decreased sucker production (carbofuran) (Sarah, 1981*a*, 1981*b*, 1983, 1987*a*). The phytotoxicity may result from direct contact with young plant tissues or physiological responses due to the systemic nature of the nematicides. Physiological disturbance caused by carbofuran and other carbamates is well documented in other plants, where the compound inhibits oxidase activity resulting in increased levels of IAA (Jamet & Piedallu, 1980). Fenamiphos causes the same phenomenon in pineapple (Milne *et al.*, 1977*b*) and this may explain fenamiphos induced stimulation of growth in the absence of nematodes.

Biological management

Linford was one of the pioneers in biological control of nematodes. Many nematode-parasitizing fungi have been identified in Hawaiian soils, including *Arthrobotrys oligospora* Fresenius, *Catenaria anguillulae* Sorokin, *Harposporium anguillulae* Lohde, and *Stylopage hadra* Drechsler (Linford, 1937). In lab experiments Linford (1937) examined the potential of incorporating organic matter to stimulate the activity of nematode predators and parasites in the soil. The incorporation of organic matter resulted in increased populations of free-living nematodes that are prey for nematode-parasitizing fungi, resulting in the increase of fungal populations. The addition of chopped pineapple material to soil at a rate of 50–150 tons per acre-foot of soil significantly reduced galling caused by root-knot nematode as determined by bioassay (Linford, 1937; Linford *et al.*, 1938). Linford also investigated the potential for using several fungi as manipulable biological control agents (Linford & Yap, 1939). In small pot tests they observed that addition of *Dactylella ellipsospora* reduced plant injury caused by the root-knot nematode, although the results were confounded by the presence of other natural enemies of nematodes in the treatment.

Potential biological control agents must be tested in field soil. Results obtained in greenhouse experiments may differ from those in the field because the activity level of the biological control agent will depend on the biotic and abiotic characteristics of the soil (Linford & Yap, 1939). The majority of Linford's work was completed before the widespread use of soil fumigation, and the above mentioned caveats are even more important today. Although there is potential for using manipulable biological control as part of a nematode management programme in pineapple, it is

not currently used as a major part of nematode management in any of the world's pineapple growing areas.

Summary of nematode management in pineapple

Fallow periods play an important role in the crop cycle by reducing nematode populations prior to nematicide treatments in the next planting. Manipulation of the fallow period and soil moisture during fallow holds promise for increasing nematicide efficacy. Cover crops, living mulches, and nematode antagonists may eventually augment or replace effective nematicides. Drip irrigation may play an increasingly important role in nematode management by improving the plants tolerance of nematode damage. However, the most effective means of controlling plant parasitic nematodes on pineapple in intensive production systems is with chemical nematicides. The use of volatile, fumigant nematicides and non-fumigant nematicides is a very effective management technique.

Methods of diagnosis

Sampling

Soil samples should be taken before planting to a depth of approximately 30–40 cm with a trowel or soil-sampling tube. Ideally, the soil should be in a condition of good tilth suitable for sampling. A composite soil sample consisting of 30 cores/100 m^2 is adequate for most analyses. If the nematode population density estimates are required to a certain level of accuracy, then pre-treatment samples taken on a quadrant basis can be used to estimate the numbers of samples required for a given degree of accuracy (Barker *et al.*, 1986).

Samples taken from the growing crop are removed from between two plants within the plant row and in the root zone to a depth of approximately 30 cm. Commencing from about 2 months post-planting, samples are taken on a monthly basis in research work. This sampling regime should be followed during the plant crop to allow assessment of nematode population dynamics. A composite sample consists of from 10 cores per 15–20 m of row (as practiced in Hawaii) to approximately 12 cores per 30 m of row (as practiced in the Ivory Coast). Samples should be placed in plastic bags and protected from temperature extremes until they are processed.

Nematode extraction

The nematode extraction technique used depends on the objectives of the sampling programme, the nematode species present in the soil or the roots, and the stage in the crop cycle. Root-knot nematode juveniles can be recovered by processing known volumes of soil with Baermann funnels, by a combination of Cobb sieving and centrifugation-flotation, or by processing root-samples using mist apparatus or staining egg masses within roots. Females and associated egg masses can be visualized by staining root segments. Staining females is sometimes inefficient as pineapple roots are heavily suberized and do not clear readily (see Barker *et al.*, 1986). Each of previously mentioned techniques allows enumeration of specific root-knot or reniform nematode stages.

Soil-dwelling juvenile and adult stages of reniform nematode are easily recovered from soil using Baermann funnels or by Cobb sieving and centrifugation-flotation. The Baermann funnel technique typically yields a lower estimate of reniform nematode population density than the centrifugation-flotation technique.

Because of the endoparasitic nature of the root-lesion nematode, population density estimates are obtained by extracting the life stages of the root-lesion nematode from soil and roots using centrifugal-flotation with magnesium sulfide (Coolen & d'Herde, 1972; Hendricks *et al.*, 1976). Roots can be macerated to release endoparasites for counting (Alvarado & Lopez, 1981; Barker *et al.*, 1986).

The inoculum of root-lesion nematode prior to planting is sometimes estimated in the Ivory Coast by a maize bioassay. The bioassay is especially helpful if initial population levels are low and is performed by placing the soil sample into several pots and sowing maize in the pots. The root-

lesion nematodes are extracted from soil and roots after 5 weeks to allow nematode reproduction, increasing the probability of detecting the nematode.

In some instances it is desirable to estimate the number of nematodes in the rhizosphere. This can be accomplished by gently shaking the roots to remove adhering soil, and then rinsing the remaining soil that is closely associated with the root system into a bucket. This wash is passed through a set of nested sieves, and may be subsequently passed through the centrifugation-flotation technique.

Determination of populations and crop loss

In the Ivory Coast studies on the impact of nematodes on the plant are undertaken in plots of 80–120 plants (two or three beds of 40 plants per double-row bed). Planting distances are 90 cm x 40 cm x 25 cm, yielding a planting density of approximately 61 500 plants per hectare for fresh fruits; and 90 cm x 40 cm x 28 cm, yielding a plant density of approximately 55 000 plants per hectare for canned fruits. Each treatment should have a minimum of 4 replications, with 5 used in general practice. Experimental plots in Hawaii are similar, typically consisting of 3 or 4 beds, with the centre bed(s) reserved for yield determination. Each experiment should include appropriate controls; a non-treated control, a standard treatment control (plantation practice), and an irrigated control (if the experiment is irrigated) (Apt & Caswell, 1988).

Observations on plant growth are typically non-destructive, using "D" leaf measurements and estimated plant weights. Plants are sometimes uprooted for inspection, or soil profile samples are taken to assess root development and nematode distributions within the soil profile. Soil samples for nematode assessment are taken at random from those beds designated "non-yield". Nematode soil samples are taken from the inside edge of these beds in the treated area, while the centre beds are reserved for yield assessment and are not sampled to prevent root system damage. In the Ivory Coast, soil samples are taken on a monthly rotation basis, so that each month soil cores are removed from soil around plants that have not previously been sampled.

At harvest, fruits are picked, size-classed, and the fruit and crown weights determined per size class. In Hawaii, approximately 100 fruits are harvested per treatment replication, but this depends on the length of the rows in the experiment. In the Ivory Coast, all the fruits of each plot (80–120 fruit) are harvested, and 20 plants per treatment are selected at random for analysis of plant growth, enumeration of fruitlets, size and form of fruits, and fruit analysis (sugar and acidity). The specifics of the analysis are determined by the objectives of the research.

Acknowledgements

We thank N. Marbán M. and G. R. Sterling for information on pineapple production in Mexico and Australia respectively, and B. A. Jaffee and J. J. Lacoeuilhe for critical review of the manuscript.

References

Alvarado-Soto, M. & Lopez-Chaves, R. (1981). Efficacia de dos metodos y sus modificaciones en la extraccion de nematodos endoparasiticos migratorios de raices de pina y plantano. *Nematropica*, 11 : 129–136.

Anon. (1982). Les nématodes. In: *La culture de l'ananas d'exportation en Côte d'Ivoire – Manuel du planteur.* Abidjan. IRFA, Les Nouvelles Editions Africaines : 21–25.

Anon. (1987). Complexe sol-racines: les ravageurs. *Fruits, special Ananas*, 42 (11) : 669–677.

Apt, W. J. (1976). Survival of reniform nematodes in desiccated soils. *Journal of Nematology*, 8 : 278.

Apt, W. J., & Caswell, E. P. (1988). Application of nematicides via drip irrigation. *Annals of applied Nematology (Journal of Nematology 20, Supplement)*, 2 : 1–13.

Ayala, A. (1961). An analysis of the quantitative and qualitative composition of the nematode populations in pineapple fields in Puerto Rico. *Journal of Agriculture, University of Puerto Rico*, 45 : 265–299.

Ayala, A. (1968). Nematode problems of pineapple in Puerto Rico. In: G. C. Smart Jr. & V. G. Perry (Eds), *Tropical nematology*. Gainesville, Univ. Florida Press : 49–60.

Ayala, A., Gonzales-Tejera, E. & Irizarry, H. (1969). Pineapple nematodes and their control. In: Peachey, J. E. (Ed.), *Nematodes of tropical crops*. C.A.B. : 210–224.

Ayala, A. A., Roman, J., & Tejera, E. G. (1967). Pangola grass as a rotation crop for pineapple nematode control. *Journal of Agriculture, University of Puerto Rico*, 51 : 94–96.

Bafokuzara, N. D. (1982). Nematodes associated with pineapples in Uganda. *Nematropica*, 12 : 45–49.

Barker, K. R., Townshend, J. L., Bird, G. W., Thomason, I. J., & Dickson, D. W. (1986). Determining nematode population response to control agents. In: Hickey, K. D. (Ed.), *Methods for evaluating pesticides for control of plant pathogens*. American Phytopathological Society, St. Paul, Minnesota : 283–296.

Birchfield, W., & Brister, L. R. (1962). New hosts and nonhosts of reniform nematode. *Plant Disease Reporter*, 46 : 683–685.

Bird, A. F. (1984). Growth and moulting in nematodes: moulting and development of the hatched larva of *Rotylenchulus reniformis*. *Parasitology*, 89 : 107–119.

Collins, J. L. (1968). *The pineapple*. Leonard Hill, London, 294 p.

Collins, J. L. & Hagan, H. R. (1932). Nematode resistance of Pineapples: Varietal resistance of pineapple roots to the nematode *Heterodera radicicola* (Greef) Muller. *Journal of Heredity*, 23 : 459–511.

Coolen, W. A. & d'Herde, C. J. (1972). *A Method for the quantitative extraction of nematodes from plant tissue*. State Agricultural Research Centre. Ghent, Belgium, 77 p.

Dalldorf, E. R. (1977). Selection and preparation of pineapple planting material. In: *Pineapple cultivation in South Africa*. Citrus and Subtropical Fruit Research Institute, Nelspruit. sh. D–3.

Dasgupta, D. R., & Seshadri, A. R. (1971). Races of the reniform nematode, *Rotylenchulus reniformis* Linford & Oliveira, 1940. *Indian Journal of Nematology*, 1 : 21–24.

Davide, R. G. (1988). Nematode problems affecting agriculture in the Philippines. *Journal of Nematology*, 20 : 214–218.

Egunjobi, O. A. & Larinde, M. A. (1975). Nematodes and maize growth in Nigeria. II. Effects of some amendments on populations of *Pratylenchus brachyurus* and on the growth and production of maize (*Zea mays*) in Nigeria. *Nematologia mediterranea*, 3 : 65–73.

Endo, B. Y. (1959). Responses of root-lesion nematodes, *Pratylenchus brachyurus* and *P. zeae*, to various plants and soil types. *Phytopathology*, 49 : 417–421.

Evans, D. O., Sanford, W. G., & Bartholomew, D. P. (1988). *Pineapple*. University of Hawaii Cooperative Extension Service, Commodity Fact Sheet PIN–3(A).

Garcia-Espinosa, R. & Adam, A. V. (1972). Major diseases of pineapple in Oxaca, Mexico, and their control. *FAO Plant Protection Bulletin*, 20 : 79–87.

Godfrey, G. H. (1929). A destructive root disease of pineapple and other plants due to *Tylenchus brachyurus* n. sp.. *Phytopathology*, 19 : 611–629.

Godfrey, G. H. (1936). The pineapple root system as affected by the root-knot nematode. *Phytopathology*, 26 : 408–428.

Godfrey, G. H. & Hagan, H. R. (1933). Influence of soil hydrogen-ion concentrations on infections by *Heterodera radicicola* (Greef) Muller. *Soil Science*, 35 : 175–184.

Godfrey, G. H. & Hagan, H. R. (1937). Some measurements of detrimental effects of the root-knot nematode on the pineapple plant. *Phytopathology*, 27 : 515–530.

Godfrey, G. H. & Hoshino, H. M. (1933). Studies on certain environmental relations of the root-knot nematode, *Heterodera radicicola*. *Phytopathology*, 23 : 41–62.

Godfrey, G. H. & Oliveira, J. M. (1932). The development of the root-knot nematode in relation to root tissues of pineapple and cowpea. *Phytopathology*, 22 :325–348.

Godfrey, G. H., Oliveira, J. M. & Gittel, E. B. H. (1933). The duration of life of the root-knot nematode, *Heterodera radicicola*, in soils subjected to drying. *Soil Science*, 35 : 185–195.

Guérout, R. (1965). Compétition *Pratylenchus brachyurus – Meloidogyne* sp. dans les cutures d'ananas de Côte

d'Ivoire. In *Proceedings of 8th International Nematology Symposium, Antibes*. E. J. Brill, Leiden : 64–69.

Guérout, R. (1969). Action des plantes améliorantes en culture d'ananas. III. Bilan nématologique. *Fruits*, 24 (9–10) : 436–443.

Guérout, R. (1975). Nematodes of pineapple: a review. *Pest Articles & News Summaries*, 21(2) : 123–140.

Guyot, A., Pinon, A. & Py, C. (1974). L'ananas en Côte d'Ivoire. *Fruits*, 29 : 85–117.

Hagan, H. R. (1933). Hawaiian pineapple field soil temperatures in relation to the nematode *Heterodera radicicola* (Greef) Muller. *Soil Science*, 36 : 83–95.

Hagan, H. R. & Collins, J. L. (1935). Studies on varietal resistance of pineapple plants. II. Plant resistance to *Heterodera marioni* (Cornu) Goodey. *Journal of Heredity*, 26 : 35–46.

Haroon, S. & Smart, G. C. (1983*a*). Root extracts of pangola digitgrass affect hatch and larval survival of *Meloidogyne incognita*. *Journal of Nematology*, 15 : 646–649.

Haroon, S. & Smart, G. C. (1983*b*). Effects of pangola digitgrass on *Meloidogyne arenaria, M. javanica* and *M. hapla*. *Journal of Nematology*, 15 : 649–650.

Heald, C. M. (1978). Effect of the reniform nematode on vegetable yields. *Plant Disease Reporter*, 62 : 902–904.

Heald, C. M. & Inserra, R. N. (1988). Effect of temperature on infection and survival of *Rotylenchulus reniformis*. *Journal of Nematology*, 20 : 356–361.

Hendricks, G. J., Coolen, W. A. & Moernans, R. (1976). Influence de la nature de la densitié des liquides de séparation sur les nématodes pendant le processus de centifugation-flottation. *Nematologia Mediterranea*, 4 : 31–40.

Hoshino, H. M. & Godfrey, G. H. (1933). Thermal death point of *Heterodera radicicola* in relation to time. *Phytopathology*, 23 : 260–270.

Jamet, P. & Piedallu, M. A. (1980). Comportement des nématicides organophosphorés et carbamates dans le sol et les plantes. Etude bibliographique. *Phytiatrie-Phytopharmacie*, 29 : 175–199.

Jepson, S. B. (1987). *Identification of root-knot nematodes (*Meloidogyne *species). Commonwealth Agricultural Bureau*, Wallingford, U.K., 265 p.

Kahn, F. A. (1985). Hatching response of *Rotylenchulus reniformis* to root leachates of certain hosts and nonhosts. *Revue de Nématologie*, 8 : 391–393.

Keetch, D. P. (1977). Nematodes in pineapple. In: *Pineapple cultivation in South Africa*. Citrus and Subtropical Fruit Research Institute, Nelspruit. sh. H–18.

Keetch, D. P. (1982). Nematode pests of pineapple. In: Keetch, D. P. & Heyns, J. (Eds.), *Nematology in South Africa*. Department of Agriculture and Fisheries, Pretoria, Republic of South Africa : 19–29.

Keetch, D. P. & Dalldorf, E. R. (1980). The use of grass and legume rotations for pineapple nematode control in the Eastern Cape. *Citrus and Subtropical Fruit Journal*, 557 : 10–12.

Keetch, D. P. & Webster, G. (1977). Experimental control of pineapple nematodes. *Information Bulletin of the Citrus Subtropical Fruit Research Institute*, Nelspruit 55, : 14–15.

Lacoeuilhe, J. J. & Guérout, R. (1976). Action du nématode *Pratylenchus brachyurus* sur la croissance, la nutrition et les rendements de l'ananas. Influence de la localisation de la fumure. *Fruits*, 33 : 147–156.

Lacoeuilhe, J. J. & Guyot, A. (1979). Les techniques culturales de l'ananas en Côte d'Ivorie. *Fruits*, 34 : 159–168.

Linford, M. B. (1937). Stimulated activity of natural enemies of nematodes. *Science*, 85 : 123–124.

Linford, M. B., & Oliveira, J. M. (1940). *Rotylenchulus reniformis*, nov. gen., n. sp., a nematode parasite of roots. *Proceedings of the helminthological Society of Washington*, 7 : 35–42.

Linford, M. B. & Yap, F. (1939). Root-knot nematode injury restricted by a fungus. *Phytopathology*, 29 : 596–609.

Linford, M. B. & Yap, F. (1940). Some host plants of the reniform nematode in Hawaii. *Proceedings of the helminthological Society of Washington*, 7 : 42–44.

Linford, M. B., Yap, F. & Oliveira, J. M. (1938). Reduction of soil populations of the root-knot nematode during decomposition of organic matter. *Soil Science*, 45 : 127–141.

Luc, M. & de Guiran, G. (1960). Les Nématodes associés aux plantes de l'Ouest Africain. *L'Agronomie tropicale, Nogent*, 4 : 434–449.

Magistad, O. C., & Oliveira, J. M. (1934). Changes in plant-food intake caused by a population of *Heterodera marioni* (Cornu) Goodey on *Ananas comosus*. *Phytopathology*, 24 : 276–283.

Milne, D. L. (1974). Dips for the control of pineapple eelworms. *Citrus and Subtropical Fruit Journal*, 484 : 11–13.

Milne, D. L., De Villiers, E. A. & Smith, B. L. (1977*a*). Response of nematode populations and pineapple yields to foliar application of systemic nematicides. *Citrus and Subtropical Fruit Journal*, 525 : 12–14.

Milne, D. L., Van Lelyveld, L. J. & De Villiers, E. A. (1977*b*). The response to peroxidase and indolacetic acid oxidase in pineapple roots to foliar applications of fenamiphos. *Agrochemophysica*, 9 : 65–70.

Nakasono, K. (1973). Relationship between cultivation of *Tagetes* plants and changes in population of the reniform nematode, *Rotylenchulus reniformis*. *Japanese Journal of Nematology*, 3 : 38–41.

Nakasono, K. (1977). Sexual attraction of *Rotylenchulus reniformis* females and some differences in the attractiveness between amphimictic and parthenogenetic populations (Nematoda: Nacobbidae). *Applied Entomology and Zoology*, 12 : 154–161.

Nakasono, K. (1983). Studies on morphological and physio-ecological variations of the reniform nematode, *Rotylenchulus reniformis* Linford & Oliveira, 1940 with an emphasis on differential distribution of amphimictic and parthenogenetic populations in Japan. *Bulletin of the National Institute of Agricultural Sciences, Japan*, Series C, 38 : 1–67.

Olowe, T. & Corbett, D. C. M. (1976). Aspects of the biology of *Pratylenchus brachyurus* and *P. zeae*. *Nematologica*, 22 : 202–211.

Py, C., Lacoeuilhe, J. J. & Teisson, C. (1984). *L'ananas: sa culture, ses produits*. Paris, Maisonneuve & Larose, 564 p.

Rebois, R. V. (1973). Effect of soil temperature on infectivity and development of *Rotylenchulus reniformis* on resistant and susceptible soybeans, *Glycine max*. *Journal of Nematology*, 5 : 10–13.

Rohrbach, K. G. & Apt, W. J. (1986). Nematode and disease problems of pineapple. *Plant Disease*, 70 : 81–87.

Roman, J. & Triantaphyllou, A. C. (1969). Gametogenesis and reproduction of seven species of *Pratylenchus*. *Journal of Nematology*, 1 : 357–362.

Sarah, J. L. (1980). Utilisation de nématicides endothérapiques dans la lutte contre *Pratylenchus brachyurus* (Godfrey) en culture d'ananas. I. Activité préventive et curative sur les infestations racinaires par applications foliaires. *Fruits*, 35 : 745–757.

Sarah, J. L. (1981*a*). Utilisation de nématicides endothérapiques dans la lutte contre *Pratylenchus brachyurus* (Godfrey) en culture d'ananas. II. Effets secondaires d'applications foliaires sur la phase végétative du cycle de développement de l'ananas. *Fruits*, 36 : 275–283.

Sarah, J. L. (1981*b*). Utilisation de nématicides endothérapiques dans la lutte contre *Pratylenchus brachyurus* (Godfrey) en culture d'ananas. III. Effets secondaires d'applications foliaires sur la réponse au traitement d'induction florale et sur la floraison. *Fruits*, 36 : 491–500.

Sarah, J. L. (1983). Utilisation de nématicides endothérapiques dans la lutte contre *Pratylenchus brachyurus* (Godfrey) en culture d'ananas. IV. Effets secondaires d'applications foliaires sur le développement des plantes après le traitement d'induction florale et sur la maturation des fruits. *Fruits*, 38 : 523–540.

Sarah, J. L. (1986). Influence of *Pratylenchus brachyurus* on the growth of development of pineapple in the Ivory Coast. XVIII Int. Symp. E. S. N., Antibes. *Revue de Nématologie*, 9 : 308–309.

Sarah, J. L. (1987*a*). Influence des traitements nématicides sur la production des rejets d'ananas. *Fruits*, 42 : 71–75.

Sarah, J. L. (1987*b*). Utilisation d'une jachère travaillée pour lutter contre les nématodes parasites de l'ananas. *Fruits*, 42 : 357–360.

Towson, A. J. & Apt, W. J. (1983). Effect of soil water potential on survival of *Meloidogyne javanica* in fallow soil. *Journal of Nematology*, 15 : 110–115.

Tsai, B. Y., & Apt, W. J. (1979). Anhydrobiosis of the reniform nematode: survival and coiling. *Journal of Nematology*, 11 : 316.

Wallace, H. R. (1963). *The biology of plant parasitic nematodes*. London, E. Arnold Ltd., 282 p.

Zeck, W. M. (1971). The systemic nematicide potential of Nemacur. *Pflanzenschutz-Nachrichten Bayer*, 24 : 114–140.

Zem, A. C. & Reinhardt, D. H. (1978). Nematoides associados – cultra do abacaxi no estado da Bahia. In: Mendes, B. V. (Ed.), *Resumos dos trabalhos cientificos e conferencias, III Reuniao Brasileira de Nematologia, Sociedade Brasileira de Nematologia et da Escola Superior de Agricultura, Mossoro* : 17–20.

Chapter 17

Nematode Parasites of Cotton and Other Tropical Fibre Crops

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Cotton

Cotton (*Gossypium* spp.) belongs to the family Malvaceae. It has about thirty species and subspecies of shrubs or small tress, distributed in the tropical and sub-tropical regions of Africa, Asia Australia and America (Purseglove, 1975). Hutchinson *et al.* (1974) recognised four cultivated species (Table 1). The wild form of *G. herbaceum* race *africanum* is thought to be the the common ancestor of modern cottons (Hutchinson, 1962) and is still to be found growing in its native habitat; hot dry savannah areas of Southern Africa from Angola to Mozambique (Prentice, 1972). Subsequent breeding has adapted the cultivated cultivars for survival in less arid and even mesophytic environments and commerical cotton production now extends as far north as the Ukraine and as far south as Argentina.

TABLE 1. Domesticated species of *Gossypium*.

Species	Genetics	Origin
G. hirsutum	*allotetraploid*	*New World (Brazil & Mexico)*
G. barbadense	*allotetraploid*	*New World (Brazil)*
G. arboreum	*diploid*	*Old World (Arabia & Syria)*
G. herbaceum	*diploid*	*Old World (Africa)*

Cotton is susceptible to many pest species in addition to nematodes. Insect and arthropod pests are especially important, Ridgeway (1984) lists 46 such pests from 32 countries, with the majority of the losses being due to six species (three *Heliothis* sp., pink boll worm, boll weevil, and the Egyptian cotton leaf worm). Seedlings diseases, vascular wilts (*Fusarium* and *Verticillium*), bacterial

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blight and boll rots are among the most important diseases (Bell, 1984). Over 100 species of plants have been identified as weeds relative to cotton production (Chandler, 1984).

Cotton is a drought resistant crop by virtue of its long tap root which may reach depths of more than one metre (Prentice, 1972). Any damage to this tap root can severly restrict the uptake of water and nutrients, leading to loss of vigour in the rest of the plant. Plant parasitic nematodes can disrupt the meristematic zone, which may lead to the slowing down, or even complete cessation of tap root growth. Cotton is particularly prone to nematode attack because of the cultivation system to which it is commonly subjected. For some peasant farmers in marginal areas of Africa, cotton is the only cash crop which they can grow successfully, consequently it may be monocropped on the same land for many years. This cropping system inevitably results in the "selecting out" of one or two nematode species which are the best adapted parasites for the major crop. Therefore, nematode problems tend to be most severe in cotton grown under intensive and irrigated conditions. It is interesting to note that many nematode problems develop first in cotton plots on government research stations, usually in places where protracted field trials have been conducted!

Nematodes of Cotton

Numerous nematodes have been identified as parasites, or pathogens, of cotton. In this chapter we concentrate on those species which have been shown to suppress cotton growth or yield. Little attention will be devoted to those species for which cotton is a host (a species upon which the nematode can complete its life cycle) but which have not been proven to be pathogens (i.e., they are simply parasites). For other reviews of nematodes pathogenic or parasitic on cotton the reader is referred to Sasser (1972), Heald and Orr (1984), and Veech (1984). Unless otherwise noted we have used the general name of cotton to denote genotypes of *G. hirsutum;* generalized life cycles of the nematode pathogens of cotton are given elsewhere in this text.

Meloidogyne

Distribution

Two species of *Meloidogyne*, root-knot nematodes, are known to parasitize cotton, *M. incognita* and *M. acronea*. *M. incognita* has two races which attack cotton (races 3 and 4). These races have world wide distribution and are frequently associated with crops other than cotton. Taylor *et al.* (1982) reported that of 662 populations of root-knot nematodes from predominately subtropical and tropical regions 46.7% were *M. incognita*. Of these, 10.3% and 1.9% were race 3 and 4, respectively (or 4.8 and 0.9% of the total). Only 16% of these populations came from cotton fields. Taylor *et al.* (1982) estimates world wide cotton losses due to *M. incognita* as 3.1%. Orr and Robinson (1984) estimated yield losses due to *M. incognita* in the southern high plains of Texas to be 12%. If these losses were the only losses due to root-knot in the U.S.A. they would represent $25 million of the total U.S. crop. Taylor *et al.* (1984) observed a low positive correlation between sand content of soil and occurrence of root-knot, less than 4% of the populations came from soils with greater than 50% silt or 40% clay. Robinson *et al.* (1987) found that infestations of *Meloidogyne* spp. in Texas were correlated with soil type (coarser textured sandy soils) and that crop sequence had little effect. Populations of *M. incognita* are most frequent where mean annual temperatures are 24–30°C, with the peak occurrence at 28°C. *M. acronea* has, so far, been found only in two isolated areas of southern Africa; the lower Shire Valley of Malawi and Cape Province in South Africa. These areas both border the natural habitat for the wild precurser of cotton, *G. herbaceum* var. *africanum*, which extends from Botswana, through the northern Transvaal and the Save Valley of Zimbabwe to Mozambique. This is largely a neglected area, as far as nematology is concerned and it is possible that *M. acronea* is indigenous to this semi-arid region of southern Africa. In Malawi, infected cotton was stunted and chlorotic in clearly defined patches. Affected root systems were severely distorted;

the tap root was poorly developed and appeared to be "turned aside", while there was profuse proliferation of the secondary roots. Yield losses of 50% have been reported (Page, 1983).

Symptoms

As with most nematode diseases, foliar symptoms of root-knot nematodes on cotton are not diagnostic. The general symptoms of damage by *Meloidogyne* species include stunting, chlorosis, incipient wilting, and a general unthrifty appearence. Damage by *M. incognita* and *M. acronea* can be distinguished, however, based on differences in root symptoms. *M. incognita* attacks both the tap and lateral roots and, under heavy infections, causes a distinct galling of the roots. With more moderate, yet still damaging, levels of infection, the galling may be indistinct (Plate 15C, D).

Biology

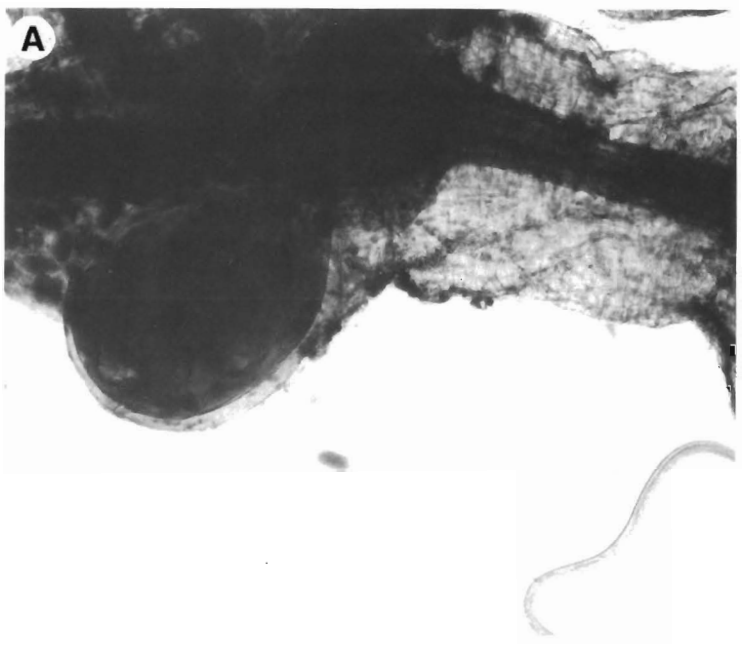
The biology of *M. acronea* in cotton is similar to that of *M. incognita* , except that the mature female is semi-endoparasitic, a feature that is thought to be connected with its almost entirely amphimictic mode of reproduction (Fig. 1A) (Page, 1983). Host reaction is markedly different from that stimulated by *M. incognita* ; there is an almost complete absence of root galling, further extension of the infected root ceases, while one or two root initials are produced adjacent to the nematode feeding site. These root intitials develop into laterals which provide new invasion sites for the next generation of infective juveniles. The so-called "turned-aside" tap root is actually a series of secondary and tertiary roots that have each taken over the function of the true tap root, as its normal downward growth has been checked by nematode invasion. This results in the root system being confined to the upper, drier layers of soil, where it is unable to absorb sufficient water or nutrients and gives rise to a plant that is stunted, wilted and chlorotic (Page, 1983).

When attempting to examine cotton roots to determine if root-knot nematodes are present, it is important that the roots are carefully dug from the ground rather than simply pulling up the plant. Pulling a plant from the ground will strip off most of the lateral roots, making if difficult to observe nematode symptoms. This is especially true for *M. acronea* because it mainly attacks the lateral roots (Fig. 1B).

Population dynamics

Given suitable soil type, favourable temperatures, and adequate soil moisture, the host will govern nematode population densities and dynamics. Cotton is a good host for *M. incognita* supporting populations as high as 10 000 eggs and juveniles/500 cm^3 (Starr & Veech, 1986). In situations with a single growing season devoted to a single crop, with an intervening period unfavourable for either host growth or nematode activity (e.g., cold winter temperatures or a prolonged drought season), populations of *M. incognita* are at a minimum at the beginning of the cropping season and at a maximum at crop maturity (Minton, 1964; Kraus-Schmidt & Lewis, 1979). Maximum population densities of *M. incognita* on cotton are governed in part by host genotype and by initial population densities (Pi). Starr and Veech (1986) reported that the Pf/Pi ratios were negatively correlated with Pi. Total populations can increase several hundred-fold in a single season on cotton if initial populations are low (10 eggs and J2/500cm^3). During the growing season the population exsits primarily as developing nematodes within the roots and as eggs within the eggmass (Barker *et al.* 1987). Therefore in assaying population densities it is important to utilize methods which will allow direct egg quantification (Barker *et al., 1987*), or allow the eggs to hatch (Rodrguez-Kabana & Pope, 1981).

The presence of other nematode species pathogenic on cotton can affect the population dynamics of *M. incognita.* Gay and Bird (1973) reported that *Pratylenchus brachyurus* suppressed population development of *M. incognita* on cotton in pot studies. Bird *et al.* (1974) and Kraus-Schmidt and Lewis (1981) reported that *M. incognita* could not compete with *Hoplolaimus columbus* on cotton in field situations, but that *H. columbus* would eventually replace root-knot as the dominant species in fields with concomitant populations. *M. incognita* populations are also suppressed by concomitant



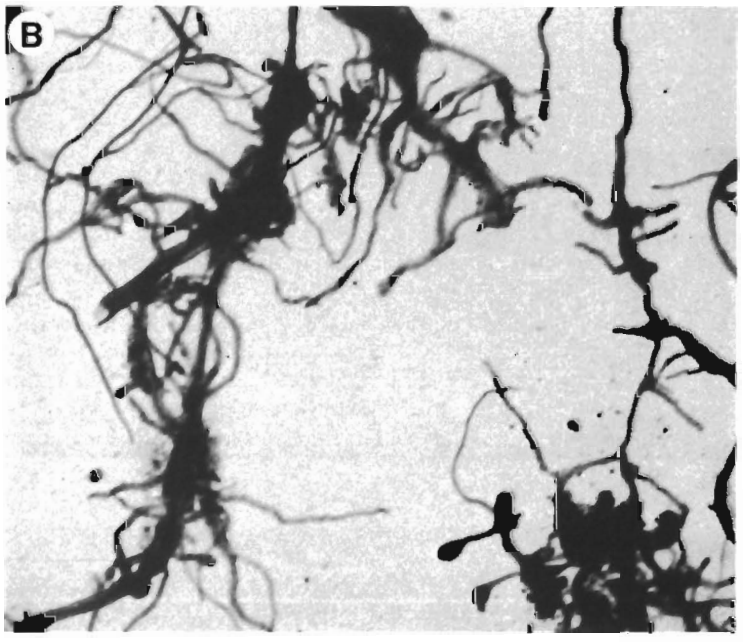


Fig. 1. *Meloidogyne acronea*. A. Female protruding from cotton root and male. B. Extensive production of secondary lateral cotton roots caused by feeding of *M. acronea* (Photo: J. Bridge).

populations of the vascular wilt pathogen *Fusarium oxysporum* f. sp. *vasinfectum* (Starr *et al.*, 1989). The Fusarium wilt/root-knot disease complex causes increased plant mortality which inhibits development of root-knot populations.

Survival

With regard to overseasoning of *M. incognita* populations, most studies have dealt with winter survival. Starr and Jeger (1985) reported that percent winter survival was negatively correlated with population densities in the autumn. Ferris (1985) observed a similar trend with respect to winter survival of *M. incognita* on tomato. Egg populations decline exponentially during winter survival due to egg hatch mortality. Viable eggs can be recovered as late as March in Texas (five months after crop harvest). Juvenile populations, on the other hand, increase initially as a result of egg hatch, then decline exponentially. By late spring J2 are the predominate part of the surviving population. Jeger and Starr (1985) have developed a simple model to quantify rates of egg hatch and J2 mortality during winter survival. *M. acronea* survives the 6–7 month long dry season of southern Africa as eggs within either the gelatinous matrix or the thickened body cuticle of the moribund female. The eggs are maintained in a viable but dormant condition only in soils in which the relative humidity does not fall below 97.7%. This could account for the limited distribution of this nematode within the Shire Valley, as it appears to be confined to alluvial soils with a high water-holding capacity (Page, 1984).

Damage thresholds

The relationship between population densities of *M. incognita* and growth and yield of cotton has been studied by several investigators. Roberts and Matthews (1985) and Starr and Veech (1986) reported a linear, negative correlation between log transformed Pi and seed cotton yields. Roberts and Matthews (1984) reported that yield suppression by the nematodes was not due to increased boll abscission, a common stress response in cotton, but was due to a decrease in plant height and number of fruiting positions. Nematode infection also altered patterns of dry weight accumulation with more dry weight being partitioned into the leaves and roots and less into the stem and fruits. Duncan and Ferris (1984) examined the relationship between nematode population densities and cotton yields in field plots using the Seinhorst model, they reported a tolerance value (T) of 27 eggs and J2/1000 g soil and a relative minimum yield value (M) of 0.66. Starr *et al.* (1989) reported values of T = 7.5–9.7 eggs and juveniles/100 cm3 soil and values of M = 0.11–0.23 from microplot studies. Both studies utilized sandy soils.

In comparing the two races of *M. incognita* which attack cotton Kirkpatrick and Sasser (1983) concluded that populations of race 3 were generally more aggressive than populations of race 4, based on reproduction of these populations on common cotton cultivars. Veech and Starr (1986), however, using regression analysis of the relationship between Pi and seed cotton yields, concluded that there was no difference between the populations of race 3 and 4 they tested. Nor was it possible to detect any difference between the two races with respect to rate of development or fecundity.

Disease complexes

In addition to crop damage directly attributable to nematode pathogenesis, *Meliodogyne* species are frequently involved in disease complexes involving other organisms. *M. incognita* on cotton is known to be involved in several disease complexes (Powell, 1971; Sikora & Carter, 1988; Webster, 1985). Among the most notable are the Fusarium wilt/root knot complex, and the seedling disease complexes involving *Pythium, Rhizoctonia, Fusarium,* and *Thielaviopsis* spp. *Meloidogyne incognita* can also increase the incidence of infection of cotton by *Verticillium dahliae* in pot studies (Khoury & Alcorn, 1973). There is little evidence, however, to suggest that these two pathogens interact to form a disease complex in field situations (Bazan de Segura & Aguilar, 1955; McCellan *et al.*, 1955). Little information is available on the effect of such disease complexes on the relationship of *M. incognita* population densities and growth or yield of cotton. Roberts *et al.* (1984) reported that in the presence

of *F. oxysporum* f. sp. *vasinfectum* the slope of the damage function was more negative, i.e., the damage caused by the nematode was greater in the presence of the wilt pathogen than in its absence. Starr *et al.* (1989) examined the effect of *F. o.* f. sp. *vasinfectum* on the relation between *M. incognita* and cotton growth in microplant studies. They found that at high nematode population densities (Pi > 10 eggs and J2/100cm^3) and intermediate *Fusarium* populations (ca. 10^3 colony-forming units/g soil), that both pathogens had significant effects on cotton mortality. Suppression of plant height and yield were due to primarily to the nematode and not *Fusarium*. When the yield responses were analysized by the Seinhorst model, no significant effect of *Fusarium* on the tolerance parameter (*T*) was observed but *Fusarium* did consistently reduce the relative minimum yield parameter (*M*). Population densities of each pathogen determined whether or not a significant interaction was observed. Very high densities of either pathogen could mask the effects or the input of the other. At low populations of either pathogen no interaction was detectable.

When *M. acronea* first discovered parasitizing cotton in the lower Shire Valley it was thought to be capable of forming tanned, cyst-like structures (Bridge *et al.*, 1976). This tanning process was later found to be under the influence of enzymes from the black root-rot fungus, *Thielaviopsis basicola*. This fungus secretes a polyphenol oxidase which converts certain polyphenolic compounds to melanin, a dark brown polymer. It is thought that during invasion by the *T. basicola* hypyhae benzoic acids present in the nematode are melanised, together with tannins in the host tissue, resulting in the cyst-like appearance of *M. acronea* females (Page, 1983).

Control tactics

Chemical

Control of root-knot nematodes on cotton in the USA has traditionally relied heavily on the use of nematicides. Orr and Robinson (1984), in a summary of 80 research plots over a 16 year period, reported average yield increases of 26% when infested fields were fumigated with either DBCP or EDB, with yield increases of threefold being observed in some fields. Although use of both of these nematicides has been banned in most countries, nonfumigant nematicides such as aldicarb or phenamiphos will also provide an acceptable but somewhat lower level of control of root-knot nematodes. Despite the apparent benefit which can be derived from the use of nematicides, they are not used in many cotton production areas. This may be due to several factors including the expected value of the crop versus production costs, lack of suitable financing systems for purchasing the nematicides, and lack of knowledge of the need or benefit of nematicide use.

Resistance

Resistance to *M. incognita* has been identified within the *G. hirsutum* germplasm (Jones *et al.*, 1988) and resistant cultivars (Shepherd, 1983) have been developed. However, such resistance is not in wide scale use, because these cultivars generally lack the yield potential and quality characteristics required by the industry today. The resistance in cultivar Auburn 623 provides greater control of *Meloidogyne* populations than does fumigation with DBCP (Shepherd, 1982).

In the USA, there have been several cotton cultivars released which are reported to be resistant to the Fusarium wilt/root-knot complex (Anon., 1987). However, at least some of these cultivars are highly susceptible to the nematode (Starr & Veech, 1986). These cultivars are resistant to *F. oxysporum* f. sp. *vasinfectum*. For other cultivars data supporting claims of resistance are lacking. In selected cases, the claims of nematode resistance are based on resistance to Fusarium wilt symptom development without direct evidence of nematode resistance (Kappleman & Bird, 1981). Shepherd (1982, 1986) has demonstrated that effective field resistance to Fusarium wilt can be achieved by resistance to *M. incognita,* however resistance to Fusarium wilt does not mean that the genotype is resistant to the nematode. Based on resistance germplasm known to exist and current breeding efforts, commercially acceptable cottons with high level of resistance to *M. incognita* should be available in the near future.

Crop rotation

Crop rotation is effective in reducing and maintaining low population densities of *M. incognita*. Barley and clean fallow will significantly reduce population densities after nine months (Carter & Nieto, 1975). Duncan and Ferris (1984) found a cotton/cowpea cropping system to be effective in managing *M. incognita* on cotton and *M. javanica* on cowpea. Kirkpatrick and Sasser (1984) reported that a cotton/groundnut cropping sequence was effective in managing *M. incognita,* but that a cotton/maize sequence was not. Highest yields and lowest root-knot gall indices were observed for cotton following two years of peanut, but even one year of peanut gave significant differences in yield and root-galling of cotton. As cotton is nonhost for the major root-knot species attacking peanut (*M. hapla* and *M. arenaria*) the cotton/peanut sequence should benefit both crops. The use of a resistant cotton cultivar (Auburn 623) in rotation with susceptible cultivars will increase seed cotton yields of the susceptible cultivars by suppression of nematode population densities (Shepherd, 1982).

Control of *M. acronea* should be based on rotation with crops such as pearl millet (*Pennisetum typhoides*), finger millet (*Eleusine coracana*) maize (*Zea mays*), groundnut (*Arachis hypogea*), guar bean (*Cyamopsis tetragonoloba*), or leucaena (*Leucaena glauca*) that are poor or non-hosts for *M. acronea*. There is no known resistance in cotton to this nematode (Page, 1983). Cotton hosts for *M. acronea* include *G. barbadense* var. *brasiliense, G. arboreum, G. herbaceum* var. *africanum,* and several cultivars of *G. hirsutum,* including Makoka 72, Auburn 623, and Clevewilt. The latter two cultivars are resistant to *M. incognita*. Other hosts are okra (*Hibiscus esculentus*) cvs West African, pigeon pea (*Cajanus cajan*) tomato (*Lycopersicon esculentum*) cv Harvester and Moneymaker, sorghum (*Sorghum vulgare*) cvs Thengalamanga, Lindse 555 and Gonkho.

Biological control

Cotton roots containing vesicles of vesicular-arbuscule endomycorrhizal fungi, showed increased resistance to *M. acronea*. Unfortunately these vesicles did not develop until the cotton plants were at least eight weeks old and although it would be possible to ratoon this crop to preserve the beneficial mycorrhizal relationship, this practice is not advisable due to the possiblity of encouraging the survival of other serious pests (Page, 1983).

Pasteuria penetrans has been found to be an effective biocontrol agent for all stages of *M. acronea* and *M. incognita* under experimental conditions, but this obligate nematode parasite is unlikely to be of practical use for cotton production systems, due to its requirement for high soil moisture content for passive dispersal in the field (Page & Bridge, 1985). Biocontrol systems as reliable as host resistance or crop rotation for control of root knot are not yet available.

Rotylenchulus

Distribution and symptoms

Two species of *Rotylenchulus* the reniform nematode are pathogenic on cotton. *R. reniformis* (Fig. 2), with a host range of 115 plant species, is distributed throughout the subtropical and tropical regions of the world (Heald & Thames, 1984). *R. parvus* is reported only from Africa. Although both species are considered to be tropical species, one population of *R. reniformis* has survived for more than five years in northern Texas, where soils are subjected to subzero temperatures annually (Orr, pers. comm.). Unlike *M. incognita, R. reniformis* is favoured by fine textured soils with a relativity high content of silt and (or) clay (Robinson *et al.*, 1987). Yield losses due to *R. reniformis* as high as 40–60% have been documented (Birchfield & Jones, 1961) in heavily infested fields. Symptoms of reniform nematode damage include dwarfing, premature decay and loss of secondary roots, and plant mortality. Yield suppression due to the nematodes is not accompanied by a reduction in fibre quality (Jones *et al.*, 1959).

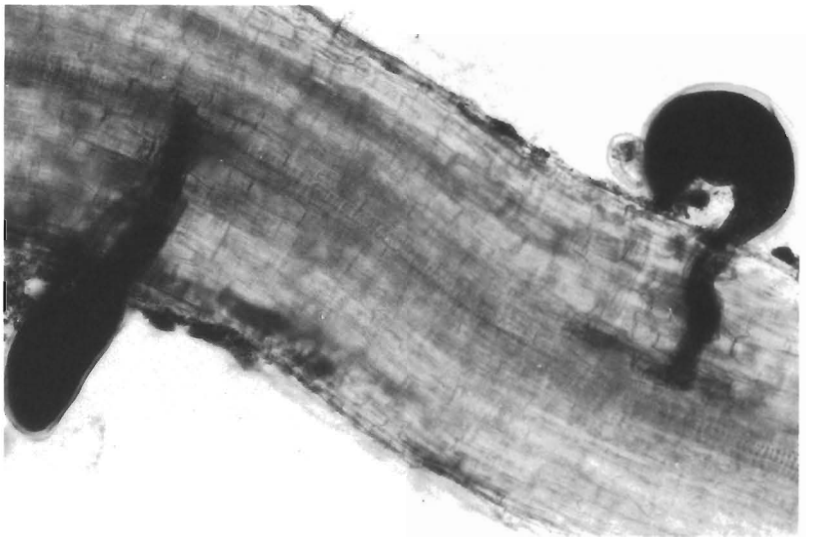


Fig. 2. *Rotylenchulus reniformis* semi-endoparasitic females on cotton root (Photo: J. Bridge).

Population dynamics and damage thresholds

In general, populations of *R. reniformis* are at a minimum in the late spring and during the first 45 days of the cropping season, and a maximum in the autumn as the cotton crop nears maturity (Bird *et al.*, 1973) with soil populations as high as 49 000/100 g soil being detected (Jones *et al.*, 1959). Thames and Heald (1974) reported Pf/Pi values of 16.7 in nematicide treated plots with the population peak occurring 5.3 months after planting. The population density peaked at 2.5 months after planting in the untreated control plots. Brathwaite (1974) reported that population densities of *R. reniformis* declined by 86% and 75% under the non-host maize and fallow, respectively.

Precise damage function studies with *R. reniformis* on cotton have not been reported. Sud *et al.* (1984) examined the relationship between nematode population densities and growth responses of cotton in pot tests. Using the Seinhorst model, they reported a tolerance value of $T = 16$ nematodes/200 cm^3 soil with a relative minimum yield value of $M = 0.5$ for shoot growth. With respect to root growth responses to *R. reniformis*, $T = 2$ nematodes/200 cm^3 soil with $M = 0.5$. In field trials, Thames and Heald (1974) observed a significant cotton yield response to nematicide treatment when Pi was 100 nematodes/100 g of a loamy sand soil, but not when Pi was 6–40 nematodes/100 g soil. Gilman *et al.* (1978) reported a significant yield response to fumigation of a silt loam soil when Pi was greater then 240 nematodes/ 100 cm^3 soil. Palanisamy and Balasubramanian (1983) reported significant yield losses in clay loam soil when Pi were 115–135 nematodes/100 g soil. Collectively, these data suggest a tolerance value of 100 nematodes /100 g soil.

Disease complexes

The reniform nematode forms a disease complex with both *Fusarium oxysporum* f. sp. *vasinfectum* and *Verticillium dahlia*. Prasad and Padeganur (1980) reported substantially higher nematode populations associated with *Verticillium*-wilted plants (925–2000 nematodes/100 cm^3) than associated with fields not exhibiting wilt symptoms (225–565 nematodes/100 cm^3). Tchatchaua and Sikora (1983) reported that plants exposed to both pathogens did not exhibit an increase in wilt symptoms, but there was a significant interaction with respect to suppression of shoot growth in pot tests. The Fusarium-wilt reniform nematode disease complex has been observed on both *G. hirsutum* (Neal,

1954) and *G. barbadense* (Khadr *et al.*, 1972). *R. reniformis* also increases the incidence and severity of seedling disease on cotton (Brodie & Cooper, 1964). As with *M.incognita*, the effects of nematode infection on plant maturity are believed to increase cotton susceptibility to the numerous seedling pathogens (Brodie & Cooper, 1964).

Control tactics

In fields where the Pi exceeds the tolerance level, application of fumigant nematicides will result in significant yield increases (Thames & Heald, 1974; Palanisamy & Balasubramanian, 1983; Gilman *et al.*, 1978). Use of nematicides for control of the reniform nematode, however, is not widespread.

Resistance to *R. reniformis* has been identified in several *Gossypium* species. Yik and Birchfield (1984) reported high levels of resistance within *G. stocksii, G. somalense, and G. barbadense,* while moderate resistance, with nematode reproduction at 20% of the susceptible check, was identified within *G. arboreum* and *G. herbaceum*. They also found one primitive line of *G. hirsutum* from Haiti to be resistant to *R. reniformis*. Beasley and Jones (1985) reported that several "Texas race stocks" of *G. hirsutum* were resistant to *R. reniformis,* supporting nematode reproduction which was only 24–50% of the susceptible check. Jones *et al.* (1988) released several germplasm lines of *G. hirsutum* with resistance to both *R. reniformis* and *M. incognita*. With appropriate effort it should be possible to develop locally adapted, commercially acceptable cotton cultivars with useful levels of resistance to both of these nematode pathogens.

Crop rotation has been reported to be effective in suppressing population densities of *R. reniformis,* despite the nematodes wide host range, and in reducing cotton yield losses. Thames and Heald (1974) reported grain sorghum to be a good rotation crop and Brathwaite (1974) recommended maize. Gilman *et al.* (1978) showed that population densities of reniform nematodes were lower and cotton yields were higher following two years of reniform resistant soybean than after one year.

Pratylenchus

Pratylenchus brachyurus has long been considered a pathogen of cotton in the southeastern region of the USA, however data supporting this belief are contradictory. Smith (1950) reported that the distribution of a *Pratylenchus* sp. was closely correlated with the incidence of Fusarium wilt but gave no data to support any effect of the nematode on cotton growth. In 1951, Graham reported *P. brachyurus* to be the causal agent of a root-rot of several crops, including cotton. Population densities of the nematode in this study were seldom greater than 30 nematodes/g root: such a population level being lower than usually required to cause plant damage. Bird *et al.* (1971) implicated *P. brachyurus* in the cotton stunt disease syndrome, but, although they found cotton to be a good host, no definitive evidence of pathogenicity by *P. brachyurus* was presented. Hussey and Roncadori (1978) examined the interrelationship of *P. brachyurus,* the mycorrhizal fungus *Gigaspora margarita,* and cotton growth in pot tests. They found cotton to be a good host for the nematode with population densities increasing from 5000/plant to 30 000/plant over a 77-day period, but did not observe any effect of the nematodes on plant growth, or interaction with the mycorrhizal fungus. Two seperate studies provide data that cotton is not a good host for *P. brachyurus*. Johnson *et al.* (1974) observed little or no increase in the densities of a mixed population of *P. brachyurus* and *P. zeae* over four seasons in a field planted solely to cotton. Similarly, Starr and Mathieson (1984) reported that cotton was a poor host for *P. brachyurus* in pot or microplot tests, with a maximum Pf/Pi ratio of 1.5. They did observe suppression of root growth at high Pi levels, 10 000 nematodes/plant.

The apparent confusion with regard to *P. brachyurus* as a pathogen of cotton may be due to a number of factors, including differing susceptibility of cotton genotypes and (or) differences in aggressiveness among *Pratylenchus* populations. It is possible that the nematode is important only as part of a disease complex such as the cotton stunt syndrome or with Fusarium wilt.

In the Sudan, Yassin (1974) reported that *P. sudanensis* increased the amount of Fusarium wilt observed on cultivars of *G. barbadense* but did not affect wilt on cultivars of *G. hirsutum*. In these

studies the nematode populations remained relatively low at 26–69/200g soil and 1 g root. Soil treatment with fumigant or nonfumigant nematicides increased *G. barbadense* yields by 56–88% (Yassin, 1980). *P. sudanensis* has not been reported from other cotton regions.

Belonolaimus longicaudatus

Distribution and survival

The sting nematode, *Belonolaimus longicaudatus*, is an aggressive pathogen of cotton and is distributed with low frequency of occurrence throughout the coastal plain of the southeastern USA. The nematode is restricted to soils with greater than 85% sand content (Robbins & Barker, 1974). Soil temperatures, in addition to soil textural class, affect the survival of *B. longicaudatus*. In July, when temperatures are high in Florida, Boyd and Perry (1971) found that sting nematode populations were higher at the 15–30 cm depth than at the 0–15 cm depth. Populations generally exhibit a marked decline during the winter months, with less than 10% of the population surviving from autumn until spring.

Symptoms

Heavy infestations of the sting nematode result in a stunted, chlorotic growth habit for cotton. Infected plants may exhibit premature wilting and senescence. *B. longicaudatus* feeds ectoparasitically at the root tips and in the cortical regions, resulting in poorly developed root systems. Graham and Holdeman (1953) observed that cotton roots attacked by the nematode were severely damaged and ultimately destroyed. In the early stages of attack, dark, sunken lesions could be seen along the root axis. These lesions may spread laterally to girdle the root and cause it to break off, or advance longitudinally with the root remaining intact. Abu-Garbieh and Perry (1970) demonstrated the existence of three physiological races of *B. longicaudatus* based on differences in host range populations from Florida. Robbins and Barker (1974) showed that populations from North Carolina were generally smaller, adapted to cooler temperatures, and unable to reproduce on cucumber (*Cucumis sativus*) relative to populations from Georgia.

Control tactics

Control of *B. longicaudatus* on cotton has been accomplished primarily through the use of nematicide treatments (Johnson, 1970) and by crop rotation. The nematode has a wide host range that includes the grain crops barley (*Hordeum vulgare*), oats (*Avena sativa*), maize (*Zea mays*), and pearl millet (*Pennisetum americanum*)(Orton Williams, 1974). Vegetable hosts include bean (*Phaseolus vulgaris*), cabbage (*Brassica oleracea* var. capita), cowpea (*Vigna unguiculata*), potato (*Solanum tuberosum*). Groundnut (*Arachis hypogaea*) and soyabean (*Glycine max*) are also hosts for the sting nematode. Tobacco (*Nicotiana tabacum*) is a nonhost for *B. longicaudatus* and has been used as a rotation crop to control sting nematodes (Holdeman & Graham, 1953). *Crotalaria spectabilis* and *Tagetes minuta* give excellent control of sting nematode populations when used as cover crops in infested fields (Good *et al.*, 1965). Tomerlin (1969) found that the numbers of sting nematodes were reduced in soils amended with alfalfa meal, cottonseed meal, or rice straw.

Hoplolaimus

Four lance nematodes (*Hoplolaimus* spp.) are considered to be pathogens of cotton: *H. aegypti, H. columbus, H. indicus, and H. seinhorsti* (Fig. 3) (Shafie & Koura, 1969; Lewis & Smith, 1976; Guar & Mishra, 1981). All species exhibit both endoparasitic and ectoparasitic feeding habits, feeding mostly in the cortical regions (Luc, 1958; Lewis *et al.*, 1976). *H. columbus* is reported from the southern USA (Plate 15E) and the Giza Experiment Station in Egypt (Fassuliotis *et al.*, 1968; Koura

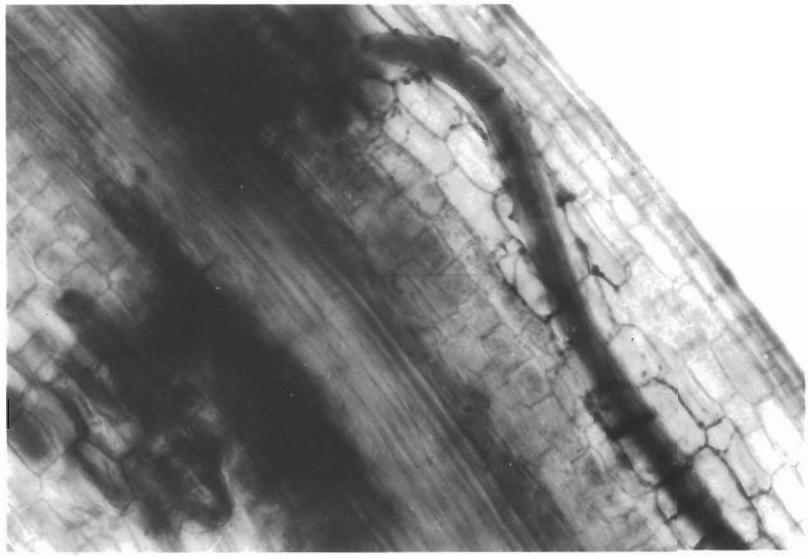


Fig. 3. *Hoplolaimus seinhorsti* endoparasitic in the cortex of cotton root causing cell damage and necrosis (Photo: J. Bridge).

& Osman, 1984). *H. seinhorsti* is widely distributed, having been reported from numerous different crops from Africa, Asia, India, and South America (van den Berg, 1976). Hussey (1977) reported control of lance nematode in the southern USA by nematicide treatments and (or) subsoiling to a depth of 35 cm. Subsoiling resulted in deeper soil penetration by the cotton roots.

Xiphinema and *Longidorus*

A new species of *Xiphinema*, the dagger nematode, was recently found associated with severly stunted cotton in the Middle Save Valley of Zimbabwe (Page, unpubl.). Death of some cotton plants had occurred in large areas of the field (Plate 15F), surviving plants were only 10–15 cm tall two months after planting. Tap roots of affected plants were less than 10 cm long and terminated in a lobed gall. Lateral roots also had terminal gall. The affected field had been planted to irrigated cotton in rotation with wheat for more than 20 years. The wheat crops exhibited a similar stunted growth habit. High population densities of *Xiphinema sp.* (2500/dm^3 soil), along with high populations of *Longidorus* sp. (4000/dm^3), were found associated with stunted cotton near Sande in the lower Shire Valley of Malawi (Bridge & Page, 1975).

Jute

Nematodes of Jute

Two species of jute, *Corchorus capsularis* and *C. olitorius*, are grown mainly as commercial fibre crops although the latter can be used as a vegetable. The most important nematode pathogens of jute are probably the root-knot species *M. incognita, M. javanica,* and *M. arenaria*. They have been reported on jute from Brazil (Silva *et al.*, 1977; Ponte & Santos, 1981), Pakistan (Maqbool *et al.*, 1985), West Africa (Germani & Delattre, 1981), and India (Mishra & Singh, 1985). Other nematodes frequently found in association with jute and of possible importance in India are *Hoplolaimus*

indicus, Helicotylenchus spp., and *Rotylenchulus reniformis* (Laha *et al.*, 1988; Mishra *et al.*, 1985). Nematodes are also described as pests of jute in China (Gu & Chen, 1985).

Meloidogyne spp. produce large galls on roots of infected jute causing a reduction in growth if nematode populations are great enough. *Hoplolaimus indicus* and *Helicotylenchus digonicus* feed endoparasitically in the root cortex of jute. General symptoms of nematode damage are stunting, yellowing, and wilting.

Disease complexes

M. incognita but not *Rhizoctonia bataticola* (= *Macrophomina phaseolina*) reduces the height and weight of jute in the presence of both pathogens, whereas the fungus causes a root-rot. Plant mortality is increased significantly by both pathogens together, but is not affected by either alone (Mishra *et al.*, 1988). Both *M. incognita* and *Hoplolaimus indicus* form a disease complex with *Macrophomina phaseolina* on jute (Haque & Mukhopadhyaya, 1979).

Economic importance and control

Root-knot nematodes are considered to be important and damaging pathogens of the crop in jute growing areas of India (Saikia & Phukan, 1986; Mishra *et al.*, 1987). Experiments in microplots and pots have determined that *M. javanica* can cause significant reduction in fibre yield at initial populations of 1000 J2 per plant (Mishra & Singh, 1985) and *M. incognita* can reduce fibre yields by 50% at initial populations of 2000 J2 per plant (Saikia & Phukan,1986).

Numerous pot and small plot studies suggest that several methods might be used to reduce nematode damage to jute. An integrated control system suggested for root-knot in India is a combination of cultural practices and application of organic waste over a two year period (Mishra *et al.*, 1987). Weeding and removal of jute stubble combined with rotation to paddy rice, followed by a crop of wheat, increased yields of jute in these experiments. Crop rotations involving combinations of fallow, mustard, gourd, and wheat were effective in reducing populations of *M. incognita* (Saikia & Phakan, 1986). Organic soil amendments increased jute growth and reduced population densities of *M. incognita,* however, fumigant nematicides were more effective (Bora & Phukan, 1983; Roy, 1983). Moderate resistance to *M. javanica* has been reported in a study of a limited number of jute cultivars (Srivastava *et al.*, 1974).

Kenaf and Roselle

Nematodes

Kenaf (*Hibiscus cannabinus* L.) and roselle (*H. sabdariffa* L.) are fibre crops which are widely grown in the tropics. One or more *Meloidogyne* spp. have been reported as pathogens of both crops, but no other nematode species have been reported to damage these crops.

Kenaf is generally susceptible to *M. arenaria, M. javanica,* and *M. incognita,* whereas roselle has some resistance to *M. javanica* and *M. incognita* but is highly susceptible to *M. arenaria* (Minton *et al.*, 1970). Summers and Seale (1958) reported increased rates of kenaf seedling death in fields with high populations of *M. incognita*; surviving plants were stunted and yielded less dry matter then did non-infected plants. Both kenaf and roselle develop large root galls when infected by the root-knot nematodes. McSorley and Parrado (1986) were able to relate amount of root galling to the growth of kenaf (height) in fields infested with *M. incognita* using the Seinhorst model. They obtained a tolerance value of 8 galls or egg masses per plant at two months after planting in a fine sandy loam soil. Tu and Cheng (1971) reported the development of a root disease complex when kenaf was exposed to both *M. javanica* and *Macrophomina phaseolina*.

Control

Both fumigant and nonfumigant nematicides will protect kenaf from root-knot nematode damage. Minton and Adamson (1979) increased kenaf yields by as much as 440% with ethylene dibromide or dibromochloropropene. Aldicarb reduces root galling but did not give a significant increase in plant height (Addoh & Amanquah, 1968). Several studies have shown the presence of resistance to *M. javanica* and *M. incognita (Summers et al.,* 1958; Adeniji, 1970; Adamson *et al.,* 1974). Roselle lines with resistance to all three *Meloidogyne* spp. have been reported (Adeniji, 1970; Minton *et al.*,1970; Minton & Adamson, 1979). Minton and Adamson (1979) found resistance to be equally effective as nematicides in controlling damage by root-knot nematodes. Some roselle lines which are resistant to root galling symptoms did support significant levels of reproduction of *M. javanica* and *M. incognita,* although at lower levels than a susceptible line of kenaf (Adamson *et al.,* 1975).

References

Abu-Garbieh, W. I., & Perry, V. G. (1970). Host differences among Florida populations of *Belonolaimus longicaudatus,* Rau. *Journal of Nematology,* 2:209–216.

Adamson, W. C., Stone, E. Q., & Minton, N. A. (1974). Field resistance to the javanese root-knot nematode in kenaf. *Crop Science,* 14:334–335.

Adamson, W. C., Martin, J. A., & Minton, N. A., (1975). Rotation of kenaf and roselle on land infested with root-knot nematodes. *Plant Disease Reporter,* 59:130–132.

Adeniji, M. O. (1970). Reaction of kenaf and roselle varieties to the root-knot nematodes in Nigeria. *Plant Disease Reporter,* 54:547–549.

Addoh, P. G., & Amanquah, S. Y. (1968). The effectiveness of Temik, a systemic pesticide, for controlling root-knot nematodes and its influence on the growth and seed yield of kenaf, *Hibiscus cannabinus* L. *Ghana Journal of Agricultural Science,* 1:55–57.

Anonymous. (1987). Cotton production. In: *Southwest Agricultural Digest.* Clarksdale, USA Farm Press Publications: 18–60.

Barker, K. R., Starr, J. L. & Schmitt, D. P. (1987). Usefulness of egg assays in nematode population density determinations. *Journal of Nematology*19:130–134.

Bazan de Segura, C., & P. Anguilar F. (1955). Nematodes and root rot diseases of Peruvian cotton. *Plant Disease Reporter,* 39:12.

Beasly, J. P., & Jones, J. E. (1985). The current status of the development of resistance to the reniform nematode in cotton in Louisiana. *45th Cotton Disease Council, Proceedings Beltwide Cotton Production Research Conference, National Cotton Council. Memphis, Tn:* 23–45.

Bell, A. A. (1984). Cotton protection practices in the USA and world. Section B: Diseases. In: R. J. Kohel and C. F. Lewis (Eds.) *Cotton.* Agronomy Monograph no. 24, ASA-CSSA-SSSA, Madison, WI: 288–309.

Birchfield, W., & Jones, J. E. (1961). Distribution of the reniform nematode in relation to crop failure of cotton in Louisiana. *Plant Disease Reporter,* 45:671–673.

Bird, G. W., Brooks, O. L., & Perry, C. E. (1974). Dynamics of concomitant field populations of *Hoplolaimus columbus* and *Meloidogyne incognita. Journal of Nematology,* 6:190–194.

Bird, G. W., Crawford, J. L., & McGlohon, N. W. (1973). Distribution frequency of occurrence and population dynamics of *Rotylenchulus reniformis* in Georgia. *Plant Disease Reporter,* 57:399–401.

Bird, G. W., McCarter, S. M., & Roncadori, R. W. (1971). Role of nematodes and soil-borne fungi in cotton stunt. *Journal of Nematology,* 3:17–22.

Bora, B. C., & Phukan, P. N. (1983). Organic amendments for the control of root-knot nematode on jute. *Journal of Research, Assam Agricultural University,* 4:50–54.

Boyd, F. T., & Perry, V. G. (1971). Effects of seasonal temperatures and certain cultural treatments on sting nematodes in forage grass. *Proceedings of Soil and Crop Science Society of Florida, 30:360–365.*

Brathwaite, C. W. D. (1974). Effect of crop sequence on populations of *Rotylenchulus reniformis* in fumigated and untreated soil. *Plant Disease Reporter,* 58:259–261.

Bridge, J., & Page, S. L. J. (1975). Plant parasitic nematodes associated with cotton in the lower Shire Valley and other cotton growing regions of Malawi. *United Kingdom Overseas Development Administration Technical Report, 40p.*

Bridge, J., Jones, E., & Page, S.L. J. (1976). *Meloidogyne acronea* associated with reduced growth of cotton in Malawi. *Plant Disease Reporter, 60:5–7.*

Brodie, B. B., & Cooper, W. E. (1964). Relation of parasitic nematodes to post-emergence damping-off of cotton. *Phytopathology, 54:1023–1027.*

Carter, W. W., & Nieto, S. (1975). Population development of *Meloidogyne incognita* as influenced by crop rotation and fallow. *Plant Disease Reporter*, 59:404–403.

Chandler, J. M. (1984). Cotton protection practices in the USA and world. Section E: Weed Control. In: Kohel, R. J. & Lewis, C. F. (Eds.). *Cotton.* Agronomy Monograph no. 24, ASA-CSSA-SSA, Madison, WI:330–365.

Duncan, L. W., & Ferris, H. (1984). Effects of *Meloidogyne incognita* on cotton and cowpeas in rotation. *43rd Cotton Disease Council, Proceedings Beltwide Cotton Production Research Conference, National Cotton Council. Memphis, Tn.* :22–26.

Fassuliotis, G., Rau, G. J., & Smith, F. M. (1968). *Hoplolaimus columbus,* a nematode parasite associated with cotton and soybeans in South Carolina. *Plant Disease Reporter*, 52:571–572.

Ferris, H. (1985). Density-dependent nematode seasonal multiplication rates and overwinter survivorship: A critical point model. *Journal of Nematology*, 17:93–100.

Gay, C. M., & Bird, G. W. (1973). Influence of concomitant *Pratylenchus brachyurus* and *Meloidogyne* spp. on root penetration and population dynamics. *Journal of Nematology*, 5:212–217.

Germani, G. & Delattre, R. (1981). Les nématodes phytoparasites la cotonnier et des plantes a fibres jutieres. Observations et expérimentation au Béin. *Coton et Fibres tropicales*, 36:319–333.

Gilman, D. F., Jones, J. E., Williams, C. & Birchfield, W. (1978). Cotton-soybean rotation for control of reniform nematodes. *Louisiana Agriculture*, 21:10–11.

Good, J. M., Minton, N. A., & Jaworski, C. A. (1965). Relative susceptibility of selected cover crops and coastal bermudagrass to plant nematodes. *Phytopathology*, 55:1026–1030.

Graham, T. W. (1951). Nematode root rot of tobacco and other plants. South Carolina Agriculture Experiment Station Bulletin 390.

Graham, T. W., & Holdeman, Q. L. (1953). The sting nematode, *Belonolaimus gracilis* Steiner: a parasite on cotton and other crops in South Carolina. *Phytopathology*, 43:434–439.

Gu, Q. F., & Ehen, Z. Y. (1985). [An analysis of yield potential of jute and kenaf under the microclimatical conditions given by sprinkler irrigation during the drought seasons.] *China's Fibre Crops*, 3:7–11.

Guar, H. S., & Mishra, S. D. (1981). Pathogenicity of the lance nematode, *Hoplolaimus indicus* to cotton, *Gossypium hirsutum. Indian Journal of Nematology*, 11:87–88.

Haque, S., & Mukhaopadhyaya, M. C. (1979). Pathogenicity of *Macrophomina phaseoli* on jute in the presence of *Meloidogyne incognita* and *Hoplolaimus indicus. Journal of Nematology*, 11:318–321.

Heald, C. M., and Orr, C. C. (1984). Nematode parasites of cotton. In: Nickle, W. R. (Ed.). *Plant and Insect Nematodes,* M. Dekker, New York: 147–166.

Heald, C. M. & Thames, W. H. (1982).The reniform nematode, *Rotylenchulus reniformis. Nematology in the Southern Region of the United States.* USDA-CSRS Southern Cooperative Series, Bulletin 276:139–143.

Hussey, R. S. (1977). Effects of subsoiling and nematicides on *Hoplolaimus columbus* populations and cotton yield. *Journal of Nematology*, 9:83–86.

Hussey, R. S., & Roncadori, R. W. (1978). Interaction of *Pratylenchus brachyurus* and *Gigaspora margarita* on cotton. *Journal of Nematology*, 10:16–20.

Hutchinson, J. B., Silow, R. A., & Stephens, S. G. (1947). *The evolution of Gossypium and the differentiation of the cultivated cottons.* London: Oxford University Press, 160p.

Hutchinson, J. B. (1962). The history and relationships of the worlds cottons. *Endeavor*, 21:5–15.

Jeger, M. J., & Starr, J. L. (1985). A theoretical model of winter survival dynamics of *Meloidogyne* spp. eggs and juveniles. *Journal of Nematology*, 17:256–260.

Johnson, A. W. (1970). Cotton (Coker 413–67):Sting nematodes (*Belonolaimus longicaudatus*). *Fungicide and Nematicide,* 25:135–136.

Johnson, A. W., Dowler C. C., & Hauser, E. W. (1974). Seasonal dynamics of selected plant-parasitic nematodes on four moncultured crops. *Journal of Nematology*, 6:187–190.

Jones, J. E., Beasly, J. P., Dickson, J. I. & Caldwell, W. D. (1988). Registration of four cotton germplasm lines with resistance to reniform and root-knot nematodes. *Crop Science*, 28:199–200.

Jones, J. E., Newsom, L. D. & Finley, E. L. (1959). Effect of the reniform nematode on yield, plant characters, and fiber qualities of upland cotton. *Agronomy Journal*, 51:353–356.

Kappelman, A. J., Jr., & Bird, L. S. (1981). Indirect selection for resistance to the Fusarium wilt-root-knot nematode complex in cotton. *Crop Science*, 21:66–68.

Khadr, A. S., Salem, A. A., & Oteifa, B. A. (1972). Varietal susceptibility and significance of the reniform nematode, *Rotylenchulus reniformis,* in Fusarium wilt of cotton. *Plant Disease Reporter*, 56:1040–1042.

Khoury, F. Y., & Alcorn, S. M.(1973). Effect of *Meloidogyne incognita acrita* on the susceptibility of cotton plants to *Verticillium albo-atrum. Phytopathology*, 63:485–490.

Kirkpatrick, T. L., & Sasser, J. N. (1983), Parasitic variability of *Meloidogyne incognita* populations on susceptible and resistant cotton. *Journal of Nematology*, 14:302–307.

Kirkpatrick, T. L., & Sasser, J. N. (1984).Crop rotation and races of *Meloidogyne incognita* in cotton root-knot management. *Journal of Nematology*, 16:323–328.

Koura, F. H. & Osman, H. A. (1984). The relation between population density of *Hoplolaimus* and damage to cotton and soybean. *Annals Agriculture and Science, Faculty of Agriculture, Ain-Shams University, Cairo, Egypt.*, 29:521–529.

Koura, F. H. (1984). Reaction of Egyptian cotton cultivars to *Hoplolaimus aegypti* infection. *Annals Agriculture and Science, Faculty of Agriculture, Ain-Sahms University, Cairo, Egypt.*, 29:513–519.

Kraus-Schmidt, H., & Lewis, S. A. (1979). Seasonal fluctuations of various nematode populations in cotton fields in South Carolina. *Plant Disease Reporter*, 63:859–863.

Kraus-Schmidt, H., & Lewis, S. A. (1981). Dynamics of concomitant populations of *Hoplolaimus columbus, Scutellonema brachyurum,* and *Meloidogyne incognita* on cotton. *Journal of Nematology*, 13:41–48.

Laha, S. K., & Pradhan, S. K. (1987). Susceptibility of bast fibre crop to *Meloidogyne incognita. Nematologia mediterranea*, 15:163–164.

Lee, J. A. (1984), Cotton as a world crop. In: R. J.Kohel & Lewis, C. F. (Eds). *Cotton.*Agronomy Monograph no. 24, ASA-CSSA-SSSA, Madison, WI: 1–25.

Lewis, S. A., Smith, F. M. & Powell, W. M. (1976), Host-parasite relations of *Hoplolaimus columbus* on cotton soybean. *Journal of Nematology*, 8:141–145.

Lewis, S. A. & Smith, F.H. (1976), Host-plants, distribution and ecological associations of *Hoplolaimus columbus. Journal of Nematology*, 8:264–269.

Luc, M. (1958), Les nématodes et le flétrissement des cotonniers dans le Sud-Ouest de Madagascar. *Coton et Fibres tropicales*, 13:239–256.

Maqbool, M. A., Hashmi, S., & Ghaffar, A. (1985). New host records of root-knot nematodes *Meloidogyne* spp. in Pakistan and identification of physiological races. *Pakistan Journal of Nematology*, 3:49–52.

McClellan, W. D., Wilhelm, S. & George, A. (1955), Incidence of Verticillium wilt in cotton not affected by root-knot nematodes. *Plant Disease Reporter*, 39:226–227.

McSorley, R. & Parrado, J. L. (1986). Relationship between height of kenaf and root galling by *Meloidogyne incognita. Nematropica*, 16:205–211.

Minton, E. B. (1964), Population dynamics of 7 nematode species under 10 cotton selects. *Phytopathology*, 54:625. (Abstr)

Minton, N. A., Adamson, W. C. & White, G. A. (1970). Reaction of kenaf and roselle to three root-knot nematode species. *Phytopathology,* 60:1844–1845.

Minton, N. A. & Adamson, W. C. (1979), Control of *Meloidogyne javanica* and *M. arenaria* on kenaf and roselle with genetic resistance and nematicides. *Journal of Nematology, 11:37–41.*

Mishra, C., Singh, B. & Chakrabarati, N. K. (1985). Host-parasite relationship of some nematode pests with jute (*Corchorus capsularis* and *C. olitorus*). *Annals of Agricultural Research*, 6:162–167.

Mishra, C. & Singh, B. (1985). Pathogenicity of root-knot nematode *Meloidogyne javanica* (Treub) Chitwood on jute, *Corchorus* spp. *Indian Journal of Nematology*, 15:245–246.

Mishra, C. Singh, B. & Laha, S. K. (1987), Integrated approach for root-knot nematode management in jute. *Indian Journal of Nematology*, 17:285–287.

Mishra, C., Som, D. & Singh, B. (1988). Interaction of *Meloidogyne incognita* and *Rhizoctonia bataticola* in white jute (*Corchorus capsularis*). *Indian Journal of Agricultural Sciences*, 58:234–235.

Neal, C. D. (1954). The reniform nematode and its relationship to the incidence of Fusarium wilt of cotton at Baton Rouge, Louisiana. *Phytopathology*, 44:447–450.

Orr, C. C. & Robinson, A. F. (1984). Assessment of cotton losses in Western Texas caused by *Meloidogyne incognita. Plant Disease*, 68:284–285.

Orton Williams, K. J. (1974). *Belonolaimus longicaudatus.* C.I.H. Descriptions of Plant Parasitic Nematodes. Set 3, No. 40.

Page, S. L. J. (1983). *Biological studies of the African cotton root nematode* Meloidogyne acronea, Ph. D. Thesis. London University, 294 p.

Page, S. L. J. (1984), Effects of the physical properties of two tropical soils on their permanent wilting point and relative humidity, in relation to survival and distribution of *Meloidogyne acronea. Revue de Nématologie,* 7:227–232.

Page, S. L. J. (1985) *Meloidogyne acronea.* C.I.H. Description of Plant-Parasitic Nematodes. Set 8, No. 114., 3p.

Page, S. L. J. & Bridge, J. (1985). Observations on *Pasteuria penetrans* as a parasite of *Meloidogyne acronea. Nematologica,* 31:238–240.

Palanisamy, S., and Balasubramanian. (1983). Assessment of avoidable yield loss in cotton (*Gossypium barbadense* L.) by fumigation with metham sodium. *Nematologia mediterranea*, 11:201–201.

da Ponte, J. J. & Santos, C. D. G. (1981). Novos hospedeiros de nematoides da galhas assinaldos no nordeste do Brazil. *Fitossanidade,* 1981:39–40.

Powell, N. T. (1971). Interactions between nematodes and fungi in disease complexes. *Annual Review of Phytopathology*, 9:253–274.

Prasad, K. S. & Padeganur, G. M. (1980). Observations on the association of *Rotylenchulus reniformis* with Verticillium wilt of cotton. *Indian Journal Nematology,* 10:91–92.

Prentice, A. N. (1972). *Cotton with special references to Africa.* London; Longman. 282p.

Purseglove, J. W. (1974). *Tropical crops. Vol I: Dicotyledons.* London, Longman. 719 p.

Ridgway, R. L. (1984). Cotton protection practices in the USA and world. Section A: Insects. In: Kohel, R. J. & Lewis, C. F. (Eds.). *Cotton.* Agronomy Monograph no. 24, ASA-CSSA-SSSA, Madison, WI: 266–287.

Roberts, P. A. & Matthews, W. C. (1984). Cotton growth responses to root-knot nematode infection. *44th Cotton Disease Council, Proceedings Beltwide Cotton Production Research Conference, National Cotton Council, Memphis, Tn.* :17–19.

Roberts, P. A., Smith, S. N. & Matthews, W. C. (1985). Quantitative aspects of the interaction of *Meloidogyne incognita* with Fusarium wilt on Acala cotton in field plots. *45th Cotton Disease Council, Proceedings Beltwide Cotton Production Research Conference, National Cotton Council, Memphis TN.* :21.

Robbins, R. T. & Barker, K. R. (1974). The effects of soil type, particle size, temperature and moisture on reproduction of *Belonolaimus longicaudatus. Journal of Nematology*, 6:1–6.

Robinson, A. F., Heald, C. M., Flanagan, S. L, Thames, W. H. & Amador, J. (1987). Geographical distribution of *Rotylenchulus reniformis, Meloidogyne incognita,* and *Tylenchulus semipenetrans* in the lower Rio Grande valley as related to soil texture and land use. *Annals of applied Nematology*, 1:20–25.

Rodriguez-Kabana, R. & Pope, M. H. (1981). A simple incubation method for the extraction of nematodes from soil. *Nematropica,* 11:175–186.

Roy, A. K. (1983). Comparison of efficacy of decaffeinated tea waste with nemagon on the control of root-knot nematode on jute. *Journal of Research, Assam Agricultural University,* 4:63–64.

Saikia, D. K. & Phukan, P. N. (1986*a*). Estimation of loss in jute due to root-knot nematode, *Meloidogyne incognita. Indian Journal Nematology,* 16:190–109.

Saikia, D. K. & Phukan, P. N. (1986*b*). Effect of crop rotation on the development of root-knot nematode, *Meloidogyne incognita* on the jute crop. *Indian Journal Nematology*, 16:110–111.

Sasser, J. N. (1972). Nematode disease of cotton. In:Webster, J. M. (Ed.) *Economic Nematology* London Academic Press Inc. :187–214.

Shafie, M. F. & Koura, F. H. (1969). *Hoplolaimus aegypti* n. sp. (Hoplolaimidea:Tylenchida; Nematoda) from U.A.R. *The zoological Society of Egypt Bulletin,* 22:117–120.

Shepherd, R. L. (1982). Genetic resistance and its residual effects for control of the root-knot nematode-Fusarium wilt complex in cotton. *Crop Science*, 22:1151–1155.

Shepherd, R. L. (1983). New sources of resistance to root-knot nematodes among primitive cottons. *Crop Science,* 23:999–1002.

Shepherd, R. L. (1986). Cotton resistance to the root-knot nemtode-Fusarium wilt complex. II. Relation to root-knot resistance and its implications on breeding for resistance. *Crop Science,* 26:233–237.

Sikora, R. A. & Carter, W. W. (1987). Nematode interactions with fungi and bacterial plant pathogens-fact or fantasy. In:Veech, J. A. & Dickson D. W. (Eds) *Vistas on Nematology,* Hyattsville, Maryland Society. Nematologists: 307–312.

Silva, A. B., Freire, F. C. O., & Mota, M. G. C. (1977). Meloidoginose da juta. *Trabalhos apresentados a II Reuniao de Nematologia, Piracicaba, Brazil, 14–16 Setembro 1976*:149–152.

Smith, A. L. (1950). Distribution and relation of meadow nematode, *Pratylenchus pratensis,* to Fusarium wilt of cotton in Georgia. *Phytopathology,* 40:710. (Abstr)

Srivastava, A. S., Verma, R. S. & Ram, S. (1974). Susceptibility of jute varieties to root-knot nematode. *Meloidogyne javanica* (Treub, 1885) Chitwood, 1949. *Indian Journal of Nematology,* 2:198–199.

Starr, J. L. & Jeger, M. J. (1985). Dynamics of winter survival of eggs and juveniles of *Meloidogyne incognita* and *M. arenaria. Journal of Nematology,* 17:252–256.

Starr, J. L., Jeger, M. J. Martyns, R. D. & Schilling, K. (1989). Effects of *Meloidogyne incognita* and *Fusarium oxysporum* f. sp. *vasinfectum* on plant mortality and yield of cotton. *Phytopathology,* 79:640–646.

Starr, J. L., & Matheison, T. (1985). Reproduction of *Pratylenchus brachyurus* on cotton and growth response to infection by the nematode. *45th Cotton Disease Council. Proceedings Beltwide Cotton Production Research Conference, National Cotton Council, Memphis, TN. :25.*

Starr, J. L. & Veech, J. A. (1986). Susceptibility to root-knot nematodes in cotton lines resistant to the Fusarium wilt/root knot complex. *Crop Science,* 26:543–546.

Sud, U. C., Varaprasad, K. J., Seshadri, A. R. & Kher, K. K. (1984). Relationship between initial densities of *Rotylenchulus reniformis* and damage to cotton with fit to Seinhorst curves. *Indian Journal of Nematology,* 14:148–151.

Summers, T. E., Pate, J. B., & Wilson, F. D. (1958). Extent of susceptibility within kenaf, *Hibiscus cannabinus* L., to root-knot nematodes. *Plant Disease Reporter,* 42:591–593.

Summers, T. E., & Seale, C. C. (1958). Root-knot nematodes, a serious problem of kenaf in Florida. *Plant Disease Reporter,* 42:792–795.

Taylor, A. L., Sasser J. N., & Nelson, L. A. (1982). *Relationship of climatic and soil characteristics to geographical distribution of species in agricultural soils.* Raleigh, North Carolina State University and US-AID, NC., 65p.

Tchatchoua, J. & Sikora, R. A. (1983). Veränderungen in der anfälligkeit welkerestitenter Baumwollpflazen gegenüber *Verticillium dahliae,* verursacht durch *Rotylenchulus reniformis. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz,* 90:232–237.

Thames, W. H., & Heald, C. M. (1974). Chemical and cultural control of *Rotylenchulus reniformis* on cotton. *Plant Disease Reporter,* 58:337–341.

Tomerlin, A. H., Jr. (1969). *The influence of organic amendments on numbers of nematodes and other microorganisms in the soil.* Ph. D. Dissertation., Univ. Florida, Gainesville., 56 p.

Tu, C. C. & Cheng, Y. H. (1971). Interaction of *Meloidogyne javanica* and *Macrophomina phaseoli* in kenaf root-rot. *Journal of Nematology,* 3:39–42.

Veech, J. A. (1984). Cotton protection practices in the USA and world. Section C:Nematodes. In: Kohel, R. J. & Lewis, C. F. (Eds.) *Cotton.* Agronomy Monograph no. 24, ASA-CSSA-SSSA, Madison, WI: 309–330.

Veech, J. A. & Starr, J. L. (1986). Comparison of development, reproduction, and aggressiveness of *Meloidogyne incognita* races 3 and 4 on cotton. *Journal of Nematology,* 18:413–415.

Webster, J. M. (1985). Interaction of *Meloidogyne* with fungi on crop plants. In : Sasser, J. N. and Carter, C. C. (Eds.) *An Advanced Treatise on Meloidogyne, Vol 2,* Raleigh, North Carolina State University Graphics: 183–192.

Yassin, A. M. (1974). Role of *Pratylenchus sudanensis* in the syndrome of cotton wilt with reference to its vertical distribution. *Sudan Agricultural Journal,* 9:48–52.

Yassin, A. M. & Mohamed, Z. E. (1980). Studies on the biology and chemical control of root-lesion nematode, *Pratylenchus sudanensis* loof and Yassin 1970, from the Gezira. *Zeitschrift für angewandte Zoologie,* 67:225–231.

Yik, C. P. & Birchfield, C. (1984). Resistant germplasm in *Gossypium* species and related plants to *Rotylenchulus reniformis. Journal of Nematology,* 16:146–153.

Chapter 18

Nematode Parasites of Spices

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Spices are strongly flavoured or aromatic substances of plant origin commonly used for seasoning and preserving food stuffs. They consist of rhizomes, barks, leaves, fruits, seeds and other parts of plants. These plants belong to different families, genera and species (Table I). The bulk of the dry matter of their products consist of carbohydrates, volatile oils, fixed oils, proteins, tannins, resins, pigments and mineral elements. These constituents differ in their composition and content in different spices. Most of the spices are crops of the humid tropical regions. India is considered as the home of spices from ancient times and produces a large proportion of all spices. There are innumerable biotic and abiotic problems on spice crops which adversely affect production including plant parasitic nematodes which can cause considerable damage to some of these crops.

Nematode problems of the spices, chilli and garlic are not included as they are discussed under vegetables (Chapter 7). Nematode problems of betel vine (*Piper betle*) and kava (*Piper methysticum*) have also been included in this chapter.

Black Pepper

Black pepper (*Piper nigrum* L.) is a branching and climbing perennial shrub belonging to the family Piperaceae and is cultivated in the hot and humid parts of the world. India, Indonesia, Malaysia and Brazil, contributing 24, 23, 22 and 14% respectively, are the major pepper producing countries in the world today. World production of pepper during 1985–86 was 125 990 t and covered an area of 2 44 250 ha (Anon., 1988). Its origin is considered to be in the hills of south-western India where it is known as the "King of spices". It is used in culinary seasonings, as a preservative for meat and other perishable foods, and in medicine. Piperine, the bite factor of pepper, is used to impart a pungent taste to brandy. Pepper oil is used in perfumery. The pepper vine can be propagated either vegetatively or by seed. Raising plants through cuttings is universally adopted. Two pepper vines entwined about a teak wood or concrete post, set in the field, is known as "pepper tree". In India, live trees are used as supports (standards) for climbing pepper.

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds) © CAB International 1990

TABLE 1. Important spice crops in the tropics and subtropics.

	Scientific Name	Family	Common Name	Origin	Major Areas of Production
1.	*Allium sativum* L.	Liliaceae	Garlic	Europe	China, Turkey, Spain
2.	*Capsicum frutescens* L.	Solanaceae	Chillies	Tropical America	China, Nigeria, Turkey
3.*	*Trachyspermum ammi* L.	Umbelliferae	Bishop's weed	Egypt	India, Egypt, Iran
4.*	*Cinnamomum cassia* Blume	Lauraceae	Cassia	Egypt	China, Laos, Cambodia
5.*	*C. tamala* (Buch.-Ham) Nees & Eberm	Lauraceae	Tejpat	Egypt	India, Nepal
6.	*C. verum* Presl.	Lauraceae	Cinnamon	Sri Lanka & South India	Indonesia, Sri Lanka, Seychelles
7.	*Coriandrum sativum* L.	Umbelliferae	Coriander	Europe & Asia	Morocco, India, Pakistan
8.	*Cuminum cyminum* L.	Umbelliferae	Cumin	Egypt & Mediterranean	India, Iran, Morocco
9.	*Curcuma domestica* Val.	Zingiberaceae	Turmeric	South-East Asia	India, Bangladesh, Pakistan
10.	*Elettaria cardamomum* Maton.	Zingiberaceae	Cardamom	Indian Peninsula	India, Guatemala, Tanzania
11.	*Eugenia caryophyllus* (Sprengel) Bullock & Harrison	Myrtaceae	Clove	Indonesia	Indonesia, Zanzibar, Madagascar
12.*	*Foeniculum vulgare* Mill.	Umbelliferae	Fennel	Southern Europe	India, Europe, Russia
13.	*Myristica fragrans* Houtt.	Myristicaceae	Nutmeg	Indonesia	Indonesia, Grenada, Sri Lanka
14.*	*Pimenta dioica* (L.) Merrill	Myrtaceae	Allspice	West Indies	West Indies, Guatemala, Honduras
15.*	*Piper longum* L.	Piperaceae	Indian long pepper	India	Indonesia, Singapore, Sri Lanka
16.	*P. nigrum* L.	Piperaceae	Black pepper	India	India, Indonesia, Brazil
17.	*Trigonella foenum-graecum* L.	Leguminosae	Fenugreek	Southern Europe	India, France, Lebanon
18.	*Vanilla fragrans* (Salisb.) Ames	Orchidaceae	Vanilla	Mexico	Madagascar, Indonesia, Comoros
19.	*Zingiber officinale* Rosc.	Zingiberaceae	Ginger	South-Eastern Asia	India, Jamaica, Japan

*No report of nematodes

Nematodes on Black Pepper

Many nematodes have been reported on black pepper (Table 2), but the only two known to cause serious damage to the crop are *Radopholus similis* and *Meloidogyne* spp.

Radopholus similis

Association of the burrowing nematode, *R. similis*, with the yellows disease of pepper was first reported by Van der Vecht (1950), who made extensive field studies and also demonstrated its pathogenicity under laboratory conditions. The nematode is notorious for being associated with the loss of 22 million pepper vines within 20 years in Bangka Island, Indonesia due to "yellows disease" (Christie, 1957; 1959). Subsequently, *R. similis* was reported from black pepper from India (Venkitesan, 1972; Koshy *et al.*, 1978), Malaysia, Thailand (Sher *et al.*, 1969; Reddy, 1977) and Sri Lanka (Gnanapragasam *et al.*, 1985). The nematode is also involved in "slow-wilt" disease of black pepper in India, which is almost identical to pepper yellows in Indonesia (Van der Vecht, 1950; Mohandas & Ramana, 1987*b*; Ramana *et al.*, 1987*a*) hence, they are dealt with together. Intensive surveys carried out on the role of plant parasitic nematodes in the slow-wilt disease complex of black pepper

in India showed that high populations of *Radopholus similis* occurred more frequently in slow-wilt disease affected plants than in healthy plants. Discriminate analysis indicated the positive involvement of *R. similis* in slow-wilt disease (Ramana *et al.*, 1987*a*).

Black pepper was introduced to Indonesia from Kerala, India (Nambiar, 1977) and it is quite likely that the burrowing nematode was also introduced along with the rooted cuttings of black pepper.

Symptoms of damage

The primary symptom of the yellows (slow-wilt) disease is the appearance of pale yellow or whitish yellow drooping leaves on the vines. The number of such leaves increases gradually until large numbers of leaves or even the entire foliage becomes yellow (Plate 16A). Yellowing is followed by shedding of leaves, cessation of growth and die-back symptoms (Fig. 1, Plate 16B). The symptoms are well pronounced when soil moisture is depleted. In the very early stage of the disease in India, the symptoms may disappear with the onset of the South-west monsoon resulting in an apparently healthy appearance of such plants in the following years because of new leaf growth and shedding of yellowed leaves. This has often given a mistaken impression of the disease being caused by soil moisture stress rather than nematodes. However, within three to five years of initiation of yellowing all the leaves are shed and death of the vine takes place and hence the name "slow-wilt" disease.

Fig. 1. Black pepper growing on arecanut palms in India showing defoliation and dieback due to *Radopholus similis*.

In bearing vines, shedding of spikes (inflorescences) is a major symptom. Large numbers of shed spikes are seen at the base of affected vines. In large plantations, affected patches become conspicuous initially as yellowed plants (Plate 16C), and later with large numbers of barren standards that have lost the vines, or standards supporting dead vines without any leaves (Plate 16D). Young and old plants are affected and the replanted vines normally die within two years.

The tender thin, white, feeding roots show typical orange to purple coloured lesions. Lesions are not clearly seen on older roots, being brown in colour. The root system exhibits extensive rotting and the main roots are devoid of fine feeder roots that rot quickly. Extensive necrosis of larger lateral roots develops subsequently.

Biology and life cycle

The nematode penetrates roots within 24 hours of inoculation and the cells around the site of penetration become brown (Venkitesan & Setty, 1977). Nematodes do not enter the stelar portions of the root, but plugging of xylem vessels with a gum-like substance has been reported (Freire & Bridge, 1985*a*). It completes its life cycle within 25–30 days, at a temperature range of 21–31°C and the black pepper isolate of the nematode is easily cultured on carrot discs at 25°C (Koshy, 1986*b*). The *R. similis* populations in Indonesia and Kerala (India) have a haploid number (n=4) of four chromosomes (Huettel *et al.*, 1984; Koshy, 1986*b*).

In India, the maximum nematode population in roots of pepper occurs during September-October and minimum during April-June (Ramana, 1986; Mohandas & Ramana, 1987*b*). A low soil temperature coupled with adequate soil moisture and availability of fresh tender roots help in the build up of the population during September-October.

Other hosts

A large number of tree species such as, coconut (*Cocos nucifera*), arecanut (*Areca catechu*), jack fruit (*Artocarpus integrifolia*), mango (*Mangifera indica*), gliricidia (*Gliricidia maculata*), dadap (*Erythrina indica*), garuga (*Garuga pinnata*) and Vatta (*Macaranga indica*) are used as live standards. Among these, coconut and arecanut are good hosts of *R. similis* (see Chapter 11). Crops like banana, ginger and turmeric that are susceptible to *R. similis* are also intercropped with pepper.

Disease complexes

It has been speculated that yellows disease in Indonesia is caused by a nematode – fungus complex (Hubert, 1957; Bridge, 1978) involving *R. similis, Fusarium* spp. and possibly other fungi. There is little direct evidence to support the hypothesis, however, Freire (1982) showed that an Indonesian isolate of *R. similis* predisposed black pepper seedlings to attack by a weakly pathogenic isolate of *Fusarium solani* causing severe root damage.

Economic importance and population damage threshold levels

The slow-wilt disease was first reported from Wynad area in Kerala as early as 1902 and Krishna Menon (1949) reported mortality up to 10% of the vines due to the disease. Reduction in plant growth has been reported in sterile soil when 55-day-old rooted cuttings of black pepper in pots are inoculated with 2300 nematodes.

The onset of yellows disease in Sumatra, Indonesia is correlated with *R. similis* populations of 2/100g of soil and 25/10g of roots, and *Meloidogyne* spp. populations of 47/100g of soil and 305/10g of roots (Mustika, 1978), but Bridge (1978) thought that a low population of less than 310 nematodes/10g roots may not alone cause the disease. A population level of 250 nematodes/g of roots was constantly recorded with slow-wilt affected pepper vines in Kerala (Ramana, 1986).

Control measures

At present there are no effective control measures for control of slow-wilt or pepper yellows. The price of black pepper is known to fluctuate greatly and with the fall in prices, the farmer often loses

interest in the crop and tends to neglect adoption of even agronomic practices. Control methods need to be adopted every year for black pepper, being a perennial crop, especially under Indian conditions where live standards are used. The perennial multi-cropping systems involving coconut, arecanut, black pepper, betel vine, banana, ginger, turmeric, etc. that have developed over many years in the west coast of South India are ideal situations where the burrowing nematode multiplies and causes heavy damage to all the susceptible crops (Plate 16E). Black pepper, betel vine and banana are crops that succumb to nematode attack early. In later years, the farmers abandon pepper cultivation in arecanut based farming systems where arecanut is the live standard. Although application of phorate at 3 g a.i./vine twice a year has been found to control *R. similis*, the high density multispecies cropping pattern does not permit use of nematicides, as most of the crops are export oriented and some products are consumed without any processing or cooking, such as banana, betel leaves, etc. This situation is further complicated because arecanut and coconut that are used as live standards are also very good hosts of *R. similis* which warrants higher dosages and more frequent use of nematicides, especially under irrigated conditions.

Cultural practices

Symptoms of slow-wilt/pepper yellows are known to be ameliorated with mulching. Pasril (1976) has recorded 18% reduction in disease incidence in Bangka Island, Indonesia after mulching. He also observed a reduction in disease symptoms after application of nematicide with a corresponding increase of yield in the first year of treatment.

De Waard (1979) suggested application of fertilizers at a dose of 400 kg N, 180 kg P, 480 kg K, 425 kg Ca and 112 kg Mg in combination with a mulch for effective control of yellows disease in Bangka, Indonesia. Further, foliar yellowing and necrosis of distal ends of laminae of slow-wilt affected vines in Kerala, India were attributed to N and K deficiencies respectively (Wahid *et al.*, 1982).

Resistance and tolerance

Eighteen cultivars of black pepper, four *Piper* species and five wild *Piper* collections were screened against *Radopholus similis*. Wild collection Vittal No. 430, *Piper hymenophyllum* and *P. attenuatum*, recorded least (less than 30%) root reduction and minimum (xl.5) nematode reproduction. The hybrid pepper variety Panniyur-I recorded 91.4% root reduction and x7.6 nematode reproduction (Venkitesan & Setty, 1978). However, a local cultivar at Peringamala, Kerala, India was found not to be invaded by *R. similis* (Jacob & Kuriyan, 1979*b*). No resistance or tolerance was found to the nematode in a total of 106 cultivated germplasm, 36 wild related *Piper* spp., 20 intercultivar hybrids, 90 selections of cultivar Karimunda and 12 200 open pollinated seedlings of popular pepper cultivars screened against *R. similis* (Ramana *et al.*, 1987*b*).

Chemical

A number of pesticides have been found effective in reducing *R. similis* populations on black pepper in pot trials as well as in preliminary field trials. Aldicarb sulphone at 8 kg a.i./ha was most effective for control of *R. similis* on pepper in pot trials (Venkitesan, 1976; Venkitesan & Setty, 1979). DD, Vapam, Nemagon, Temik, Furadan, Nemacur, Mocap, Hostathione, Dasanit and Dasudin were found to reduce populations of *Meloidogyne* spp. and *R. similis* on *P. nigrum* in greenhouse trials (Mustika & Zainuddin, 1978). Under Indian conditions, aldicarb/carbofuran/phorate at 3 g a.i./vine applied in May/June and again in September/October results in the remission of foliar yellowing and reduction in nematode populations. Among the above three nematicides, phorate is superior (Ramana, 1986; Mohandas & Ramana, 1987*a*). The chances of rehabilitating the severely affected vines by application of nematicides are slim because of the heavy damage already caused to the root system and the inability of such plants to put out fresh roots for quick rejuvenation.

Although chemicals have been reported to reduce the nematode population and ameliorate slow-wilt symptoms, the cost benefit ratio has not been calculated.

Summary of control measures

Integrated methods of nematode management that can be suggested are:

1. Planting of nematode-free rooted cuttings.
2. Uprooting of affected vines and replanting after a period of 9–12 months.
3. Use of non-living supports or standards.
4. Exclusion of *R. similis* susceptible trees as standards for trailing black pepper vines, and exclusion of susceptible intercrops such as banana, ginger and turmeric.
5. Application of phorate at 3 g a.i./vine with the onset of monsoon and again after three months. The nematicide may be applied after removing the top soil without causing damage to the roots, followed by replacement of the soil. The susceptible intercrops, e.g. banana, may also be treated with nematicides.
6. Application of organic amendments, such as 200 g neem oil cake (*Azadirachta indica*), green foliage (3–5 kg), or farm yard manure (1 kg) per vine.
7. Earthing-up after application of nematicides, NPK fertilizers and organic amendments in September/October.

Methods of diagnosis

Sampling

The presence of nematodes and their association with the disease can be diagnosed by soil sampling at a distance of 25–50 cm from the base of the vine at a depth of 20–30 cm. A soil sample of 200 cm^3 and root sample of 0.5 to 1.0 g thin, tender, feeder roots will yield maximum nematode population (Koshy, 1986*b*, 1987*a*, 1988).

Extraction

Infested roots, showing lesions and rotting, may be split longitudinally and cut to a length of 1 to 2 cm. When such roots are submerged in water contained in Petri dishes or shallow pans and incubated at 20–25°C, 50% of nematodes are released in 72 h. For collecting active nematode populations for culturing and other studies, tease out individual root lesions in water contained in a watch glass under a stereoscopic microscope and quickly transfer the nematodes into fresh water.

Meloidogyne

The root-knot nematode, *Meloidogyne* sp., was the first nematode to be recorded on black pepper (Delacroix, 1902) in Cochin-China. In 1906, Butler reported root-knot nematodes from black pepper in Wynad, Kerala (India). *Meloidogyne javanica* and *M. incognita* have been reported from India, Brazil, Sarawak, Borneo, Cochin-China, Malaysia, Brunei, Kampuchea, Indonesia, Philippines, Thailand and Vietnam (Winoto, 1972; Castillo, 1974; Lordello & Silva, 1974; Ichinohe, 1975; Reddy, 1977; Freire & Monteiro, 1978; Kueh & Teo, 1978; Sundararaju *et al.*, 1979*a*; Ramana & Mohandas, 1983) and *M. arenaria* from Sri Lanka (Lamberti *et al.*, 1983).

Symptoms of damage

A gradual decline characterized by unthrifty growth and yellowing of leaves are the prominent symptoms. Leaves of vines infested with *Meloidogyne* spp. exhibit dense yellowish discolouration of the interveinal areas making the leaf veins quite prominent with a deep green colour, whereas leaves of the vines infested with *Radopholus similis* show uniform pale yellow or whitish discolouration and typical drooping. Root systems become heavily galled. In the cv Panniyur I, the galls are smooth and bigger in size compared to the small galls with exposed egg masses giving a pitted rough appearance to roots of cv Karimunda.

Other hosts

Among the commercially used standards *Oroxylum indicum* Vent., *Erythrina lithosperma* Blume, *Ceiba pentandra* (L.) Gaerth. and *Bombax malabaricum* DC. are highly susceptible to root-knot nematodes, whereas *Garuga pinnata* Roxb. and *Macaranga indica* Wight are not susceptible. The popular live standards, *Erythrina indica* Lank. and *Gliricidia sepium* (Jacq.) Walp. are less susceptible (Koshy *et al.*, 1977). Large numbers of weeds that are found in pepper gardens have been recorded as hosts of the root-knot nematode (Ramana, 1986).

Disease complexes

Meloidogyne spp. do not significantly enhance the susceptibility of pepper vines to foot-rot in Sarawak (Holliday & Mowat, 1963). *M. incognita* and *Fusarium solani* were found associated with black pepper vines in Paraba State, Brazil. Infested plants showed wilting, yellowing of leaves, rotting of stems and roots and cracking of stems; cracked stems 5–10 cm above the soil surface were heavily infected. Both organisms together were found to do more harm than either of them alone (Lopes & Lordello, 1979), but Winoto (1972) reported increased susceptibility of *M. incognita* and *M. javanica* infested pepper cv Kuching to *Phytophthora* infection in Malaysia. *Rotylenchulus reniformis* was found to inhibit the multiplication of *M. incognita* and the resultant damage on black pepper in autoclaved soil in pots under greenhouse conditions in Brazil (Ferraz & Sharma, 1979). The root gall development and population build up of *M. incognita* was suppressed in black pepper on inoculation with *R. similis* in succession in sterile soil under pot conditions (Sheela & Venkitesan, 1981).

Economic importance and population damage threshold levels

As much as 91% root-knot nematode infestation was reported from Para, Brazil (Ichinohe, 1975) and Kerala, India (Ramana *et al.*, 1987*a*; Ramana & Mohandas, 1987*b*). An initial population of ten juveniles per rooted cutting reduces growth by 16%, while, a maximum of 50% reduction is observed at an inoculum level of 100 000 over a period of one year in sterile soil under potted conditions (Koshy *et al.*, 1979*b*). *M. incognita* was found highly pathogenic at 100–10 000 juveniles per seedling (Freire & Bridge, 1985*c*). In Indonesia, yellow symptoms appeared on plants with *Meloidogyne* spp. at population levels of 47/100 g soil and 305/10 g roots (Mustika, 1978).

Control measures

Root-knot infestation in black pepper nurseries has been a serious problem in several government nurseries in Kerala, India. Fumigation of nursery potting mixture with methyl bromide is effective in checking the infestation (Koshy, 1974, 1986*a*; Mohandas & Ramana, 1987*a*).

Cultural

Growing of the non-host cover plant siratro (*Macroptilium atropurpureus*) in the interspace and mulching with Guatemala grass are recommended to reduce populations of *M. incognita* on black pepper in the Amazonian region (Ichinohe, 1980).

Resistance and tolerance

Among the seven popular cultivars screened, the hybrid cultivar, Panniyur-I was the most susceptible and the cultivar Valiakaniakadan was the least susceptible (Koshy & Sundararaju, 1979). The intensity of damage on infestation with *M. incognita* was less in cultivar Karimunda compared with that of Panniyur-I (Mohandas & Ramana, 1983). Of eight cultivars screened against *M. incognita*, Kalluvalli, Balancotta, Karimunda, Narayakodi and Padapan had fewer galls than Panniyur-I, Cheriyakaniakadan and Kottanadan (Jacob & Kuriyan, 1979*a*). A total of 101 cultivars, 74 accessions of wild *Piper* sp. and 140 inter cultivar hybrids were screened against *M. incognita* of which one cultivar, CLT-P–812, was found resistant (Ramana & Mohandas, 1986, 1987*b*; Koshy, 1987*b*).

Infection by nematodes is known to cause biochemical changes in plants. The cv Cingapura

recorded high concentrations of total phenols on inoculation with 6000 *M. incognita* juveniles/pot 95 days after planting although no resistance was shown (Ferraz *et al.*, 1984). Changes in levels of amino acids, organic acids and sugars in *M. incognita* infected plants, compared with uninfected plants were reported by Freire and Bridge (1985*b*).

Chemical

Most nematicides have been found effective in reducing root-knot nematode populations on black pepper, but information on their practical use is limited. Under Indian conditions when a live standard is used, the dosage has to be different depending upon the susceptible/resistant reaction of the standard to the root-knot populations. Thus, generalizations on the dosage of nematicides are not possible, and recommendations have to be location specific depending upon the standard, variety of black pepper, rainfall pattern and flowering and harvesting period of black pepper. Green berry yields can be doubled by four applications of carbofuran incorporated into mound soil at 114 g per vine per application in black pepper fields infested with *M. incognita* and *M. javanica* in Malaysia (Kueh & Teo, 1978). Application of Temik 10G at 12.5 g/plant or Furadan 5 G at 50 g/plant twice a year, including at planting around cuttings, can reduce populations of *M. incognita* on black pepper in the Amazonian region (Ichinohe, 1980). Phenamiphos at one per cent a.i./vine followed by carbofuran and ethoprophos was effective in controlling nematodes in cv Kuching in Malaysia (Leong, 1984).

When aldicarb at 1 g a.i./vine applied twice a year (May/June and October/November) is integrated with fertilizers (N=100g, P=40g, K=140g/vine) in two equal split doses, plus earthing up to 50 cm radius at the base of the vines and mulching the vine base with leaves, there is a reduction in foliar yellowing of 83% and *M. incognita* juvenile populations by 33–88% (Venkitesan & Jacob, 1985).

Biological

Nematode-free cuttings could be raised by incorporating a biological control agent in the potting mixture. The only attempt known to have been made in this direction is by Friere and Bridge (1985*d*). However, the rates of infection by *Paecilomyces lilacinus* and *Verticillium chlamydosporium* of *M. incognita* egg masses on black pepper seedlings were only 15 and 12% respectively, and this would be totally inadequate for effective control.

Other nematodes of black pepper

The nematodes that have been found associated with black pepper (Table 2) in various countries (Timm, 1965; Sher *et al.*, 1969; Castillo, 1974; Sharma & Loof, 1974; Ichinohe, 1975; Reddy, 1977; Bridge, 1978; Sundararaju *et al.*, 1979*b*; Rama, 1987; Dasgupta & Rama, 1987; Ramana & Mohandas, 1987*a*) are, apart from *R. similis* and *Meloidogyne* spp., probably of minor economic importance. The nematode that could prove to be damaging to the crop is *Trophotylenchulus piperis*. *T. piperis* has been reported as a widespread parasite of black pepper roots in South India, but its damaging potential has yet to be studied (Mohandas & Ramana, 1982; Mohandas *et al.*, 1985).

Future prospects

Developing cropping systems, avoiding susceptible live supports or standards, incorporating an integrated nematode management system with minimum or no nematicide application, should be the main thrust of research to increase black pepper yield in areas infested with damaging nematodes.

Cardamom

Cardamom is a fruit (capsule) of the plant, *Elettaria cardamomum* Maton, belonging to the family Zingiberaceae. It is a perennial plant having an underground stem (rhizome) with aerial shoots. A mature cardamom plant may measure about 2 to 4 m in height. Flowers are borne on panicles which emerge directly from the swollen base of the aerial shoot. The fruits are small, trilocular capsules containing 15 to 20 seeds. Cardamom, known as the "Queen of spices", has its origin in the evergreen rain forests of South India and is basically a shade loving plant. India and Guatemala are the main producers and exporters of cardamom. Tanzania, Sri Lanka, El Salvador, Vietnam, Laos, Kampuchea and Papua New Guinea are also cardamom growers. The area under cardamom cultivation in India during 1985–86 was 95 370 ha and the total world production was 10 660 t (Anon., 1988). Cardamom is used for flavouring various food preparations, confectionery, beverages, liquors and medicines. Cardamom can be propagated through seedlings as well as suckers. Suckers are better suited for gap filling and multiplication of selected high yielding types.

Nematodes on Cardamom

Nematological investigations on this crop have been undertaken in India, where a number of plant parasitic nematodes have been found with cardamom (Table 2). The most important nematode problem is caused by the root-knot nematodes, *Meloidogyne* spp., although the lesion nematode, *Pratylenchus coffeae* and the burrowing nematode, *Radopholus similis*, are also known to cause root rotting (D'Souza *et al.*, 1970; Kumar *et al.*, 1971; Khan & Nanjappa, 1972; Viswanathan *et al.*, 1974; Sundararaju *et al.*, 1979*b*).

Meloidogyne

Widespread occurrence of root-knot nematodes, *Meloidogyne incognita* and *M. javanica* has been reported in cardamom nurseries and plantations in India (Kumar *et al.*, 1971; Koshy *et al.*, 1976; Ali, 1982, 1986).

Symptoms of damage

Heavy root-knot nematode infestation in mature plants in a plantation causes stunting, reduced tillering, yellowing, premature drying of leaf-tips and margins, narrowing of leaf blades, a delay in flowering, immature fruit-drop and reduction in yield. Unlike several other plant species, galling of roots is not a conspicuous symptom on mature plants. The infested roots, however, exhibit a "witches broom" type of excessive branching (Plate 16E).

In the primary nurseries, more than 50% of the germinating seeds do not emerge as a consequence of infection of the radicle and plumule by the second stage juveniles of the root-knot nematode. The infested seedlings at the two-leaf stage show marginal yellowing and drying of leaves and severe galling of roots. On transplantation to a secondary nursery, they exhibit curling of the unopened leaves. These leaves mostly emerge after the breaking open of the pseudostem. Up to 40% of such seedlings do not establish in the secondary nursery. In secondary nurseries, the infested plants are stunted and yellowed with poor tillering, drying of leaf-tips and margins, and heavy galling of roots (Ali & Koshy, 1982).

Survival and means of dissemination

The heavily shaded, hot, humid atmosphere and continuous availability of soil moisture prevalent in cardamom plantations are congenial conditions for the multiplication of root-knot nematodes. The nematodes are disseminated through infested seedlings and rhizomes used for propagation. Most plantations have their own permanent nursery sites situated in areas having easy access to water sources like forest streams.

Other hosts

A large number of annual weeds present in the cardamom plantations and the common shade trees, *Erythrina indica* and *E. lithosperma*, are hosts of root-knot and help in the build up of nematode populations.

Disease complexes

The incidence of rhizome rot and damping-off diseases caused by the fungus, *Rhizoctonia solani* increases in the presence of *M. incognita* in the nurseries (Ali, 1986; Eapen, 1987).

Economic importance

A yield loss of 32–47% due to root-knot has been reported from the results of a nematicide experiment (Ali, 1984, 1986). An initial population level of 100 nematodes per plant causes discernible damage to cardamom (Eapen, 1987).

Control measures

Nematological investigations have helped in creating a general awareness among the planters as well as administrators in India that the root-knot nematode is a major factor. However, planters have not yet adopted recommended control measures. No resistance to root-knot nematodes has been found and the popular cardamom cultivars, Malabar, Mysore and Vazhuka are all susceptible.

It is advisable to change nursery sites every year, but this is not always practicable in view of the difficulties involved in getting suitable sites having facilities for irrigation. Hence, disinfestation of the nursery beds need to be carried out every year. Disinfestation of nursery beds with methyl bromide at 500 g/10m^2 is effective in controlling root-knot infestation in both primary and secondary nurseries.

It has been demonstrated that application of aldicarb at 5 kg a.i./ha, three times, every three months, results in increased growth and vigour of seedlings both in primary and secondary nurseries (Koshy *et al.*, 1979*a*; Ali, 1986). Aldicarb, carbofuran, phorate at 5, 10 or 15 kg a.i./ha respectively, have been applied in primary nurseries of cardamom for control of *M. incognita*. None of the nematicide treatments totally prevented nematode infestation but there was significant reduction in root-knot densities. Aldicarb at the very high level of 15 kg a.i./ha reduced nematode numbers by 90% (Ali, 1987). Application of aldicarb/carbofuran/phorate at 5g and 10g a.i./plant and neem oil cake at 500g and 1000g/plant twice a year increases yield of cardamom plants infested with *M. incognita* from 47 to 88%. Maximum yield was obtained from the plants receiving neem oil cake at a rate of 1000g/plant followed by 500g/plant (Ali, 1984).

Ginger

Ginger is the rhizome or underground stem of *Zingiber officinale* Rosc., a herbaceous perennial, belonging to the family Zingiberaceae. Although the country of origin is not known with certainty, it is presumed to be either India or China. It is grown in many countries of the tropics and subtropics and is used widely in food, beverages, confectionery and medicines. India is the largest producer and exporter of dry ginger. The total area in India under cultivation during 1986–87 was 52 460 ha. India contributes (127 000 t) nearly half of the worlds production. The other ginger producing countries are Jamaica, Sierra Leone, Nigeria, Southern China, Japan, Taiwan and Australia (Anon., 1988).

Ginger is propagated by seed rhizomes or setts. Seed rhizomes are cut into small pieces of 2.5 to 5 cm length, weighing 20 to 25 g each, having one or two good buds. It is grown either as a monocrop or as an intercrop in many farming systems. In India, mulching of ginger beds with green leaves is a traditional practice to enhance the germination of seed rhizomes and conservation of soil moisture. The first mulching is done at the time of planting itself, with green leaves at 10 to 12 t/ha

and repeated with 5t/ha, 40 and 90 days after planting, immediately after weeding and application of fertilizers.

Nematodes on Ginger

Although a large number of nematode species have been recorded from ginger (Table 2) (Colbran, 1958; Reddy, 1977; Sundararaju *et al.*, 1979*b*; Rama & Dasgupta, 1985; Kaur, 1987) the most important parasites are *Meloidogyne* spp., *Radopholus similis* and *Pratylenchus coffeae*.

Meloidogyne

Nagakura (1930) in Japan was the first to report *Meloidogyne* sp. on ginger and subsequently the species *M. arenaria, M. hapla, M. incognita* and *M. javanica* have been reported as parasites of ginger in various countries.

Symptoms of damage

The root-knot nematodes cause galling and rotting of roots and underground rhizomes. The second stage juveniles of *M. incognita* invade the rhizome through the axils of leaf sheaths in the shoot apex. In fibrous roots, penetration occurs in the area of differentiation and, in fleshy roots, the entire length of root is invaded. In both fleshy and fibrous roots the nematode develops to maturity in 21 days but in rhizomes it requires 40 days at 30°C (Cheng & Tu, 1979). Galls are formed on the fibrous roots. Abnormal xylem and hyperplastic parenchyma are observed in all infested tissues except rhizome meristems. Extensive internal lesions are formed in the fleshy roots and rhizomes. Wound cork around the lesions is suberized only in old rhizomes after harvest (Huang, 1966; Shah & Raju, 1977). Infested rhizomes have brown, water-soaked areas in the outer tissues, particularly in the angles between shoots. Nematodes continue to develop after the crop has matured and been harvested and induce breakdown of the seed rhizomes. Heavily infested plants are stunted and have chlorotic leaves with marginal necrosis. Infested rhizomes serve as a source of infection and means of dissemination.

Disease complexes

The fungus *Pythium myriotylum* is antagonistic to *M. incognita* on ginger in the rhizosphere, although concomitant infection by the two organisms does not affect the soft rot disease syndrome (Lanjewar & Shukla, 1985).

Other hosts

Most of the weeds that are present in ginger growing areas are known hosts of root-knot nematodes.

Economic importance and population damage threshold levels

In Queensland, Australia severe infestation of rhizomes reduces yields by 57% as determined by fumigation (Pegg *et al.*, 1974). Treatment of infested soil with DD before planting nematode-free seed rhizomes has increased yields by 80%. A reduction of 74% rhizome weight has been recorded with an initial inoculum level of 10 000 nematodes per plant over a period of six months under potted conditions and significant reduction in yield can be expected with a population of one juvenile/30g of soil (Sukumaran & Sundararaju, 1986).

Both *M. incognita* and *M. hapla* cause significant reduction in shoot length and shoot and root weight following inoculation with 50 juveniles/100 cm^3 soil in pots whereas, 2 juveniles/cm^3 of soil is required to produce measurable effects when ginger is grown in soil naturally infested with *M. incognita*. At higher initial inoculum levels, *M. incognita* and *M. hapla* cause partial or complete withering of aerial shoots, and typical symptoms of drying and twisting of leaves are observed with *M. arenaria* (Kaur, 1987).

Significant damage is noticeable at 0.5 and 1.25 nematodes/g of soil and above in sterilized soil under potted conditions. The fibrous roots are very much reduced at two nematodes/g soil (Parihar, 1985; Routaray *et al.*, 1987*a*).

Control measures

Pegg *et al.* (1974) suggested the following control measures for root-knot nematodes in Queensland:

1. Production of nematode-free planting material by:
   a) Selecting an area where ginger has not been grown in the previous season and has no history of severe nematode infestation.
   b) Preparation of land and fumigation with DD or EDB 15 at 330 l/ha in August. Application of fumigants at a depth of 20 cm in rows, 30 cm apart. The time interval between fumigation and planting should be at least two weeks.
   c) Selection of nematode-free planting material and treatment in hot water at 40°C for 20 min. It is followed by cooling the rhizomes before cutting and dipping in benomyl.
   Seed should be planted within one week of hot water treatment.
   d) Growing under sawdust mulch. If sawdust is not available, nemacur granules should be sprinkled over the soil between the plants at 11 kg/ha in mid-November and again in mid-January. The rhizomes should be held for planting in the following season. Seed rhizomes with external symptoms of nematode infestation should be discarded.
2. Fumigation of land two or more weeks before planting.

In Fiji, hot water treatment of ginger seed material at 50°C for ten minutes has been recommended (Anon., 1971).

The efficacy of granular nematicides such as Mocap, Nemacur, Vydate and Temik was assessed in Queensland against *M. javanica*. Nemacur was found to be the most effective, increasing rhizome yield by up to 15%. Split and late applications at 22.4 kg/ha are more promising than higher doses applied early in the season (Colbran, 1972). A high level of control of root-knot nematodes has been obtained with sawdust mulching at a depth of 5–7.5 mm, combined with post-plant application of Nemacur. The control schedule for *M. javanica* involving the use of clean seed and a ginger-taro-fallow rotation has been recommended in Fiji (Haynes *et al.*, 1973).

In India, the traditional practices of applying well decomposed cattle manure or compost at 25–30 t/ha, neem cake at 2 t/ha, and mulching with green leaves at 10–12 t/ha at planting and repeating the mulching during the growth period help in reducing nematode multiplication. Application of phenamiphos at 3 kg a.i./ha has resulted in a 70 to 144% increase in yield of ginger in fields infested with *M. incognita* and *Pratylenchus coffeae* either singly or in combination (Kaur, 1987).

Radopholus similis

Parasitism of ginger by the burrowing nematode, *R. similis*, was first reported by Hart (1956) in Florida, USA. Later, Butler & Vilsoni (1975) reported heavy infestation of ginger by *R. similis* in Fiji and its further spread through infested seed rhizomes. Occurrence of *R. similis* along with *M. incognita, Pratylenchus* sp. and *Helicotylenchus* sp. has also been reported from roots of ginger in India (Charles, 1978; Charles & Kuriyan, 1979).

Symptoms of damage

Infected plants exhibit stunting, reduced vigour and tillering. The topmost leaves become chlorotic with scorched tips. Affected plants tend to mature and dry out faster than unaffected healthy plants. Incipient infections of the rhizomes are evidenced by small, shallow, sunken, water-soaked lesions (Vilsoni *et al.*, 1976; Sundararaju *et al.*, 1979*a*). The nematodes migrate intracellularly through tissues producing large infection channels or galleries within the rhizomes.

Means of dissemination

R. similis infestation in Fiji of ginger fields appears to have originated through bananas as the areas once used for banana cultivation have been used for growing ginger (Vilsoni *et al.*, 1976). The coconut isolate of *R. similis* in Kerala (India) also reproduces well on ginger (Koshy & Sosamma, 1975, 1977). The perpetuation and dissemination of the nematode is through infested seed rhizomes used for planting.

Economic importance and population damage threshold levels

In Fiji, *R. similis* has been reported from more than 50% of the total area with a rate of infection ranging from 10–50% resulting in yield reductions of about 40%. An initial inoculum level of 10 000 nematodes per plant has been reported to cause 74% reduction in rhizome weight and an initial inoculum level of ten nematodes per plant reduced shoot weight, root weight and rhizome weight by 43, 56 and 40% respectively, in a pot experiment (Sundararaju *et al.*, 1979*c*).

Control measures

Few studies have been done on the control of *R. similis* on ginger, but the measures suggested for control of root-knot nematodes could help in reducing the loss.

Pratylenchus coffeae

The lesion nematode, *P. coffeae* is widely distributed in ginger in Kerala (Charles & Kuriyan, 1979) and Himachal Pradesh, India. The nematode is highly pathogenic to 15 day old ginger seedlings even with an initial inoculum level of ten nematodes in sterilized soil (Kaur, 1987).

Future prospects

Systematic nematode surveys have not been carried out in most of the ginger growing areas of the world except for stray reports. The burrowing nematode, root-knot nematode and the lesion nematode are well-known potential pathogens that can cause considerable reduction in yield of ginger.

Turmeric

Turmeric (*Curcuma domestica* Val.) is best known as a condiment although the plant has uses in the social and religious lives of people in South-east Asia, its probable origin. The commercial turmeric is the processed rhizomes of *C. domestica*. It is grown mostly in India, and to a small extent in China, Indonesia, Peru and Jamaica. In India, the total area under cultivation during 1986–87 was 102 500 ha with a production figure of 280 600 t (Anon., 1988). It is cultivated either as a monocrop or an intercrop in many farming systems.

It is indispensable in the preparation of curry powder, and is an important source of natural yellow dye. It is also used as a colouring matter in the drug, confectionery and food industries. The rhizomes of *C. aromatica* Salisb., a close relative of *C. longa*, is also a source of turmeric.

Nematodes on Turmeric

A number of species of plant parasitic nematodes have been reported in association with turmeric in India (Table 2) (Nirula & Kumar, 1963; Sundararaju *et al.*, 1979*b*; Dasgupta & Rama, 1987; Gunasekharan *et al.*, 1987; Rama, 1987; Routaray *et al.*, 1987*b*) of which *Meloidogyne* spp., *Radopholus similis* and *Pratylenchus coffeae* are of economic importance. *M. incognita* has also been recorded as an important parasite of turmeric in China (Chen *et al.*, 1986).

Meloidogyne

Two species of root-knot nematodes, *M. incognita* and *M. javanica*, have been reported on turmeric, but most investigations have been concerned with *M. incognita*.

Symptoms of damage

Turmeric plants infested with *M. incognita* have stunted growth, yellowing, marginal and tip drying of leaves and reduced tillering with galling and rotting of roots. In the field, high densities of *M. incognita* cause yellowing, and severe stunting and withering in large patches. Plants die prematurely leaving a poor crop stand at harvest. Infested rhizomes tend to lose their bright yellow colour (Mani *et al.*, 1987).

Economic importance and population damage threshold levels

Significant reductions in length of shoot and leaf, width of lamina, number of leaves and weights of shoot, root and rhizome have been recorded at > 1000 juveniles/plant over uninoculated plants. A 76.6% reduction in the rhizome weight has been recorded with an initial inoculum level of 100 000 nematodes/plant after six months in pots (Sukumaran *et al.*, 1986).

Control measures

Resistance and tolerance

The cultivars and breeding lines 5379–1–2, 5363–6–3, Kodur, Cheyapuspa 5335–1–7, 5335–27, Ca–17/1, Cli–124/6, Cli–339, Armoor, Duggirala, Guntur–1, Guntur–9, Rajampet, Sugandham and Appalapadu have been reported as resistant to *M. incognita* (Mani *et al.*, 1987; Gunasekharan *et al.*, 1987). The species *C. zedoaria* is more resistant to *M. incognita* than *C. domestica* in China (Chen *et al.*, 1986).

Physical

Immersing turmeric rhizomes in hot water at 55°C for 10 min or 45°C for 50 min can kill *M. incognita* inside rhizomes (Chen *et al.*, 1986) and this could be used for establishing nematode-free multiplication plots but is unlikely to be economic for large scale field use.

Chemical

Application of DBCP at 15 l a.i./ha 15 days prior to planting results in a yield increase of 253–270% compared with 59–187% increase in yield with application of phenamiphos at 2.5 kg a.i./ha one day before planting (Patel *et al.*, 1982). Aldicarb and carbofuran applied at 1 kg a.i./ha increased yield by 71% and 68% respectively over control, with a cost benefit ratio of 1:6 in aldicarb and 1:2 in carbofuran treatments (Gunasekharan *et al.*, 1987). Carbofuran at 4 kg a.i./ha applied in rows to a 4-month-old turmeric crop has resulted in a 81.6% reduction in root-knot nematode population as against 45% increase in untreated plots (Mani *et al.*, 1987)

Radopholus similis

Symptoms of damage

Roots of turmeric damaged by *R. similis* become rotted and most of these decayed roots retain only the epidermis devoid of cortex and stelar portions. The infested plants show a tendency to age and dry faster than healthy plants. Infested rhizomes are of a yolk yellow colour compared with the golden yellow colour of healthy rhizomes and have shallow water-soaked brownish areas on the surface. The scale leaves harbour *R. similis* (Sosamma *et al.*, 1979).

Survival and means of dissemination

The nematodes are disseminated through infested planting material. Populations of *R. similis* from coconut are known to infest turmeric (Koshy & Sosamma, 1975) and the use of turmeric as an intercrop in *R. similis* infested coconut and arecanut based farming systems should be avoided.

Economic importance and population damage threshold levels

Pathogenicity studies show that an initial inoculum level of ten nematodes per plant can cause a reduction of 35% of the rhizome weight after four months and 46% reduction at the end of the season (8 months). With 100 000 nematodes, the extent of reduction in rhizome weight is 65 and 76%, after 4 and 8 months respectively (Sosamma *et al.*, 1979).

Control measures

Control has not been studied under field conditions. However, use of clean, nematode-free rhizomes for planting should be the first step in developing an integrated management system for the burrowing nematode on turmeric.

Pratylenchus coffeae

P. coffeae, has been reported to be associated with discolouration and rotting of mature rhizomes of 'wild turmeric', *C. aromatica*. In advanced stages of infection, the rhizomes become deep red to dark brown in colour, less turgid and wrinkled with dry-rot symptoms. The fingers are more severely affected than the mother rhizomes. Internally the affected rhizomes show dark brown necrotic lesions (Sarma *et al.*, 1974).

Future prospects

Turmeric has received very little input in terms of nematological research, although *M. incognita, M. javanica, R. similis* and *P. coffeae* are known to damage the crop. Detailed investigations including surveys, pathogenicity experiments and control through resistant/tolerant cultivars, cultural, chemical and biological methods are warranted.

Other Spices

Although a number of spice crops including tree spices and seed spices (Table 1) are cultivated over large areas in the tropics and subtropics, there is very little information available on the damage and yield loss caused by plant parasitic nematodes on some of these crops. This is not to say that nematode problems do not exist on these crops but only that there has been a lack of nematological investigations. The plant parasitic nematodes that have been reported in association with these crops in surveys and host range studies are given in Table 2. Nematodes have been found associated in clove (Ghesquiere, 1921; Goodey *et al.*, 1965; Sharma & Loof, 1974; Bridge, 1978; Sundararaju *et al.*, 1979*b*), nutmeg (Goffart, 1953; Goodey *et al.*, 1965; Kumar *et al.*, 1971; Sundararaju *et al.*, 1979*b*; Chawla & Samathanam, 1980), cinnamon (Goffart, 1953; Goodey *et al.*, 1965; Sundaraju *et al.*, 1979*b*; Chawla & Samathanam, 1980; Dasgupta & Rama, 1987; Rama, 1987), cumin (Swarup *et al.*, 1967; Verma & Prasad, 1969; Shah & Raju, 1977; Shah & Patel, 1979; Patel *et al.*, 1986), fenugreek (Krishnamurthy & Elias, 1967; Chandwani & Reddy, 1967; Mathur *et al.*, 1969; Khan & Khan, 1969, 1973; Rashid *et al.*, 1973; Khan, 1975), coriander (Krishnamurthy & Elias, 1967; Chandwani & Reddy, 1967; Sen & Dasgupta, 1977; Das & Sultana, 1979), vanilla (Orton Williams, 1980; Stier, 1984 in Bridge, 1988). All these spices are hosts of *Meloidogyne* spp., and roots of cumin can be severely galled by *M. incognita* and *M. javanica* (Patel *et al.*, 1986). *Pratylenchus brachyurus* is reported to be a parasite of vanilla in the Pacific island of Tonga causing reduced growth of vines (Stier, 1984 in Bridge, 1988).

TABLE 2. Plant parasitic nematodes found associated with spices

Nematodes	Spice Crops										
	Black pepper	Cardamom	Ginger	Turmeric	Clove	Nutmeg	Cinnamon	Cumin	Fenugreek	Coriander	Vanilla
Caloosia spp.			+		+						
Criconema spp.		+									
Criconemella spp.	+			+	+		+				
Crossonema tylatum		+									
Discocriconemella limitanea	+										
Dolichodorus sp.	+				+						
Helicotylenchus microcephalus											+
Helicotylenchus multicinctus		+		+							
Helicotylenchus spp.	+	+		+	+						+
Hemicriconemoides gaddi		+									
Hemicriconemoides mangiferae	+										+
Hemicycliophora spp.		+	+								
Hoplolaimus columbus	+			+							
Hoplolaimus indicus			+	+			+		+		
Hoplolaimus seinhorsti	+		+								
Hoplolaimus sp.		+			+	+					
Longidorus sp.	+			+							
Meloidogyne arenaria	+		+								
Meloidogyne hapla			+								
Meloidogyne incognita	+	+	+	+	+	+		+	+	+	
Meloidogyne javanica	+	+	+	+				+	+	+	
Meloidogyne sp.							+				+
Ogma taylatum		+									
Paratrichodorus spp.		+							+		
Paratylenchus sp.						+					
Pratylenchoides sp.	+										
Pratylenchus brachyurus			+								
Pratylenchus coffeae	+	+	+	+							
Pratylenchus exilis										+	
Pratylenchus indicus			+								
Pratylenchus pratensis			+								
Pratylenchus zeae	+						+				
Pratylenchus sp.					+						
Radopholus similis	+	+	+	+		+					
Radopholus williamsi											+
Rotylenchulus reniformis	+	+	+	+	+	+	+	+	+		+
Rotylenchus spp.		+		+		+	+				
Scutellonema siamense	+										
Trichodorus sp. (*s.l.*)	+				+						
Trophotylenchulus piperis	+										
Tylenchorhynchus spp.	+		+	+	+			+	+	+	
Xiphinema spp.	+	+	+	+	+	+	+				

Related Crops

Betel Vine

The betel vine, *Piper betle* L. is a perennial, dioecious, semi-woody creeper, probably native of Malaysia. Its leaves are used for chewing, extraction of essential oils like methyl eugenol and in traditional herbal (ayurvedic) medicines and religious ceremonies. It is grown throughout Asia also in Africa, the Philippines, Indonesia and the Pacific islands. The area under betel vine cultivation in India is about 30 000 ha with an annual turnover of Rs. 7 000 million. The yield varies from 7.5–22.5 million leaves/ha/year (Shenoy, 1985).

Its cultivation is labour intensive and requires heavy investment. Betel vine is propagated by cuttings of three to five nodes, from two-year-old vines. It is trailed on coconut, arecanut or other straight stemmed plants like *Sesbania grandiflora* Pers., *Moringa oleifera* Lam and *Erythrina variegata* L. Non-living standards like bamboo, wooden poles or granite stone supports are also used. The crop is usually heavily manured with farm yard manure, oil cakes, fish manure, sheep manure, etc.

Nematodes on Betel Vine

Numerous plant parasitic nematodes have been reported associated with the betel vine in India and elsewhere (Timm, 1965; Reddy, 1978; Ganguly & Khan, 1983; Sivakumar & Marimuthu, 1984; Sivakumar & Muthukrishnan, 1985; Jagdale *et al.*, 1986). Nematodes known to cause damage to the crop are *Meloidogyne incognita, Radopholus similis* and *Rotylenchulus reniformis.*

Meloidogyne incognita

M. incognita has been reported to be associated with betel vine decline from all areas in India (Dhande & Sulaiman, 1961; Venkata Rao *et al.*, 1973; Mammen, 1974; Sivakumar & Marimuthu, 1984; Jagdale *et al.*, 1986).

Symptoms of damage

Infested plants exhibit poor growth, yellowing of leaves, reduced vigour and wilting with heavy galling and rotting of roots (Jagdale *et al.*, 1986).

Disease complexes

Association of *M. incognita* with severe wilt symptoms of betel vine was reported from India (Mammen, 1974) and *M. incognita* is known to predispose betel vine to root-rot caused by *Phytophthora palmivora* (Sivakumar *et al.*, 1987).

Economic importance and population damage threshold levels

The root-knot nematode is pathogenic to betel vine at an initial inoculum level of 100 juveniles/plant in sterile soil in pots (Jagdale *et al.*, 1985*a*).

Control measures

Cultural

A crop rotation of betel vine – rice – banana – rice is helpful in reducing *M. incognita, Helicotylenchus* sp. and *Rotylenchulus reniformis* populations on betel vine crop raised in rice fields (Sivakumar & Marimuthu, 1986*a*; Sivakumar *et al.*, 1987). Considerable reduction in nematode populations in the soil and number of galls on roots has been reported after application of 50–75 kg K_2O/ha (Jagdale *et al.*, 1985*b*).

Application of neem oil cake at 1 t/ha and sawdust at 2 t/ha can reduce nematode populations,

number of galls and increase the number of leaves harvested significantly (Jagdale *et al.*, 1985*c*). Significant reduction (60%) in the nematode population has been observed in beds amended with chopped and shade dried leaves of *Calotropis gigantea* R. Br. at 2.5 t/ha followed by neem oil cake and poultry manure (44.4 and 40.9% respectively). Beds amended with *C. gigantea* leaves yielded 14.2 kg/4840 leaves and with neem oil cake yielded 12.1 kg/4220 leaves. Soil amendment with sawdust at 2 t/ha + NPK (3638 leaves) and neem oil cake at 2 t/ha is effective in reducing nematode numbers and increasing yields (Sivakumar & Marimuthu, 1986*b*).

Resistance and tolerance

The cvs Kakair, Bangla, Karapaku, Gachipan, Aswani pan and Berhampuri are reported to be tolerant to root-knot (Anon., 1987). The cv Karpoori is highly susceptible and cv Kuljedu had the lowest root-knot index and number of egg masses per plant (Jagdale *et al.*, 1985*a*; Sivakumar *et al.*, 1987).

Physical

Solarization by mulching the land with black and white polythene (100 gauge) before planting for 15 days was found to reduce plant parasitic nematode populations in India (Sivakumar & Marimuthu, 1987).

Chemical

Application of aldicarb and carbofuran at 0.75 kg a.i./ha reduces nematode populations by 71 and 55%, respectively, resulting in increased yields. The granules, at both the levels, degraded to non-detectable levels 41 days after application (Sivakumar *et al.*, 1987). Aldicarb, carbofuran and benfurocarb applied at 1.5, 3.0, 5.0 kg a.i./ha, respectively, in furrows on either side of the rows can reduce *M. incognita* populations in soil and galling of the roots significantly (Dethe & Pawar, 1987). However, use of aldicarb and carbofuran is generally not recommended for betel vine as the leaves are picked continuously and consumed directly without any processing.

Because of the residue problem in leaves, it is preferable to manage root-knot nematode infestation on betel vine by adopting the following non-chemical measures:

1. Crop rotation wherever possible.
2. Use of resistant/tolerant cultivars.
3. Use of dead or non-living standards or nematode-resistant live standards for supports.
4. Solarization by mulching the land with clear polythene (100 gauge) before planting.
5. Application of organic amendments such as leaves of neem and *Calotropis*, and sawdust at 2 t/ha.
6. Supply of nitrogen through neem oil cake at 2 t/ha.

Radopholus similis

The burrowing nematode, *R. similis* has been reported to cause yellows/slow wilt disease of betel vine in India. The symptoms produced on betel vine are akin to the symptoms caused by *R. similis* on black pepper vines (Koshy & Sosamma, 1975; Sundararaju & Suja, 1986; Eapen *et al.*, 1987).

The integrated management schedules suggested for control of nematodes on black pepper, other than application of nematicides, can be largely adopted with modification to suit the local conditions for controlling *R. similis* on betel vine.

Rotylenchulus reniformis

Acharya and Padhi (1987) found *R. reniformis* to be pathogenic to betel vine. At inoculum levels of 1000 and 20 000 nematodes per cutting the reduction in number of leaves was 20 and 60% respectively.

Kava

Kava or Yaqona (*Piper methysticum* Forst.) provides a popular narcotic drink for the peoples of the Pacific islands. The drink is made from the thick roots of this bushy shrub.

Nematodes of Kava

Root-knot nematodes, *Meloidogyne* spp., have been found associated with a serious disease of kava and the nematodes alone can greatly decrease growth of plants in Fiji and Tonga (Stier, 1984 in Bridge, 1988) (Plate 16F). *M. incognita* is reported causing severe root galling of *P. methysticum* in Western Samoa (Fliege & Sikora, 1981).

Other potentially damaging parasitic nematodes that have been found with kava include *Rotylenchulus reniformis, Pratylenchus coffeae* and *Radopholus similis* (Kirby *et. al.*, 1980; Orton Williams, 1980). None of these have as yet been shown to damage the crop.

Further investigations are necessary to determine the economic importance of nematodes, particularly *Meloidogyne* spp., and their means of control.

References

Acharya, A. & Padhi, N. N. (1987). Population threshold of *Rotylenchulus reniformis* in relation to its disease intensity on betelvine. *International Nematology Network Newsletter*, 4: 21–23.

Ali, S. S. (1982). Occurrence of root-knot nematodes in cardamom plantations of Tamil Nadu. *Proceedings of the Fifth Symposium on Plantation crops*, Kasaragod, Kerala, India, 15–18 December: 615–620.

Ali, S. S. (1984). Preliminary observations on the effect of some systemic nematicides and neem oil cakes in a cardamom field infested with root-knot nematodes. *Proceedings of the Sixth Symposium on Plantation Crops*, Kottayam, India, 16–20 December: 215–223.

Ali, S. S. (1986). Root-knot nematode problem in cardamom and its management. *Proceedings of the Second Group Discussions on the Nematological Problems of Plantation Crops*, April 24–25, 1987. Central Coffee Research Station, Balehonnur, Karnataka, India: 10–12.

Ali, S. S. (1987). Effect of three systemic nematicides against root-knot nematodes in a cardamom nursery. *Nematologia mediterranea*, 15: 155–158.

Ali, S. S. & Koshy, P. K. (1982). Occurrence and distribution of root-knot nematodes in cardamom plantations of Kerala. *Nematologia mediterranea*, 10: 107–110.

Anonymous (1971). *Annual report, 1971*. Department of Agriculture, Fiji, 34 pp.

Anonymous (1987). Improvement of betelvine cultivation in Mahoba. *Progress Report 1986–87*. National Botanical Research Institute, Lucknow, India.

Anonymous (1988). *Cocoa, arecanut and spices statistics, 1982 to 1986*. Directorate of Cocoa, Arecanut and Spices Development, Government of India, Ministry of Agriculture, Calicut 673005, Kerala, India, 107 pp.

Bridge, J. (1978). *Plant nematodes associated with cloves and black pepper in Sumatra and Bangka, Indonesia*. ODM Technical Report on visit to Indonesia 9–19th July 1978. UK Ministry of Overseas Development, iii + 19 pp.

Bridge, J. (1988). Plant parasitic nematode problems in the Pacific islands. *Journal of Nematology*, 20: 173–183.

Butler, E. J. (1906). The wilt disease of pigeon-pea and pepper. *Agricultural Journal of India*, 1: 25–36.

Butler, L. & Vilsoni, F. (1975). Potential hosts of burrowing nematode in Fiji. *Fiji agricultural Journal*, 37: 38–39.

Castillo, M. B. (1974). Nematodes associated with stunted black pepper, beans, peas, eggplant and celery in Benguet, Batangas, Laguna and Camarines Sur. *Philippine Agriculturist*, 57: 391–402.

Chandwani, G. H. & Reddy, T. S. N. (1967). The host range of root-knot nematode, *Meloidogyne javanica* in tobacco nurseries at Rajahmundry, Andhra Pradesh. *Indian Phytopathology*, 20: 383–384.

Charles, J. S. (1978). *Studies on the nematode diseases of ginger*. M.Sc(Ag) Thesis, Kerala Agricultural University, Vellayani, Trivandrum, Kerala, India.

Charles, J. S. & Kuriyan, K. J. (1979). Studies on nematode incidence in ginger. *Proceedings of Second Symposium on Plantation Crops*, Ootacamond, Tamil Nadu, India, 26–29 June, 1979: 50–57.

Chawla, M. L. & Samathanam, C. J. (1980). Two new species of the superfamily Longidoroidea (Dorylaimida: Nematoda) from India. *Indian Journal of Nematology*, 10: 205–210.

Chen, C. M., Li, H. Y. & Lii, O. Y. (1986). [The study on root-knot nematodes of common turmeric (*Curcuma domestica* Valet).] *Herald of agricultural Sciences*, 1: 16–22.

Cheng, Y. H. & Tu, C. C. (1979). [Pathogenesis of *Meloidogyne incognita* to edible ginger.] *Journal of agricultural Research of China*, 28: 91–99.

Christie, J. R. (1957). The yellows disease of pepper and spreading decline of citrus. *Plant Disease Reporter*, 41: 267–268.

Christie, J. R. (1959). *Plant Nematodes: Their Bionomics and Control*. Gainsville, USA, University of Florida: 256 pp.

Colbran, R. C. (1958). Studies on plant and soil nematodes. 2. Queensland host records of root-knot nematodes (*Meloidogyne* species). *Queensland Journal of agricultural Sciences*, 15: 101–136.

Colbran, R. C. (1972). Studies on root-knot nematode control in ginger with non-volatile nematicides applied at and after planting. *Queensland Journal of agricultural and Animal Sciences*, 29: 275–280.

Das, V. M. & Sultana, S. (1979). Five new species of the genus *Pratylenchus* from vegetable crops of Hyderabad (Andhra Pradesh). *Indian Journal of Nematology*, 9: 5–14.

Dasgupta, M. K. & Rama, K. (1987). Plant parasitic nematodes associated with plantation crops. *Review of tropical Plant Pathology* 4: 289–304.

Delacroix, G. (1902). Une maladie affectant le poivrier (*Piper nigrum*) en Cochinchine. *Agriculture pratique des Pays chauds*, 1: 672–680.

Dethe, M. D. & Pawar, V. M. (1987). Control of root-knot nematode on betel vine by granular carbamate pesticides. *International Nematology Network Newsletter*, 4: 6–7.

De Waard, P. W. F. (1979). "Yellows Disease" complex in black pepper on the island of Bangka, Indonesia. *Journal of Plantation Crops*, 7: 42–49.

Dhande, G. W. & Sulaiman, M. (1961). Occurrence of root-knot nematodes on betel vine in Maharashtra. *Current Science*, 30: 351–362.

D'Souza, G. I., Kumar, A. C., Viswanathan, P. R. K. & Shamanna, H. V. (1970). Relative distribution and prevalence of plant parasitic nematodes in coffee tracts of South Western India. *Indian Coffee*, 34: 329–330, 342.

Eapen, S. J. (1987). Plant parasitic nematode problem in small cardamom. *Proceedings of the Third Group Discussions on the Nematological Problems of Plantation Crops, October 29–30, 1987*, Sugarcane Breeding Institute, Coimbatore, Tamil Nadu, India: 43–44.

Eapen, S. J., Geetha, S. M. & Leemoll, M. (1987). A note on the association of *Radopholus similis* with the yellow disease of betel vine. *Indian Journal of Nematology*, 17: 137–138.

Ferraz, E. D. de A., Orchard, J. E. & Lopez, A. S. (1984). Resposta da pimenteria-do-reino a infestacao or *Meloidogyne incognita* un relacao ao teor de jenois totais. *Revista Theobroma*, 14: 217–227.

Ferraz,, E. C. A. & Sharma, R. D. (1979). Interacao e patogenicidade do *Meloidogyne incognita* (Kofoid & White, 1919) Chitwood, 1949 e o *Rotylenchulus reniformis* Linford e Oliveira, 1940 na pimenteira de reino. *Revista Theobroma*, 9: 45–53.

Fliege, F. H. & Sikora, R. A. (1981). Occurrence and distribution of plant-parasitic nematodes in W. Samoa. *Alafua agricultural Bulletin*, 6: 33–41.

Freire, F. C. O. (1982). *Interactions of fungi and nematodes of black pepper* (Piper nigrum *L.*). Thesis for Doctor of Philosophy of the Faculty of Science, University of London: 575 pp.

Freire, F. C. O. & Bridge, J. (1985*a*). Histopathology of black pepper roots infested with *Radopholus similis*. *Fitopatologia Brasileira*, 10: 475–481.

Freire, F. C. O. & Bridge, J. (1985*b*). Biochemical changes induced in roots and xylem sap of black pepper by *Meloidogyne incognita*. *Fitopatologia Brasileira*, 10: 483–497.

Freire, F. C. O. & Bridge, J. (1985*c*). Influence of different inoculum levels of *Meloidogyne incognita, Nectria haematococca* f. sp. *piperis* and *Phytophthora palmivora* on black pepper plants. *Fitopatologia Brasileira*, 10: 559–575.

Freire, F. C. O. & Bridge, J. (1985*d*). Parasitism of eggs, females and juveniles of *Meloidogyne incognita* by *Paecilomyces lilacinus* and *Verticillium chlamydosporium*. *Fitopatologia Brasileira*, 10: 577–596.

Freire, F. C. O. & Monteiro, A. R. (1978). Nematodes associaoas a pimenterira-do-reino (*Piper nigrum* L.) na regiao amazonica. III Reuniao de Nematologica. ESAM/SOC. BRAS. NEMAT. Colecao Mossoroense, Mossoro 62: 28.

Ganguly, S. & Khan, E. (1983). *Trophurus impar* sp.n. and *Scutellonema eclipsi* sp.n. (Nematoda: Tylenchida). *Indian Journal of Nematology*, 13: 230–234.

Ghesquiere, J. (1921). Laboratoire d'Entomologie d'Eala (Equateur): Rapport de l'entomologiste''. *Bulletin agricole du Congo Belge*, 12: 703–732.

Gnanapragasam, N. C., Anpalagan, V. T., Dharmasena, W. A. M., Ariyaratnam, V., Jayasinghe, P. R. R. & Navaratne, N. (1985). *Report of the Tea Research Institute, Sri Lanka*: 90.

Goffart, H. (1953). Beobachtungen an pflanzenschädlichen Nematoden I. *Nachrichten Blatt Pflschutzdienst, Stuttgart*, 5: 150–153.

Goodey, J. S., Franklin, M. T. & Hooper, D. J. (1965). T. Goodey's *The Nematode Parasites of Plants catalogued under their Hosts*. Farnham Royal, England, CAB, 214pp.

Gunasekharan, C. R., Vadivelu, S. & Jayaraj, S. (1987). Experiments on Nematodes of Turmeric – A Review. *Proceedings of the Third Group Discussions on the Nematological Problems of Plantation Crops. October 29–30, 1987*. Sugarcane Breeding Institute, Coimbatore, Tamil Nadu, India: 45–46.

Hart, W. H. (1956). Spreading decline of citrus caused by the burrowing nematode. *Bulletin of the California Department of Agriculture*, 45: 263–267.

Haynes, P. H., Partridge, I. J. & Sivan, P. (1973). Ginger production in Fiji. *Fiji agricultural Journal*, 35: 51–56.

Holliday, P. & Mowat, W. P. (1963). Foot rot of *Piper nigrum* L. (*Phytophthora palmivora*). Kew, Surrey, Commonwealth Mycological Institute, *Phytopathology* Paper No. 5, 62pp.

Huang, C. S. (1966). Host-parasite relationships of the root-knot nematode in edible ginger. *Phytopathology*, 56: 755–759.

Hubert, F. P. (1957). Diseases of some export crops in Indonesia. *Plant Disease Reporter*, 41: 55–63.

Huettel, R. N., Dickson, D. W. & Kaplan, D. T. (1984). *Radopholus citrophilus* sp.n. (Nematoda), a sibling species of *Radopholus similis*. *Proceedings of the helminthological Society of Washington*, 51: 32–35.

Ichinohe, M. (1975). Infestation of black pepper vines by the root-knot nematode, *Meloidogyne incognita*, at Tome-Acu, Para, Brazil. *Japanese Journal of Nematology*, 5: 36–39.

Ichinohe, M. (1980). Studies on the root-knot nematode of black-pepper plantation in Amazon. *Annual Report of the Society of Plant Protection of North Japan*, 31: 1–8.

Jacob, A. & Kuriyan, J. (1979*a*). Screening of pepper varieties for resistance against root-knot nematode (*Meloidogyne incognita*). *Agricultural Research Journal of Kerala*, 17: 90.

Jacob, A. & Kuriyan, J. (1979*b*). Survey of nematodes associated with pepper in Kerala. *Agricultural Research Journal of Kerala*, 17: 270–271.

Jagdale, G. B., Pawar, A. B. & Darekar, K. S. (1984). Control of root-knot nematode on betel vine with systemic nematicide. *International Nematology Network Newsletter*, 1: 4–5.

Jagdale, G. B., Pawar, A. B. & Darekar, K. S. (1985*a*). Pathogenicity of *Meloidogyne incognita* on betel vine (*Piper betle* L). *Indian Journal of Nematology*, 15: 244.

Jagdale, G. B., Pawar, A. B. & Darekar, K. S. (1985*b*). Effect of differenet levels of potash on root-knot nematodes infesting betel vine. *International Nematology Network Newsletter*, 2 (4): 8–9.

Jagdale, G. B., Pawar, A. B. & Darekar, K. S. (1985*c*). Effect of organic amendments on root-knot nematodes infecting betel vine. *International Nematology Network Newsletter*, 2 (3): 7–10.

Jagdale, G. B., Pawar, A. B. & Darekar, K. S. (1986). Seasonal population fluctuation of root-knot nematode on betel vine. *Journal of Maharashtra agricultural University*, 11: 106–107.

Kaur, K. J. (1987). *Studies on nematodes associated with ginger* (Zingiber officinale *Rosc.) in Himachal Pradesh*. Thesis submitted to Himachal Pradesh University, Shimla, India, 198pp.

Khan, F. A. (1975). Some new host records of the reniform nematode in India. *Indian Phytopathology*, 28: 386–387.

Khan, F. A. & Khan, A. M. (1969). Reaction of certain economically important plants to *Rotylenchulus reniformis. Abstracts of All India Nematology Symposium, August 21 & 22, 1969*, IARI New Delhi, India: 8–9.

Khan, F. A. & Khan, A. M. (1973). Studies on the reniform nematode, *Rotylenchulus reniformis*. I. Host range and Population changes. *Indian Journal of Nematology*, 3: 24–30.

Khan, E. & Nanjappa, C. K. (1972). Four new species of Criconematoidea (Nematoda) from India. *Indian Journal of Nematology*, 2: 59–68.

Kirby, M. F., Kirby, M. E., Siddiqi, M. R. & Loof, P. A. A. (1980) *Fiji nematode survey report: Plant parasitic nematode distributions and host associations*. Bulletin No. 68, Ministry of Agriculture and Fisheries, Fiji, 28pp.

Koshy, P. K. (1974). *Annual Report, 1973*, Central Plantation Crops Research Institute, Kasaragod, 62pp.

Koshy, P. K. (1986*a*). Research on plant parasitic nematodes at the Central Plantation Crops Research Institute, Kayangulam, Kerala, India, October 1972 to June, 1986, Report, 45pp.

Koshy, P. K. (1986*b*). The burrowing nematode, *Radopholus similis* (Cobb, 1893) Thorne, 1949. In: Swarup, G. & Dasgupta, D. R. (Eds.) *Plant parasitic nematodes of India – Problems and Progress*, IARI, New Delhi, India: 223–248.

Koshy, P. K. (1987*a*). Nematological Techniques in Plantation Crops. *Proceedings of the Third Group Discussions on the Nematological Problems of Plantation Crops. October, 29–30, 1987*. Sugarcane Breeding Institute Coimbatore, Tamil Nadu, India: 24–25.

Koshy, P. K. (1987*b*). Integrated Nematode Management in Plantation Crops. *Proceedings of the Third Group Discussion on the Nematological Problems of Plantation Crops. October, 29–30, 1987*. Sugarcane Breeding Institute, Coimbatore, Tamil Nadu, India: 49–51.

Koshy, P. K. (1988). Strategies for production of nematode free planting materials in plantation crops. *Workshop on strategy for production of planting materials in plantation crops. January 22–23, 1988*. The Central plantation Crops Research Institute, Kasaragod, Kerala, India: 37–42.

Koshy, P. K. & Sosamma, V. K. (1975). Host-range of the burrowing nematode *Radopholus similis* (Cobb, 1893) Thorne, 1949. *Indian Journal of Nematology*, 5: 255–257.

Koshy, P. K. & Sosamma, V. K. (1977). Indentification of the physiological race of *Radopholus similis* populations infesting coconut, arecanut and banana in Kerala, South India. *Indian Phytopathology*, 30: 415–416.

Koshy, P. K. & Sundararaju, P. (1979). Response of seven black pepper cultivars to *Meloidogyne incognita*. *Nematologia mediterranea*, 7: 123–125.

Koshy, P. K., Sosamma, V. K. & Sundararaju, P. (1977). Screening of plants used as pepper standards against root-knot nematode. *Indian Phytopathology*, 30: 128–129.

Koshy, P. K., Sundararaju, P. & Sosamma, V. K. (1978). Occurrence and distribution of *Radopholus similis* (Cobb, 1893) Thorne, 1949 in South India. *Indian Journal of Nematology*, 8: 49–58.

Koshy, P. K., Sundararaju, P. & Wilson, K. I. (1979*a*). Efficacy of certain systemic nematicides against *Meloidogyne incognita* in a cardamom nursery. *Nematologia mediterranea*, 7: 195–198.

Koshy, P. K., Nair, C. P. R., Sosamma, V. K. & Sundararaju, P. (1976). On the incidence of root-knot nematode in cardamom nurseries. *Indian Journal of Nematology*, 6: 174–175.

Koshy, P. K., Premachandran, D., Sosamma, V. K. & Premkumar, T. (1979*b*). Effect of *Meloidogyne incognita* population on black pepper (*Piper nigrum* L.). *Indian Phytopathology*, 32: 221–225.

Krishna Menon, K. (1949). The survey of pollu and root diseases of pepper. *Indian Journal of agricultural Science*, 19: 89–136.

Krishnamurthy, G. V. G. & Elias, N. A. (1967). Host range of *Meloidogyne incognita* causing root-knot on tobacco in Hunsur, Mysore State, *Indian Phytopathology*, 20: 374–377.

Kueh, T. K. & Teo, C. H. (1978). Chemical control of root-knot nematodes in *Piper nigrum*. *Planter*, 54: 237–245.

Kumar, A. C., Viswanathan, P. R. K. & D'Souza, G. I. (1971). A study of plant parasitic nematodes of certain commercial crops in coffee tracts of South India. *Indian Coffee*, 35: 222–224.

Lamberti, F., Rohini, H. M. & Ekanayake, K. (1983). Effect of some plant parasitic nematodes on the growth of black pepper in Sri Lanka. *FAO Plant Protection Bulletin*, 31: 163–166.

Lanjewar, R. D. & Shukla, V. N. (1985). Parasitism and interaction between *Pythium myriotylum* and *Meloidogyne incognita* in soft rot complex of ginger. *Indian Journal of nematology* 15: 170–173.

Leong, C. T. S. (1984). Pepper nematodes. *Annual Report of the Research Branch, Department of Agriculture Sarawak, Borneo:* 74–78.

Lopes, E. B. & Lordello, L. G. E. (1979). *Meloidogyne incognita, Fusarium solani* f. *piperi*, associados a murcha da pimenteira-do-reino na paraiba. *Revista de Agricultura*, 54: 263–268.

Lordello, L. G. E. & Silva, H. M. (1974). Un nematoide nocivo a Pimenta-do-reino. *Revista de Agricultura*, 49: 165–166.

Mammen, K. V. (1974). On a wilt disease of betel vine in Kerala caused by root-knot nematode. *Agricultural Research Journal of Kerala*, 12: 76.

Mani, A., Naidu, P. H. & Madhavachari, S. (1987). Occurrence and control of *Meloidogyne incognita* on turmeric in Andhra Pradesh, India. *International Nematology Network Newsletter*, 4: 13–18.

Mathur, R. L., Mathur, B. N. & Handa, D. K. (1969). Additions to host records of root-knot nematodes. *Nematologica*, 15: 160–161.

Mohandas, C. & Ramana, K. V. (1982). *Trophotylenchulus floridensis* Raski, a new endoparasite of *Piper nigrum* L. from Kerala. *Journal of Plantation Crops*, 10: 53–54.

Mohandas, C. & Ramana, K. V. (1983). Effect of different levels of *Meloidogyne incognita* on plant growth of two cultivars of black pepper (*Piper nigrum* L.) Abstracts of papers, *Third Nematology Symposium Organized by Nematological Society of India*, Himachal Pradesh Krishi Viswa Vidyalaya, Solan, Himachal Pradesh, India: 9–10.

Mohandas, C. & Ramana, K. V. (1987*a*). Slow wilt disease of Black pepper and its control. *Indian Cocoa, Arecanut and Spices Journal*, 11: 10–11.

Mohandas, C. & Ramana, K. V. (1987*b*). Pathogenicity, seasonal prevalence and control of plant parasitic nematodes Associated with Black Pepper. *Proceedings of the Third Group Discussions on the Nematological Problems of Plantation Crops. October, 29–30, 1987.* Sugarcane Breeding Institute, Coimbatore, Tamil Nadu, India: 44–45pp.

Mohandas, C., Ramana, K. V., & Raski, D. J. (1985). *Trophotylenchulus piperis* n.sp. parasitic on *Piper nigrum* L. in Kerala, India (Nemata: Tylenchulidae), *Revue de Nematologie*, 8: 97–102.

Mustika, I. (1978). An observation on the relationship between nematode population and yellow disease on black pepper in Bangka. *Pemberitaan Lembaga Penelitian Tanaman Industri, Indonesia*, 30: 11–19.

Mustika, I. & Zainuddin, N. (1978). Efficacy tests of some nematicides for the control of nematodes on black pepper *Pemberitaan Lembaga Penelitian Tanaman Industri, Indonesia*, 30: 1–10.

Nagakura, K. (1930). Über den Bau and die Lebengeschichte der *Heterodera radicicola* (Greef) Muller". *Japanese Journal of Zoology*, 3: 95–160.

Nambiar, M. C. (1977). *Proceedings of the National Seminar on Pepper. December 19, 1977.* Central Plantation Crops Research Institute, Kasaragod, Kerala, India: 4–6.

Nirula, K. K. & Kumar, R. (1963). Collateral host plant of root-knot nematodes. *Current Science*, 32: 221–222.

Orton Williams, K. J. (1980). Plant parasitic nematodes of the Pacific. *UNDP/FAO-SPEC Survey of Agricultural Pests and Diseases in the South Pacific. Technical Report.* Volume 8. St. Albans, UK, Commonwealth Institute of Helminthology, 192pp.

Parihar, A. (1985). Population level studies of the root-knot nematode, *Meloidogyne incognita* (Kofoid and White, 1919) Chitwood, 1949 on ginger (*Zingiber officinale*, Rosc) *Indian Journal of Nematology*, 15: 292. (Abstr.)

Pasril, W. (1976). Studies on yellow disease in black pepper on the island of Bangka. *Pemberitaan Lembaga Penelitian Tanaman Industri, Indonesia*, 21: 64–79.

Patel, D. J., Makadia, B. M. & Shah, H. M. (1982). Occurrence of root-knot on turmeric (*Curcuma longa* L.) and its chemical control. *Indian Journal of Nematology*, 12: 168–171.

Patel, D. J., Patel, S. T. & Jogani, D. K. (1986). Preliminary screening of Cumin varieties against root-knot nematodes. *Indian Journal of Nematology*, 16: 130.

Pegg, K. C., Moffett, M. L. & Colbran, R. C. (1974). Disease of ginger in Queensland. *Queensland agricultural Journal*, 100: 611–618.

Rama, K. (1987). *Ecology of plant parasitic nematodes affecting some major perennial crops in West Bengal.* Ph.D. Thesis, University of Visva-Bharati, India, 276pp.

Rama, K. & Das Gupta, M. K. (1985). Physical ecology of plant pathogenic nematodes associated with ginger in Darjeeling District, West Bengal. *Indian Journal of Nematology*, 15: 284–285. (Abstr.)

Ramana, K. V. (1986). Slow-wilt disease of black pepper and the role of plant parasitic nematodes in its etiology. *Proceedings of the Second Group Discussion on Nematological Problems of Plantation Crops. April 24–25, 1985.* Central Coffee Research Station, Balehonnur, Karnataka, India: 17–21.

Ramana, K. V. & Mohandas, C. (1983). Plant-parasitic nematodes associated with black pepper (*Piper nigrum* L.) in Calicut district, Kerala. *Abstracts of papers, Third Nematology Symposium Organized by Nematological Society of India. Himachal Pradesh Krishi Viswa Vidyalaya, Solan, Himachal Pradesh, India*: 9.

Ramana, K. V. & Mohandas, C. (1986). Reaction of black pepper germplasm to root-knot nematode, *Meloidogyne incognita. Indian Journal of Nematology*, 16: 138–139.

Ramana, K. V. & Mohandas, C. (1987*a*). Plant parasitic nematodes associated with black pepper (*Piper nigrum* L.) in Kerala. *Indian Journal of Nematology*, 17: 62–66.

Ramana, K. V. & Mohandas, C. (1987*b*) Nematological Problems in Black pepper (*Piper nigrum* L.) *Proceedings of the Third Group Discussions on the Nematological problems of Plantation Crops. October, 29–30, 1987*, Sugarcane Breeding Institute, Coimbatore, Tamil Nadu, India: 43–44.

Ramana, K. V., Mohandas, C. & Balakrishnan, R. (1987*a*). Role of plant parasitic nematodes in the slow-wilt disease complex of black pepper (*Piper nigrum* L.) in Kerala. *Indian Journal of Nematology*, 17: 225–230.

Ramana, K. V. Mohandas, C. & Ravindran, P. N. (1987*b*). Reaction of black pepper germplasm to the burrowing nematode, (*Radopholus similis*). *Journal of Plantation Crops*, 15: 65–66.

Rashid, A., Khan, F. A. & Khan, A. M. (1973). Plant parasitic nematodes associated with vegetables, fruits, cereals and other crops in North India. I. Uttar Pradesh. *Indian Journal of Nematology*, 3: 8–23.

Reddy, D. B. (1977). Pests, diseases and nematodes of major spices and condiments in Asia and the Pacific. *Technical Document 108–14, Plant Protection Committee for the South East Asia and Pacific Region*, FAO, Bangkok, 14pp.

Reddy, D. B. (1978). Insect pests, diseases and nematodes of areca palm (*Areca catechu* L.) and betel vine (*Piper betle*) recorded in Asia and the Pacific. *Technical Document No. 114, Plant Protection Committee for the South East Asia and Pacific Region, FAO*, 6pp.

Routaray, B. N., Mohapatra, M. P. & Das, S. N. (1987*a*). Effects of *Meloidogyne incognita* on ginger, *Zingiber officinale* Rosc. *Indian Journal of Nematology*, 17: 327–329.

Routaray, B. N., Sahoo, H. & Das, S. N. (1987*b*). Nemic associations of ginger and turmeric in Orissa. *Indian Journal of Nematology*, 17: 122–123.

Sarma, Y. R., Nambiar, K. K. N. & Nair, C. P. R. (1974). Brown rot of turmeric. *Journal of Plantation Crops* 2: 33–34.

Sen, K. & Das Gupta, M. K. (1977). Additional hosts of the root-knot nematode, *Meloidogyne* spp. from India. *Indian Journal of Nematology*, 7: 74.

Shah, H. M. & Patel, D. J. (1979). Occurrence of root-knot disease in cumin. *Indian Journal of Nematology*, 9: 179–180.

Shah, J. J. & Raju, E. C. (1977). Histopathology of ginger (*Zingiber officinale*) infested by soil nematode *Meloidogyne* sp. *Phyton*, 16: 79–84.

Sharma, R. D. & Loof, P. A. A. (1974). Nematodes of cocoa region of Bahia, Brazil. IV. Nematodes in the rhizosphere of pepper (*Piper nigrum* L.) and clove (*Eugenia caryophyllata* Thumb). *Revista Theobroma*, 4: 26–32.

Sheela, M. S. & Venkitesan, T. S. (1981). Inter-relationships of infectivity between the burrowing and root-knot nematodes in black pepper, *Piper nigrum* L. (Abstr.) *Indian Journal of Nematology*, 11: 105.

Shenoy, J. R. (1985). Betel vine cultivation. *Indian Cocoa, Arecanut and Spices Journal*, 18: 84–85.

Sher, S. A., Chunram, C. & Pholcharoen, S. (1969). Pepper yellows disease and nematodes in Thailand. *FAO Plant Protection Bulletin*, 17: 33.

Sivakumar, M. & Marimuthu, T. (1984). Parasitic nematodes associated with betel vine (*Piper betle* L.) in Tamil Nadu. *Madras agricultural Journal*, 71: 108–110.

Sivakumar, M. & Marimuthu, T. (1986*a*). Population dynamics of phytonematodes associated with betel vine (*Piper betle* L.), banana and paddy with special reference to crop rotation. *Indian Journal of Nematology*, 16: 277.

Sivakumar, M. & Marimuthu, T. (1986*b*). Efficacy of different organic amendments against phytonematodes associated with betel vine (*Piper betle* L.) *Indian Journal of Nematology*, 16: 278.

Sivakumar, M. & Marimuthu, T. (1987). Preliminary studies on the effect of solarization on phytonematodes of betel vine. *Indian Journal of Nematology*, 17: 58–59.

Sivakumar, M. & Muthukrishnan, T. S. (1985). Record of *Criconemella parvula* (Siddiqi, 1961) De Grisse & Loof 1961 in South India. *Indian Journal of Nematology*, 15: 254.

Sivakumar, M., Natarajan, S. & Balasubramaniam, M. (1987). Nematode pests of betel vine (*Piper betle* L.) and their management. *Proceedings of the Third Group Discussions on the Nematological Problems of Plantation Crops. October 29–30, 1987*, Sugarcane Breeding Institute, Coimbatore, Tamil Nadu, India: 34–35.

Sosamma, V. K., Sundararaju, P. & Koshy, P. K. (1979). Effect of *Radopholus similis* on turmeric. *Indian Journal of Nematology*, 9: 27–31.

Sukumaran, S. & Sundararaju, P. (1986). Pathogenicity of *Meloidogyne incognita* on ginger (*Zingiber officinale Rosc.). Indian Journal of Nematology* 16: 258.

Sukumaran, S., Koshy, P. K. & Sundararaju, P. (1986). Effect of root-knot nematode, *Meloidogyne incognita* on the growth of turmeric. *Abstracts of Papers. Seventh Symposium on Plantation Crops. October 16–19, 1986*, Coonnor, Nilgiris, Tamil Nadu, India: 33.

Sundararaju, P. & Suja, C. P. (1986). Occurrence of *Radopholus similis* on betel vine (*Piper betle* L.) in Karnataka. *Indian Journal of Nematology*, 16: 279.

Sundararaju, P., Koshy, P. K. & Sosamma, V. K. (1979*a*). Plant parasitic nematodes associated with spices. *Journal of Plantation Crops*, 7: 15–26.

Sundararaju, P., Koshy, P. K. & Sosamma, V. K. (1979*b*). Survey of plant parasitic nematodes associated with spices in Kerala and Karnataka. *Proceedings of the Second Symposium on Plantation Crops (Plant Protection), Ootacamund, Tamil Nadu, India*: 39–44.

Sundararaju, P., Sosamma, V. K. & Koshy, P. K. (1979*c*). Pathogenicity of *Radopholus similis* on ginger. *Indian Journal of Nematology*, 9: 91–94.

Swarup, G., Nath, R. P. & Sethi, C. L. (1967). The plant parasitic nematode genus *Rotylenchulus* in India. *Indian Phytopathology*, 20: 118–123.

Timm, R. W. (1965). *A preliminary survey of the plant parasitic nematodes of Thailand and the Philippines*. South East Treaty Organization, 71pp.

Van Der Vecht, J. (1950). Plant Parasitic Nematodes. In: Karshoven, L. G. E. & Vecht, J. V. d. (Eds). [*Diseases of cultivated plants in Indonesia Colonies*] I.S'gravenhage, W.van Woeve: 16–45.

Venkata Rao, A., Narasimhan, V., Rajagopalan, P., Vidyasekharan, P. & Muthukrishnan, T. S. (1973). Efficacy of nematicides for the control of betel vine wilt. *Indian Journal of Agricultural Science*, 43: 1072–1075.

Venkitesan, T. S. (1972). On the occurrence of plant parasitic nematodes associated with different crops in Cannanore district, Kerala. *Agricultural Research Journal of Kerala*, 10: 179–180.

Venkitesan, T. S. (1976). *Studies on the burrowing nematode*, Radopholus similis *(Cobb, 1893) Thorne, 1949 on*

pepper (Piper nigrum *L.) and its role in slow wilt disease*. Ph.D. Thesis. Department of Plant Pathology, University of Agricultural Sciences, Bangalore, India, 122pp.

Venkitesan, T. S. & Jacob, A. (1985). Integrated control of root-knot nematode, infecting pepper vines in Kerala. *Indian Journal of Nematology*, 15: 261–262.

Venkitesan, T. S. & Setty, K. G. H. (1977). Pathogenicity of *Radopholus similis* to black pepper (*Piper nigrum*). *Indian Journal of Nematology*, 7: 17–26.

Venkitesan, T. S. & Setty, K. G. H. (1978). Reaction of 27 black pepper cultivars and wild forms to the burrowing nematode, *Radopholus similis* (Cobb) Thorne. *Journal of Plantation Crops*, 6: 81–83.

Venkitesan, T. S. & Setty. K. G. H. (1979). Control of the burrowing nematode *Radopholus similis* (Cobb) on black pepper. *Pesticides*, 13: 40–43.

Verma, S. K. & Prasad, S. K. (1969). The reniform nematode, *Rotylenchulus reniformis* Linford and Oliveira, 1940. II. Studies on control. *Indian Journal of Entomology*, 32: 68–72.

Vilsoni, F., McClure, M. A. & Butler, L. D. (1976). Occurrence, host range and histopathology of *Radopholus similis* in ginger (*Zingiber officinale*). *Plant Disease Reporter*, 60: 417–420.

Viswanathan, P. R. K., Kumar, A. C. & D'Souza, G. I. (1974). Nematode association of Cardamom in South India. *Cardamom News*, 6: 5, 19.

Wahid, P. A., Kamalam, N. V. & Venugopal, V. K. (1982). Mineral nutrition of slow wilt affected black pepper (*Piper nigrum* L.). *Journal of Plantation Crops*, 10: 21–25.

Winoto, S. R. (1972). Effect of *Meloidogyne* species on the growth of *Piper nigrum* L. *Malaysian agricultural Research*, 1: 86–90.

Chapter 19

Effects of Tropical Climates on the Distribution and Host-Parasite Relationship of Plant Parasitic Nematodes

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Influence of Climate on the Distribution of Plant Parasitic Nematodes

Climate influences all components of nematode life-processes and host-parasite relationships. The importance of a single climate-related factor is demonstrated by the absolute dependence of existing nematode population models on temperature as the driving variable (Duncan & Noling, 1987). Moisture is also a principle determining factor in nematode population dynamics, but usually manifests its effects in terms of seasonal cycles due to wet/dry seasons (Egunjobi, 1974; Guiran & Germani, 1980). Otherwise, nematodes can survive wherever there is sufficient moisture for the host. On a global scale, climate affects nematode distributions primarily through influence on the geographic distribution of specific host plants. The determination of host ranges may be the most important effect of climate on global occurrences of important species. Geographic maps of nematode distributions are often no more than maps of the distributions of economically important host crops.

The effects of climate on nematode distributions can be seen in a comparison of species prominence by regions, reported by Sasser and Freckman (1987). On a worldwide basis, *Meloidogyne* is the most important plant parasitic genus, followed by *Pratylenchus*, and *Heterodera*. In the cooler climates of Europe, however, *Heterodera* is the most important genus, followed by *Globodera*, with *Meloidogyne* third in importance. Similar distribution effects can be seen within tropical countries, with distinct climatic zones ranging from hot, humid coastal lowlands to cool, temperate mountainous regions, showing corresponding shifts in cropping systems and predominate species (i.e. *Meloidogyne*-/vegetable to *Globodera*/potato).

However, it is likely that most nematode life-processes have thermic optima. Norton (1978) has tabulated optimum temperatures for a number of important species, which show a considerable range in preferred temperatures. These optima determine the ideal geographic ranges of nematodes, where host-range considerations are removed. Presumably, there are southern and northern hemisphere bands of appropriate temperatures for each nematode species. These bands would be contiguous and would meet at the Equator for true tropical species.

Plant Parasitic Nematodes in Subtropical and Tropical Agriculture M. Luc, R. A. Sikora and J. Bridge (eds)

Nematode activities also have thermic 'critical points'. There are different critical points for specific nematode life stages, and for different parts of the growing season. As an example, *Globodera rostochiensis* declines rapidly at temperatures above 26°C (Trudgill, 1970), whereas in contrast, *Pratylenchus brachyurus* and *P. zeae* develop most rapidly above 30°C (Olowe & Corbett, 1976). Temperatures above or below these seasonal, stage-specific critical points exclude species from unsuitable climatic regions. Within critical temperature ranges, host availability, parasitic fitness, soil types, and moisture determine species dominance.

Availability of moisture may determine the geographic distributions of nematodes by limiting survival during wet or dry seasons. Obviously, where long dry periods are common, only those species with drought-resistant survival stages will occur. However, moisture may have a greater effect on nematode distribution by determining host availability, crop management patterns, and irrigation practices. A nematode which attacks only soybean, such as *Heterodera glycines* is not likely to occur in a dryland farming system unsuitable for soybeans, even though this cyst-forming nematode may be quite capable of surviving long periods without moisture. Conversely, availability of irrigation on limited portions of land in dryland areas often leads to intensive, non-stop cultivation of badly needed vegetable crops. These intensive irrigated systems often give rise to nematode problems which would not build up to damaging proportions in a rainfed system.

Soil types have a definite effect on the occurrence and densities of plant parasitic nematodes. Where soil types interact with climate, or where soil types are extremely heterogeneous over a climatic zone, it is difficult to isolate effects of climate and soil characteristics. Additionally, climatic factors such as annual rainfall levels and temperature extremes will affect soil structure and chemistry, leading to further circular correlations in our attempts to separate the various effects.

Climate-dependent distributions of important genera

Meloidogyne

The four major species of *Meloidogyne, M. incognita, M. arenaria, M. hapla*, and *M. javanica* have identifiable climatic associations (Sasser, 1977; Taylor & Sasser, 1978; Abu-Gharbieh, 1982). *M. hapla* is more common in cooler climates, whereas *M. incognita* is more common in warm, humid subtropical and tropical areas. *M. javanica* prevails in extreme moisture conditions (wet or dry) (Whitehead, 1969; Abu-Gharbieh, 1982), and has a slightly higher temperature requirement than *M. incognita*. The range of *M. incognita* and *M. arenaria* overlap in terms of climate, with the prevalence of one or the other probably dependent on host suitability and the deployment of *M. incognita*-resistant cultivars (Schmitt & Barker, 1988). Other important species, such as *M. exigua* and *M. naasi*, have apparent climatic associations, but because of their specific host ranges, the distributions are confounded by the concurrent distributions of their primary hosts.

Cyst forming species

Definite climate and latitude associations occur within this group. Compared to *Meloidogyne* spp., however, the cyst nematodes have very limited host ranges, which make it difficult to distinguish climatic effects on the nematode from effects on distributions of the hosts. For most of the species on which sufficient information has been compiled, there seems to be a marked tendency to favour cooler climates. *Globodera rostochiensis* and *G. pallida* are found in cool northern climates of Europe, and in the higher elevations of the tropics (Evans & Stone, 1977; Mai, 1977; Sikora, 1982), which are also the areas suitable for growth of potato, their most significant host. Populations north of 15 degrees latitude in South America are primarily *G. pallida*, whereas south of that line most populations are *G. rostochiensis* (Evans *et al.*, 1975). Evans and Stone (1977) have suggested that potato cyst nematodes may not establish infestations where soil temperatures rise above 30°C. Trudgill (1970) also has reported that low temperatures favour survival of *Globodera*, a survival strategy which perhaps results from co-evolution with potato.

Heterodera glycines is found primarily in temperate areas (Riggs, 1977), but these are also the areas suitable for growth of soybean. There is no evidence, however, that soybean cyst is less suited to the warmer climates of the southern U.S. *Heterodera avenae* is found most frequently in temperate and semi-arid temperate regions throughout the world (Meagher, 1977; Sikora, 1988). The cereal cyst nematode has many hosts in the Graminae, which may account for its widespread occurrence, but the limitation of this distribution to temperate regions lends support the concept of low temperature optima.

Other genera

Helicotylenchus multicinctus has been looked upon primarily as a tropical pest of bananas (McSorley & Parrado, 1986), but recently this nematode has been reported in association with decline of pine trees in the Southern U.S. (Sharma *et al.*, 1989). However, there are some plant parasitic nematodes which appear to be true tropical species, i.e. with high-temperature requirements. *Radopholus similis s.l.* has more than 250 host species, including many crops widely grown in temperate climates, but occurs primarily in tropical and subtropical climates (O'Bannon, 1977). *Rotylenchulus reniformis* also has a broad host range, including many temperate crops, yet is limited to tropical/subtropical areas, including the extreme southern U.S. A relatively high optimum for development, 29.5°C, has been reported for this species (Rebois, 1975). Undoubtedly, there are other true 'tropical species', which require uniform high temperatures, regardless of host ranges.

Effect of Climate on the Distribution of Plants and Subsequent Impact on Nematode Distribution and Control

Increases in the yield of major crops worldwide has for the most part occurred in growing areas where environmental conditions were naturally favourable for the crop, or had been made so by human activities and inputs (Brinkman, 1986). Future crop production increases will depend on increasing yields of many crops in marginal areas in subtropical and tropical regions. In order to develop research programmes on crop improvement many international agricultural research centres are attempting to classify agro-ecological zones in attempts to determine the factors causing low yields in these marginal areas.

The agro-ecological environment of crop, land use or a farming system has physical, chemical and biological aspects that may vary across space and time (Brinkman, 1986). These factors influence rotations, cultivars and agronomic practices used in a particular climatic zone vary greatly.

Humboldt and Bonpland (1807) recognized this fact when they published the results of their studies on the distribution of plants in the tropics under the title "Ideas for a Geography of Plants". This new branch of botany was to study the distribution of various climates based on the main actors, temperatures, humidity, atmospheric pressure, and electric tension as well as plant communities, the spread of plant diseases and the development of botanical maps (Weltzien, 1972). "Geophytopathology" is a well understood field in plant pathology (Weltzien, 1967); the importance of "Geophytonematology" has not been seriously examined.

The study of nematode-host distribution in agro-ecological zones could have significant impact on tropical and subtropical agriculture, where crop production systems are being "modernized" away from traditional production systems and especially where new crops are being introduced into a country. There are many examples that show the negative impact endemic and introduced species of plant parasitic nematodes have on an introduced crop: *H. glycines* on soybean, *H. schachtii* on sugarbeet, *R. reniformis* on pineapple, *Tylenchulus semipenetrans* on citrus.

Because plant distribution as well as plant growth is strongly regulated by the same climatic factors, the study of these factors could be used to predict the future importance of plant parasitic nematodes (both present or still absent) on an introduced crop. The study of the distribution of plants as affected by climate and mapping of environmental factors could lead to the improvement

of nematode control by: (1) determining which growing regions of specific crops have environmental factors favourable or unfavourable for specific nematode occurrence, (2) possibility of establishment upon introduction, and severity with time under the crop and (3) give plant protection research institutions time to develop appropriate integrated control practices that would prevent nematode build-up to damaging levels while optimizing yields.

Attempts have been made to use climatic factors, in particular soil moisture, to estimate optimum yield and growing regions in a country suitable for crop production. The possibility that examination of the interrelationship between climatic factors and plant distribution can be used to predict the probable distribution and loss impact of a particular nematode needs closer study. The distribution of *R. similis*, for example, on banana seems mainly determined by plant distribution, although other climatic factors may affect population buildup. Upland bananas in Tanzania are damaged by *P. goodeyi* with *R. similis* playing a minor role (Bridge, 1988; Sikora *et al.*, 1990). The potato and cereal cyst nematodes *G. rostochiensis* and *H. avenae* are similar examples of plant driven interrelationships between an obligate parasite and its major hosts. The interrelationship is not as clear with species of *Meloidogyne*, because of their wide host range.

Experimental methods

Nematode problems develop with time following the introduction of a new crop or cultivar into a region. Severe nematode problems could be avoided by studying the effect of climate on plant distribution and simultaneously determining the effect of the climatic and environmental conditions required by the plant on potential nematode pests.

A system to determine the natural potential of land, using "agro-ecological zones" based on temperature, water supply, length of growing periods and soil conditions has been developed (FAO, 1978). Jatzold (1982) developed a system that provided extension officers with a scheme that simplified decisions on which cultivars of a particular crop were best suited for a given locality.

A model was developed of water balance according to climate-crop-soil relationships. Climatic yield probabilities are calculated by comparing effective rainfall and water storage, with the curves of crop water requirements. The yield probabilities represent estimates for major soil texture classes according to water holding capacity. The main "agro-ecological zones" were then divided into "subzones" in accordance with the expected length of the growing season, needed for proper selection of cultivars. From this data an "ecological land used potential" was developed.

Nematologists using this model should be able to extrapolate future nematode problems by using available information on the moisture, temperature, and soil type requirements of potential nematode threats. Integrated control could be developed for a crop in a region regardless of knowledge of the absence or presence of a nematode in a particular zone.

A method has also been developed for defining micro-regions within larger regions where a particular crop is important (Carter, 1986). Specific nematode threats could be projected for each micro-region, based on preliminary survey sampling and ecological requirements of identified nematode species. This method could help to identify nematode problems and set research priorities.

Crop Loss Assessment in Tropical Regions

Plant-parasitic nematodes are major pests in the tropics, more so than in temperate areas. There are many reasons why nematodes may flourish to a greater extent in the tropics. Warm, humid tropical climates favour these poikilothermous, water-inhabiting organisms, and long growing seasons give rise to more reproductive cycles, and more rapid population increases. Heat stress may enhance the damage caused by nematodes. Compounding the problems, the farmers in this region typically have fewer chemical control options, and there are no resistant cultivars available for many important tropical crops.

Determination of crop losses may be done on macro and micro scales (Noe, 1988*a*). Macro assessments consist of large-scale geographic surveys to estimate losses for large regions. Micro

assessments are directed toward the determination of nematode-host relationships in individual fields or in other experimental units (glasshouse pots, microplots, or small field plots). The potential uses for information resulting from these two types of assessment range from the formulation of management recommendation models (micro) to the allocation of resources in research and other agricultural support activities (macro).

The two levels of assessment, macro and micro, are both necessary; large scale surveys are usually concerned with determining nematode distributions, whereas micro-scale information is necessary to translate survey counts into estimates of crop damage. Usually the experimental phase and survey should proceed together, since the information obtained from nematode surveys will be of little use in assessing crop losses until damage functions are available. Sasser and Freckman (1987) have attempted to assess nematode induced crop losses directly from authoritative estimates. Such surveys provide immediate information, but need to be verified through sampling and research programmes.

In order to assess the relative importance of plant parasitic nematodes in the tropics, the prominence of various species must be determined (extensity), as well as the intensity of damage caused by each species. Determining extensity is largely a matter of survey sampling, whereas intensity of damage levels must be determined in controlled crop-loss experiments. Climate impacts nematode damage functions and reproduction directly through temperature and moisture stress and indirectly by determining the types of cropping systems adapted to each region. Tropical cropping systems are generally more complex and diverse than their temperate counterparts (Ruthenberg, 1983), which makes the task of characterizing host-parasite relationships more difficult. Other complicating factors, such as multiple-species infestations, and differences among cultivars must also be considered in the analysis of nematode host-parasite relationships, although these problems are not unique to the tropics.

Effects of habitat diversity

Within tropical climates many strikingly different habitats occur, from warm, humid lowlands, to cooler, drier, mountain regions. Moisture levels also are diverse, ranging from continuously wet rain forests to deserts. Soil types vary within climatic regions and further diversify habitat. Soil type variations may result from variations in tropical climates, which produce heavily eroded acidic clays in high rainfall areas, and alkaline sands in the drier regions. In areas where tropical subsistence farming is common, nematode habitats may change rapidly within very small landholdings.

Effect on survey sampling

Tropical habitat diversities restrict attempts to characterize the predominance and importance of various nematode species. Species-habitat associations are strong, and any attempt to characterize populations will be limited in scope to the specific habitats studied. At best, surveys are representative of specific habitat types, i.e. hot-humid lowlands, moderate slopes, or cooler mountainous regions.

Experimental methods

Statistical sampling protocols must be designed to allocate a limited number of samples for efficient and precise estimates of species levels. Sampling costs are typically quite high, and travel may be difficult in many tropical regions. Particularly useful in tropical survey applications will be stratified and two-stage cluster sampling designs, with allocation of samples proportional to habitat ratios, and to the probabilities of occurrence of individual species within habitat (Fig. 1). In a well designed survey, long-distance travel between cluster centres will be minimized, while sampling efforts will be concentrated around clusters to maximize the information obtained in each locale. Precise, unbiased estimates of population characteristics can be obtained from cluster sampling by using appropriate formulas (Cochran, 1977).

Proportional allocation of samples is a technique whereby more samples are allocated to sampling

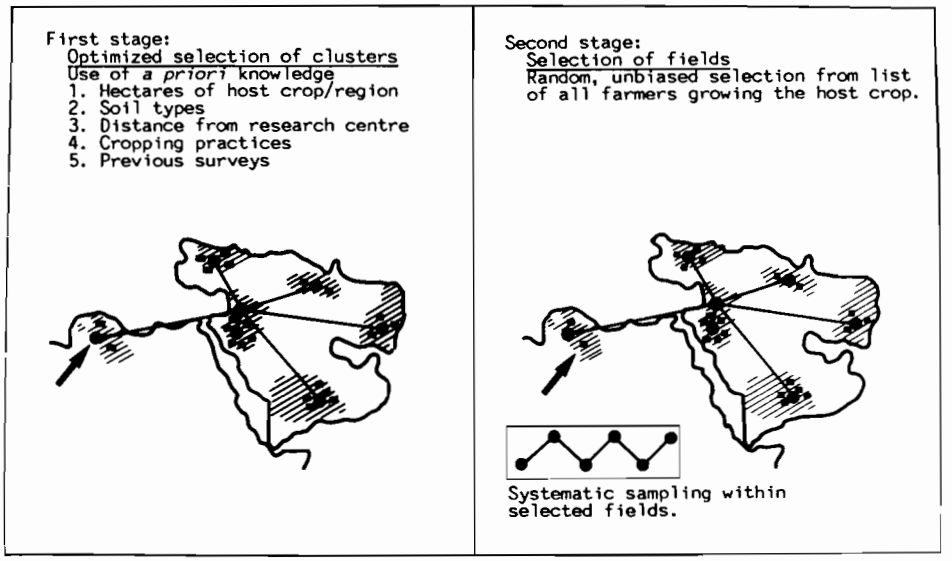

Fig. 1. Schematic diagram of two-stage cluster sampling design in which prior information is used to design the survey and allocate samples most efficiently. Such a sampling plan would provide a cost efficient and statistically valid method to survey a large region for plant parasitic nematodes.

areas that are more likely to contain the target species (based on previous knowledge) or to areas that represent a larger share of agricultural production (lowlands, river valleys, etc.). *A priori* information is critical in proportional allocation schemes, and useful data often are available in the literature. As an example, Schmiedecken (1981) has reported detailed mappings of zones of cultivation for economically important crops in Nigeria. These maps, based on isohygromenes (moisture contours) indicated distinct bands across the country containing areas ideal for cultivation of specific crops. Using these maps, a researcher could limit allocation of nematode survey samples to specific high-probability areas, and ignore regions unsuitable for cultivation of the host.

Sampling designs can be optimized for any appropriate criteria, and should be done according to the goals of the survey. Proportional allocation is simply a way to formalize utilization of existing knowledge. Specific formulas (Cochran, 1977) must be used to calculate population characteristics from proportional sampling plans, in order to obtain unbiased estimates.

Effect on host-parasite relationships

Attempts to characterize the levels of damage caused by plant-parasitic nematodes in tropical regions will be limited in usefulness by the variability of damage functions across different habitats. Moisture levels and soil types strongly affect host-parasite relationships. Variations in temperatures and rapid changes in elevations add to the complexity of determining nematode-induced crop damage.

Experimental methods

Experiments to determine crop-loss levels will require complex multifactorial designs with analyses of treatment interactions. These designs should allow determination of effects due to habitat variability, i.e. warm-humid vs cool-dry, sandy vs clay, etc., if the results are to have any general applications. Obviously, experiments conducted in the artificial uniformity of glasshouses will be of very limited predictive value. Efficient field experiments must be implemented in target habitats for accurate crop-loss determinations.

Crop losses may be predicted with a mathematical expression called a nematode damage function, relating crop performance to nematode counts at some critical point, i.e. preplant (Seinhorst, 1965;

Ferris, 1981). Preplant counts are especially important in annual crops since most management options for plant parasitic nematodes must be deployed prior to planting. In perennial crops, however, critical sampling times may vary during the growing season, and multiple-point damage functions are possible (Noling & Ferris, 1987).

Experimental methods for determining damage functions may include the use of glasshouse pots, microplots, and small field plots (Barker & Noe, 1987; Noe, 1988*a*). Regardless of the experimental unit used, the procedures are similar. A large range of nematode densities are established or identified in the soil, and crop performance is measured. Regression techniques or non-linear estimation can then be used to fit mathematical models.

Field and glasshouse research each have advantages and disadvantages. It is relatively easy to manipulate inoculum densities and to control experimental conditions in glasshouse pots. However, accurate yield estimates are difficult to obtain and results often do not correlate well with on-farm conditions. Also, relatively few nematode species lend themselves easily to culture and increase in glasshouse pots. Many nematodes, typically large ectoparasitic species, have not been increased successfully in the glasshouse, and for this reason may be overlooked in research programmes. Glasshouse methods are best suited for establishing the host status of a wide range of plant species and cultivars, but do not provide a suitable basis for management recommendation models.

Field plots offer an efficient and realistic alternative to glasshouse research in the determination of nematode host-parasite relationships. Plots can be established in naturally infested farmers' fields, and the underlying patchiness of nematode spatial patterns can be used to provide a wide range in population levels (Noe & Campbell, 1985; Barker & Noe, 1988). By locating plots in areas of high and low infestations, assaying nematode populations, and monitoring crop performance in each plot, sufficient information can be obtained to provide estimates of nematode damage functions. These estimates are likely to be more realistic than those obtained in glasshouse research, and by utilizing naturally infested fields, field designs may be more efficient in terms of minimizing resource demands. Important species that cannot be increased in glasshouse cultures need not be neglected in field research designs. Even more importantly, tropical habitat diversities can be included in the experimental design by replicating the plots in different regions/habitats. Individualized damage functions can then be formulated for each type of environment.

Microplots are small enclosed plots established in a systematic fashion in open fields, which may serve as an intermediate step between the glasshouse and field. These plots are usually fumigated before use and then infested with varying rates of nematode inoculum in a randomized design. Test crops are planted in each microplot and may be allowed to grow to maturity. Crop yields and nematode population dynamics can be monitored in each plot.

Use of microplots to determine nematode damage functions has some of the advantages and disadvantages of both glasshouse and field research. Nematode inoculum must be produced in large quantities to infest the microplots, and for many nematode species, it is not possible to produce enough inoculum to infest microplots at high population densities. It may be feasible, however, to use previously infested soil, or to allow inoculum to build up naturally. Different soil types can be placed in microplots located at the same site, which allows evaluation of the effects of soil habitat diversity without interacting climate effects. Microplots placed in open fields should provide more realistic estimations of host-parasite relationships than do glasshouse pots.

Effects of other tropical factors

Length of growing season

Although many different soil types and moisture regimes occur in the tropics, temperatures are uniformly high, and continuous cultivation of crops is possible through most of the region. Extended growing seasons affect nematode population dynamics by allowing more rapid development of degree-day dependent life stages, and ultimately increasing the number of reproductive cycles.

The lack of overwintering or fallow periods will maintain high population levels once established.

Thus, the long growing seasons may increase nematode pressures, although the underlying damage functions are unaffected. Nematodes which are typically slow to develop, and would not be a problem in temperate areas, may increase to damaging levels in the tropics. On the other hand, fallow periods in the tropics may decrease nematode levels more effectively than in temperate regions. Increased metabolic activity at higher temperatures would cause a more rapid depletion of food reserves, whereas overwintering nematodes in cooler climates are "refrigerated" during the fallow period. The typical long growing seasons found in the tropics may present additional problems for assessing and predicting crop damage, but these conditions also will offer unique opportunities in determining host-parasite relationships.

Experimental methods

If crops are grown on a more or less continuous basis, then nematode population levels must be monitored throughout the year. Information on the population dynamics of target species under each crop is essential to designing a management/recommendation programme (Barker *et al.*, 1985). To obtain the required assays, plots should be established systematically throughout each field to be monitored. McSorley (1987) has enumerated procedures for establishing field plots for use in nematological research.

In an efficient sampling scheme, soil cores (10–15 per plot) should be collected systematically from within plant rows, or root zones, and bulked for nematode extraction (Fig. 2) (Barker & Campbell, 1981). Where crops are interplanted, soil from the root zones of each crop should be

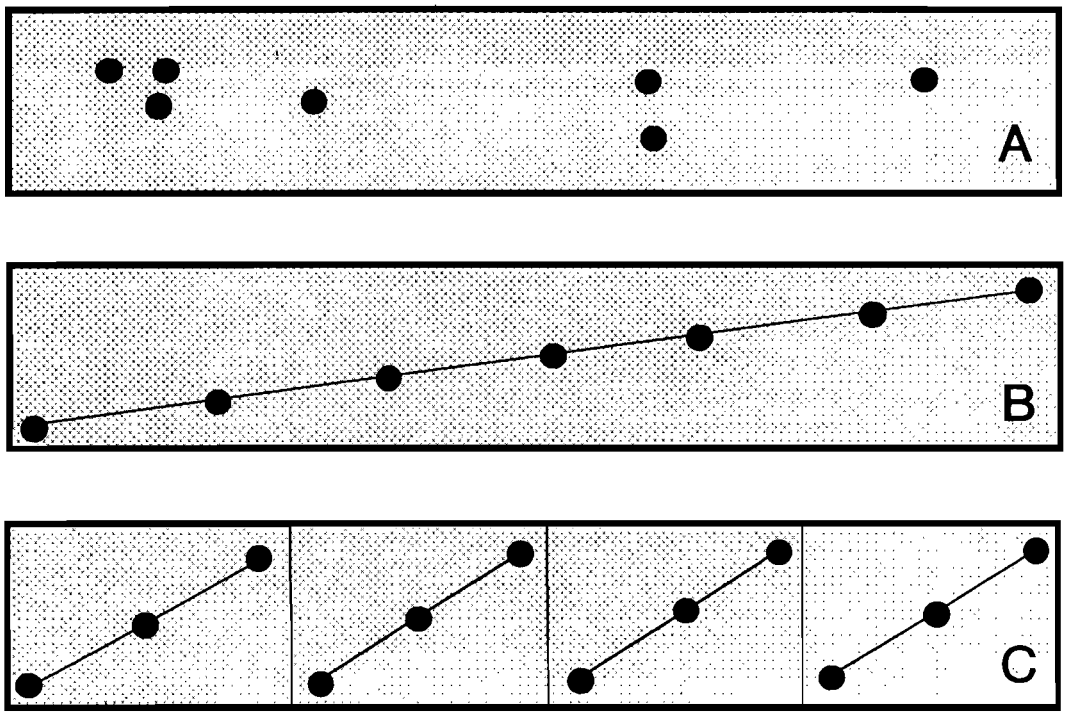

Fig. 2. Three examples of sampling patterns for nematode field assays. A truly random pattern for collecting soil cores (A) is difficult to set up, and may not be efficient for spatially aggregated populations. A systematic sample (B) is easier to implement in the field, and will provide a better estimate of overall nematode population levels. Systematic sampling often can be improved by partitioning the allocation of samples into distinct strata (C) according to soil types, or cropping histories.

processed separately, if possible. Nematode counts must be corrected for the efficiency of extraction methods used (Ferris, 1987), to allow interpretation of the results by other researchers. The same plots should be sampled at regular intervals, to facilitate determinations of density-dependent population increases and decreases. After sampling at frequent intervals in the initial phase, future sampling programmes can be established to monitor nematode populations when they are at their peaks, thus increasing the probability of detection, and precision.

Subsequent predictions of damage can be based on peak population levels under a previous crop, assuming a brief or non-existent fallow period between cycles. This procedure could provide increased precision in crop-loss predictions, by increasing sampling precision at critical times. A previously planted crop also can serve as an *in situ* bioassay (Barker, 1985). Nematode species which have obvious external signs or symptoms (root-knot, cyst) can be assayed in the field by scouts with limited training. Such a programme would not be possible in temperate regions, where the cropping season is preceded by a cold period unsuitable for on-site bioassays.

By monitoring nematode population levels periodically, predictive damage functions can be developed for multiple-cropping seasons (Noe, 1988*b*). Critical-point models may be used to describe the relationship of nematode densities under a previous crop to performance of the next crop. If the previous crop is a non-host, then a limited number of bioassay plants can be planted in infested fields along with the non-host, to serve as indicators for subsequent pressure on a host. Data from soil assays and bioassays should be monitored throughout a multiple-cropping season to determine the optimum times in a cropping sequence to plant susceptible crops.

Cropping patterns

Tropical conditions lend themselves to numerous patterns of planting and managing crops (Ruthenberg, 1983). However, much of the large-scale commercial agricultural production is done with practices similar to those used in temperate regions, and analysis of nematode-crop relationships in these systems can be done with well-established traditional research approaches (Ferris, 1981; Barker & Noe, 1987; Barker & Noe, 1988). However, other more complex production systems, such as intercropping, relay planting, and mixed plantings often are used in the tropics (Fig. 3). Also, perennial crops are more widely grown for food and export. Each of these cropping patterns will have profound effects on the experimental methods used to determine nematode host-parasite relationships. Certain land use patterns, such as slash and burn, bush fallow, and shifting cultivation are also unique to the tropical regions. Analysis of these important subsistence-level systems has been discussed by Noe (1988*b*).

Interplanted systems

Where different host plants are grown in combinations within a field, characterization of host-parasite relationships are extremely difficult. Effects on crop damage may be positive or negative. If appropriate combinations of host and non-hosts are used, interplantings may reduce nematode pressures by limiting spread and reproduction. Yield compensation may also occur, if one crop is capable of increased growth in the presence of a nematode-stunted intercrop. On the other hand, relay planting (the second crop is planted between the rows of the first crop prior to harvest) could be disastrous if both crops were hosts; relay planting would provide obligate plant parasites with a never-ending source of food. Mixed planting (where various crops are planted in an area with little regard for rows or distinct planting zones) would be functionally similar to interplanting and relay planting. The most difficult and important challenge in the experimental analysis of host-parasite relationships in these systems is to determine representative functions for each crop, and for the various combinations.

Experimental methods

Crop damage functions should be derived for each crop separately and in combination with the other crop(s) to determine compensating interactions. Basic factorial experimental designs would

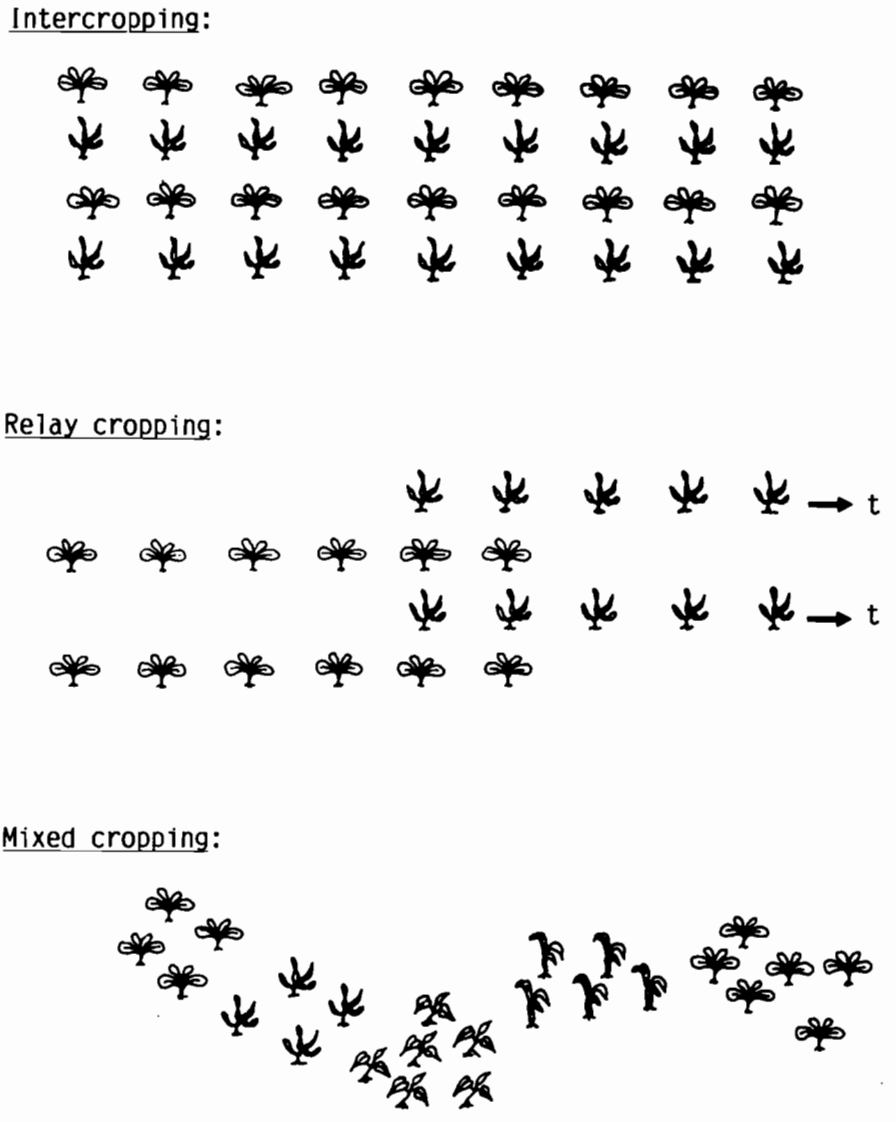

Fig. 3. Examples of interplanting schemes which may occur in tropical cropping systems. In relay cropping, a second crop is planted late in the growing season (t), but before the first crop is harvested, whereas in an intercrop both are planted at the same time. In mixed cropping, various crops are planted in small clusters at different times with no regard for delineation of rows.

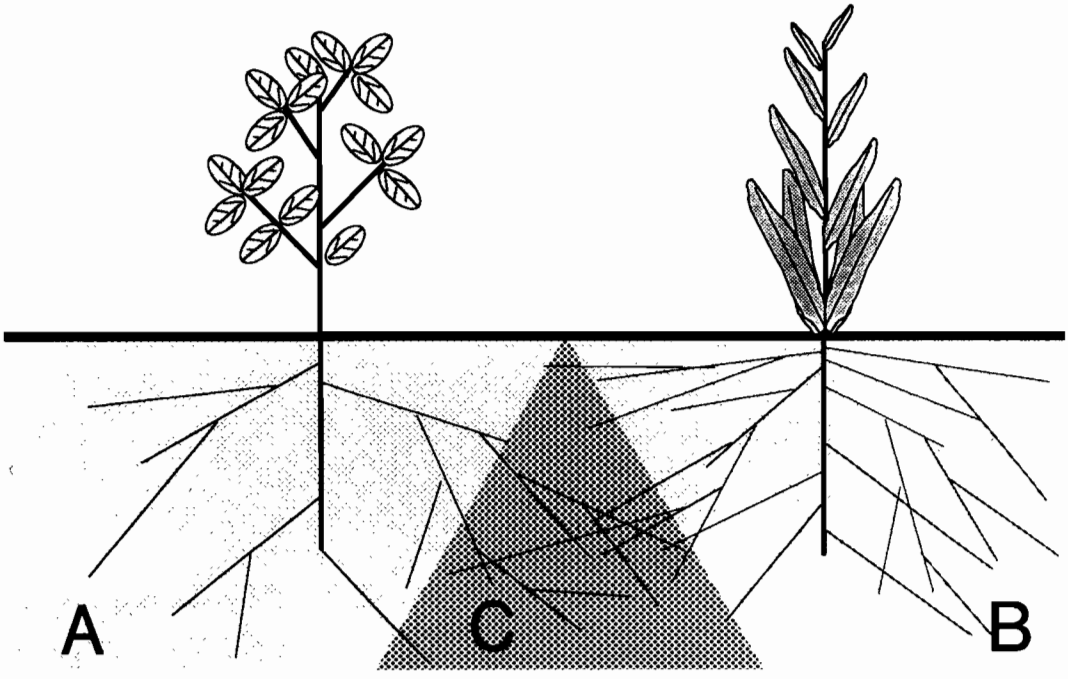

Fig. 4. Partitioning of root zones in an intercropping system. Nematode host-parasite relationships may be partitioned into functions representing the relative volumes of root zones for each crop (A+C, B+C), or into three distinct areas, with two zones representing the roots of each crop (A,B) and one zone for the area where roots overlap (C). The correct partitioning model depends on the host status of each crop in the system.

suffice, as long as all combinations are considered and statistical interactions are analyzed. For estimates representing total productivity of the interplanting, multivariate models or linked differential equation systems would be required (Noe, 1988*b*).

Although the problem of sorting out host-parasite relationships in multiple-cropping systems is complex, it is an achievable goal if approached systematically. Three discrete situations should be considered. In the simplest case, only one of the crops may be a host. In this system, the intercrop may be treated as a single crop for estimation of host-parasite relationships.

In a more complicated system, both crops may be a host, so that reproduction and feeding activities must be partitioned between the crops. An approach to the partitioning could be based on estimates of the relative root-zone sizes of the two crops, assuming that nematodes parasitize the hosts in proportion to the relative volume of roots (Fig. 4). Relative infestation levels could then be linked to damage functions for each crop. An additional refinement of the allocation would include a measure of preference for one host or the other. In a spatial context, the nematode habitats in a two-host system can be divided into three regions; two regions near each of the host plants, containing only the roots of the nearby crop, and a third region of overlap containing roots of both plants (Fig. 4).

Finally, both crops in an interplant may be non-hosts. The only complication in this system arises in analysis of population dynamics, where the nematodes may decrease more rapidly under one crop than the other. Each of these situations can be analyzed and estimates of relative relationships obtained from complete factorial research designs, utilizing field plots or microplots. Multiple species infestations can also be considered in the interplant system, by further partitioning of damage components among the important species (Noling, 1987).

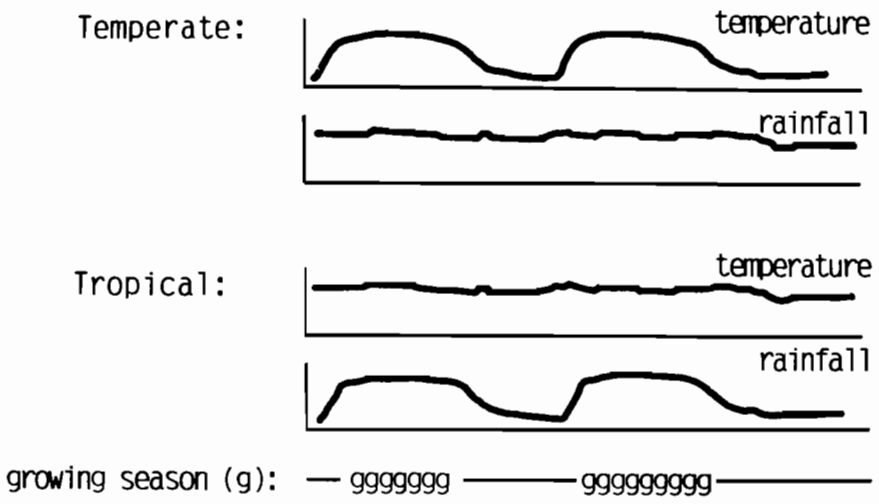

Fig. 5. Delineation of growing season cycles in temperate and tropical regions. Often, a dry season in the tropics substitutes for the overwintering period in cooler climates, for the purpose of delimiting fallow periods and defining nematode population dynamic cycles.

Perennial crops

Evaluation of the increased dependency on perennial crops in the tropics requires careful delineation of long-term host-parasite relationships. Continuous presence of the host, coupled with uniformly warm, humid climates will lead to more intense and rapid development of nematode management problems. It is unlikely that preplant treatments, such as soil fumigation, will hold up for very long. Emphasis will be placed on post-plant management practices which limit nematode population increases and/or resulting damage. Effective timing and deployment of these damage-limiting practices will depend on a careful elucidation and continuous monitoring of host-parasite relationships.

Experimental methods

Crop-loss models for perennials are based on multiple-point models, with damage estimates updated at subsequent assay points throughout the life-stages of the crop and nematode (Noling & Ferris, 1987). Population dynamics in the tropics differ from temperate systems, since there is no winter period. However, dry seasons affect population development in tropical areas in a manner similar to overwintering (Fig. 5). A detailed characterization of annual system dynamics is required to establish appropriate sampling times for multiple-point damage functions.

A suitable experimental design would begin with establishment of the required number of sampling sites systematically within a crop area. The optimum number of samples can be calculated from predetermined formulas (Barker & Campbell, 1981; Barker *et al.*, 1985). For tree crops, a single tree may constitute a sampling unit (McSorley & Parrado, 1982). Nematode assays then are obtained at frequent intervals throughout the growing season, and crop performance is monitored for each site. Nematode assays should include root and soil fractions, and identify life stages of the target nematode.

Summary

The tropics provide unique nematode environments. There are clearly tropical nematode species, which thrive only in the uniformly warm regions, and there are tropical associates of crops which are cultivated only in this region. Long growing seasons and moderate humid climates are ideal for

the development of intense nematode infestations. Even in dry tropical areas, nematode problems are enhanced by intensive cultivation of irrigated lands. In order to assess the distribution and importance of plant parasitic species in the tropics, unique experimental methods are required. We have attempted to identify aspects of the tropical regions which must be considered in the development of experimental designs for determination of nematode distributions and host-parasite relationships, and to discuss methods specific to the tropics. There is tremendous potential and need for increased agricultural production during the coming decades. Nematologists working in these vital tropical regions must be ready to meet the challenges of managing a group of organisms that seem ideally suited and positioned to severely restrain increases in tropical food production.

References

Abu-Gharbieh, W. I. (1982). Distribution of *Meloidogyne javanica* and *M. incognita* in Jordan. *Nematologica*, 28 : 34–37.

Barker, K. R. (1985). Nematode extraction and bioassays. In: Barker, K. R., Carter, C. C. & Sasser, J. N. (Eds). *An Advanced Treatise on Meloidogyne*: Vol. II, Methodology. Raleigh, NC, North Carolina State University Graphics: 19–35.

Barker, K. R. & Campbell, C. L. (1981). Sampling nematode populations. In: Zuckerman, B. M. & Rohde, R. A. (Eds). *Plant-Parasitic nematodes, Vol. 3*. New York, Academic Press: 451–472.

Barker, K. R. & Noe, J. P. (1987). Estimating and using threshold population levels. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Hyattsville, MD, Society of Nematologists: 75–81.

Barker, K. R. & Noe, J. P. (1988). Techniques in quantitative nematology. In: Kranz, J. & Rotem, J. (Eds). *Experimental Techniques in Plant Disease Epidemiology*. Berlin, Springer-Verlag: 223–236.

Barker, K. R., Schmitt, D. P. & Noe, J. P. (1985). Role of sampling for crop-loss assessment and nematode management. *Agriculture, Ecosystems, and Environment*, 12 : 355–369.

Bridge, J. (1988). Plant nematode pests of banana in East Africa with particular reference to Tanzania. In: *Nematodes and the Borer Weevil in Bananas: Present Status of Research and Outlook*. Montpellier, France; INIBAP (1988): 35–39.

Brinkman, R. (1986). Agro-ecological characterization, classification and mapping, different approaches by the international agricultural research centres. In: Bunting, A. H. (Ed.). *Proceedings of Agricultural Environments*. London, C.A.B. International: 31–42.

Carter, S. E. (1986). Collecting and organising data on the agro-socio-economic environment of the cassava crop: case study of a method. In: Bunting, A. H. (Ed). *Proceedings of Agricultural Environments*. London, C.A.B. International: 11–28.

Cochran, W. G. (1977). *Sampling Techniques*. New York, J. Wiley & Sons. 428 p.

Duncan, L. W. & Noling, J. W. (1987). Modeling nematode populations. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Hyattsville, MD, Society of Nematologists: 377–389.

Egunjobi, O. A. (1974). Nematodes and maize growth in Nigeria I. Population dynamics of *Pratylenchus brachyurus* in and about the roots of maize and its effects on maize production at Ibadan. *Nematologica*, 20 : 181–186.

Evans, K., Franco, J. & De Scurrah, M. M. (1975). Distribution of species of potato cyst nematodes in South America. *Nematologica*, 21 : 365–369.

Evans, K. & Stone, A. R. (1977). A review of the distribution and biology of the potato cyst-nematodes *Globodera rostochiensis* and *G. pallida*. *PANS*, 23 : 178–189.

FAO (1978). *Report on the agro-ecological zones project*. Rome, World Soil Resources Report 48/1.

Ferris, H. (1981). Mathematical approaches to the assessment of crop damage. In: Zuckerman, B. M. & Rohde, R. A. (Eds). *Plant parasitic nematodes: Vol. III*. New York, Academic Press: 405–420.

Ferris, H. (1987). Extraction efficiencies and population estimation. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Hyattsville, MD, Society of Nematologists: 59–63.

de Guiran, G. & Germani, G. (1980). Fluctuations of *Meloidogyne incognita* populations in a cultivated soil of the wet tropical areas. *Revue de Nématologie*, 35 : 51–60.

Humboldt, A. V. & Bonpland, A. (1807). *Ideen zu einer Geopgraphie der Pflanzen*. Neudruck Darmstadt, Wissenschaft Buchgesellschaft. 182 p.

Jatzold, R. (1982). A method to determine agro-ecological zones of the tropics, with a sample from Kenya. *Der Tropenlandwirt*, 83 : 15–34.

Mai, W. F. (1977). Worldwide distribution of potato-cyst nematodes and their importance in crop production. *Journal of Nematology*, 9 : 30–34.

McSorley, R. (1987). Plot size and design for acquisition of field data in nematology. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Hyattsville, MD, Society of Nematologists: 52–58.

McSorley, R. & Parrado, J. L. (1982). Plans for the collection of nematode soil samples from fruit groves. *Nematropica*, 12 : 257–267.

McSorley, R. & Parrado, J. L. (1986). *Helicotylenchus multicinctus* on bananas: an international problem. *Nematropica*, 16 : 73–91.

Meagher, J. W. (1977). World dissemination of the cereal-cyst nematode (*Heterodera avenae*) and its potential as a pathogen of wheat. *Journal of Nematology*, 9 : 9–15.

Noe, J. P. (1988*a*). Crop loss assessment in nematology. In: Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (Eds). *Nematodes Parasitic to Cereals and Legumes in Temperate Semi-Arid Regions*. Aleppo, Syria, International Center for Agricultural Research in the Dry Areas (ICARDA): 85–99.

Noe, J. P. (1988*b*). Theory and practice of the cropping systems approach to reducing nematode problems in the tropics. *Journal of Nematology*, 20 : 204–213.

Noe, J. P. & Campbell, C. L. (1985). Spatial pattern analysis of plant-parasitic nematodes. *Journal of Nematology*, 17 : 86–93.

Noling, J. W. (1987). Partitioning crop losses. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Hyattsville, MD, Society of Nematologists: 64–74.

Noling, J. W. & Ferris, H. (1987). Nematode-degree days, a density time model for relating epidemiology and crop losses in perennials. *Journal of Nematology*, 19 : 108–118.

Norton, D. C. (1978). *Ecology of Plant-Parasitic Nematodes*. New York, John Wiley & Sons. 268 p.

O'Bannon, J. H. (1977). Worldwide dissemination of *Radopholus similis* and its importance in crop production. *Journal of Nematology*, 9 : 16–25.

Olowe, T. & Corbett, D. C. M. (1976). Aspects of the biology of *Pratylenchus brachyurus* and *P. zeae*. *Nematologica*, 22 : 202–211.

Rebois, R. V. (1973). Effect of soil temperature on infectivity and development of *Rotylenchulus reniformis* on resistant and susceptible soybeans, *Glycine max*. *Journal of Nematology*, 5 : 10–13.

Riggs, R. D. (1977). Worldwide distribution of soybean-cyst nematode and its economic importance. *Journal of Nematology*, 9 : 34–39.

Ruthenberg, H. (1983). *Farming Systems in the Tropics*. London, Oxford University Press. 424 p.

Sasser, J. N. (1977). Worldwide dissemination and importance of the root-knot nematodes, *Meloidogyne* spp. *Journal of Nematology*, 9 : 26–29.

Sasser, J. N. & Freckman, D. W. (1987). A world perspective on nematology: the role of the society. In: Veech, J. A. & Dickson, D. W. (Eds). *Vistas on Nematology*. Hyattsville, MD, Society of Nematologists: 7–14.

Schmiedecken, W. (1981). Humidity and cultivated plants: an attempt at parallelizing zones of humidity and optimal locations of selected cultivated plants in the tropics. *Applied Geography and Development*, 17 : 45–57.

Schmitt, D. P. & Barker, K. R. (1988). Incidence of plant-parasitic nematodes in the coastal plain of North Carolina. *Plant Disease*, 72 : 107–110.

Seinhorst, J. W. (1965). The relation between nematode density and damage to plants. *Nematologica*, 11 : 137–154.

Sharma, N. K., Dwinell, L. D. & Noe, J. P. (1989). *Helicotylenchus multicinctus* found in a slash pine seed orchard in Georgia. *Plant Disease*, 73 :

Sikora, R. A. (1982). *Globodera rostochiensis* on potato in the Philippines. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*, 89 : 532–533.

Sikora, R. A. (1988). Plant parasitic nematodes of wheat and barley in temperate and temperate semiarid regions – A comparative analysis. In: Saxena, M. C., Sikora, R. A. & Srivastava, J. P. (Eds). *Nematodes Parasitic to Cereals and Legumes in Temperate Semi-Arid Regions*. Aleppo, Syria, International Center for Agricultural Research in the Dry Areas (ICARDA): 46–68.

Sikora, R. A., Bafokuzara, N. D., Mbwana, A. S. S., Oloo, G. W., Uronu, B. & Seshu Reddy, K. V. (1989). Interrelationship between Banana Weevil, Root Lesion Nematode and Agronomic Practices and Their Importance for Banana Decline in Tanzania. *FAO Plant Protection Bulletin* (in press).

Taylor, A. L. & Sasser, J. N. (1978). *Biology, Identification and Control of Root-Knot Nematodes*. Raleigh, NC, North Carolina State University Graphics. 111 p.

Trudgill, D. L. (1970). Survival of different stages of *Heterodera rostochiensis* at high temperatures. *Nematologica*, 16 : 94–98.

Weltzien, H. C., (1967). Geopathologie der pflanzen. *Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz*, 74 : 176–189.

Weltzien, H. C. (1972). Geophytopathology. *Annual Review of Phytopathology*, 10 : 277–298.

Whitehead, A. G. (1969). The distribution of root-knot nematodes (*Meloidogyne* spp.) in tropical Africa. *Nematologica*, 15 : 315–333.

PLATES

Legends for Plates

PLATE 1. Symptoms of nematode damage to rice. **A** *Ditylenchus angustus*: white patches on leaf bases of growing rice, the initial symptoms of 'ufra disease'. **B** *Ditylenchus angustus*: twisted and distorted panicles of mature rice. **C** *Aphelenchoides besseyi*: speckled chlorosis and wrinkling of leaves. **D** *Ditylenchus angustus*: large, brown patch of dead rice plants, field symptoms of 'ufra disease', Bangladesh. **E** *Meloidogyne graminicola*: drowning out of deepwater rice, Bangladesh. **F** *Hirschmanniella*: patch of yellowed plants in tidal wetland rice, The Gambia. **G** *Paralongidorus australis*: stunted and chlorotic patch of irrigated rice, Australia (Photo: G. Stirling).

PLATE 2. Symptoms of nematode damage to cereals. **A** *Heterodera avenae*: uneven growth of wheat in Israel (Photo: R. Sikora). **B** *Punctodera chalcoensis*: yellowing and stunting of maize in Mexico. **C** *Pratylenchus zeae*: poor growth of pearl millet in Zimbabwe (Photo: S. Page). **D** *Longidorus* sp.: severe damage to sorghum combined with moisture stress in Botswana (Photo: J. Starr). **E** *Anguina tritici*: black, protruding seed-galls on wheat (Photo: J. Bridge & D. J. Hunt). **F** *Anguina tritici*: *Corynebacterium michiganese* yellow ear-rot on deformed head of wheat induced by the seed gall nematode (Photo: R. Sikora). **G** *Pratylenchus* sp.: root necrosis on maize (Photo: B. Jacobsen). **H** *Xiphinema* sp.: stubby root damage on maize roots (Photo: B. Jacobsen).

PLATE 3. Symptoms of nematode damage to root and tuber crops. **A** *Globodera* spp.: cysts and females on roots of potato. **B** *Globodera rostochiensis*: yellowed and stunted potato plant. **C** *Meloidogyne incognita*: galled and distorted potato tuber, El Salvador. **D** *Meloidogyne incognita*: internal necrosis of sweet potato tubers, Papua New Guinea. **E** *Scutellonema bradys*: dry rot causing cracking and flaking of epidermis on yam tubers (*Dioscorea rotundata*), Nigeria. **F** *Pratylenchus coffeae*: dry rot of yam tuber (*Dioscorea alata*), Papua New Guinea. **G** *Hirschmanniella miticausa*: mitimiti rot disease of taro corm. **H** *Meloidogyne* sp.: galls on storage roots of arracacia, Brazil (Photo: V.P. Campos).

PLATE 4. Symptoms of nematode damage to food legumes. **A** *Heterodera ciceri*: patch of yellowed and stunted lentils, Syria. **B** *Heterodera glycines*: patch of yellowed soybean, USA (Photo: D. Schmidt). **C** *Meloidogyne* sp.: yellowing and premature senescence of haricot bean, Chile. **D** *Ditylenchus dipsaci*, giant race: stem necrosis on *Vicia faba*, Syria. **E** *Meloidogyne artiellia*: chickpea roots with large eggsacs of the nematode protruding from roots resembling cysts and no galling (Photo: M. de Vito). **F** *Heterodera ciceri*: white, lemon-shaped females on roots of chickpea. **G** *Meloidogyne incognita*: galling and rotting of haricot bean roots due to nematodes and soil fungi, Philippines. **H** *Pratylenchus* sp.: necrosis of chickpea roots.

PLATE 5. Symptoms of nematode damage to vegetables. **A** *Meloidogyne incognita*: browning and early senescence of tomato caused by the root-knot nematode, Niger. **B** *Meloidogyne incognita*: stunting of eggplant due to severe root galling (left) compared to plant with light infestation (right) (Photo: J. Bridge). **C** Tomato plants in glasshouse wilted and dying due to concomitant infection by *Meloidogyne incognita* and *Fusarium oxysporum*. **D** *Meloidogyne incognita*: galling of tomato roots, Yemen. **E** *Meloidogyne hapla*: small galls on carrot roots. **F** *Meloidogyne hapla*: deformation of taproot and "bearded-root" symptoms on carrot. **G** *Nacobbus aberrans*: bead-like root galls on tomato (Photo: J. Bridge). **H** *Meloidogyne incognita*: single female with eggs in gall of gourd root (Photo: J. Bridge).

PLATE 6. Symptoms of nematode damage to peanut. **A** *Meloidogyne arenaria*: galling of roots, pods and pegs. **B** *Meloidogyne hapla*: galling and proliferation of roots resulting in a matted root system. **C** *Meloidogyne arenaria*: peanut field in Georgia, USA, treated with aldicarb (left) and untreated (right). **D** *Pratylenchus brachyurus*: lesions on peanut pods. **E** *Aphelenchoides arachidis*: brown and wrinkled, infested seeds (top) compared to healthy seeds (bottom) (Photo: J. Bridge). **F** *Scutellonema cavenessi*: infected peanut field in Senegal treated with nematicide (left) and untreated (right) (from Germani *et al.*, 1985).

PLATE 7. Symptoms of nematode damage to citrus. **A–C** Citrus feeder roots infected by *Tylenchulus semipenetrans*, using medium power of a dissecting microscope. **A** Non-infected *vs* infected feeder root characteristically dirty in appearance due to adherence of soil particles to the gelatinous matrix in which eggs are laid. **B** Feeder root with adhering sand particles. When sand is gently removed, egg masses become visible. **C** Posterior ends of two females after soil particles and egg matrices are removed. **D** Cross-section of a feeder root showing extension of the *T. semipenetrans* female body into the root cortex and densely stained nurse cells surrounding the head (Photo: R. Inserra). **E** *Radopholus citrophilus*: cavity created in feeder root cortical tissues (Photo: D. Kaplan). **F** *Belonolaimus longicaudatus*: thickened roots and reduced root system due to feeding by the sting nematode (right). **G** *Pratylenchus coffeae*: Valencia orange trees on rough lemon rootstock, in various stages of decline (note large number of replanted trees) due to infection by the lesion nematode. **H** Adjacent, non-infested portions of the orchard have no decline symptoms.

PLATE 8. Symptoms of nematode damage to tropical fruit trees. **A** *Meloidogyne* sp.: galling of guava roots, Niger (Photo: R. Sikora). **B** *Meloidogyne* sp.: severely infested guava exhibiting dieback symptoms (Photo: R. Sikora). **C.** *Meloidogyne* sp.: infested papaya plantation, Senegal (Photo: P. Baujard). **D** Root-knot galling of young papaya roots (Photo: P. Baujard). **E** *Meloidogyne* sp.: galls on roots of fig (Photo: V. Perry & R.A. Dunn). **F** *Hemicriconemoides mangiferae*: symptoms of damage to mango, Florida (Photo: R.T. McSorley).

PLATE 9. Symptoms of nematode damage to palms. **A** *Rhadinaphelenchus cocophilus*: foliar symptoms of red ring disease on coconut palm, Trinidad. **B** *Rhadinaphelenchus cocophilus*: red ring necrosis in cut trunk of coconut palm, Trinidad. **C** *Radopholus similis*: progressive development of necrotic lesions (top to bottom) on roots of coconut palm, India. **D** *Radopholus similis*: coconut palms with and without nematodes in field tanks, India. Centre palm uninoculated, rear left inoculated with 100,000 nematodes, rear right inoculated with 100 nematodes. **E** *Rhadinaphelenchus cocophilus*: red ring symptoms in cut trunk of oil palm. **F** Foliar symptoms of red ring disease in oil palm.

PLATE 10. Symptoms of nematode damage to tea and coffee. **A** *Pratylenchus loosi*: declining patch of tea plants showing typical symptoms of early flowering and fruiting, Sri Lanka. **B** *Pratylenchus loosi*: necrotic patches on large storage roots of tea, Sri Lanka. **C** *Radopholus similis*: susceptible tea clone (TRI 2025) damaged by nematodes (right) compared to healthy plants (left). **D** *Meloidogyne incognita*: root peeling, cracking and death of lateral roots of coffee, Brazil. **E** *Meloidogyne decalineata*: round root-tip galls on roots of coffee (*Coffeae arabica*), Tanzania (Photo: J. Bridge). **F** *Meloidogyne coffeicola*: peeling and cracking of coffee root without galling, Brazil. **G** *Meloidogyne exigua*: galls on coffee roots, Nicaragua (Photo: J. Bridge).

PLATE 11. Symptoms of nematode damage to bananas. **A** *Pratylenchus goodeyi*: cooking banana plantation severely infested with nematodes, Tanzania (Photo: J. Bridge). **B** *Radopholus similis*: necrosis on surface of roots and extending to the stele in cut sections (Photo: J. Bridge). **C** *Radopholus similis*: toppling or uprooting of bananas, W. Indies. **D** *Radopholus similis*: close up of blackened, necrotic roots of toppled banana, Ecuador (Photo: J. Bridge). **E** *Pratylenchus coffeae*: outer tissues removed to show root and corm necrosis of banana, Papua New Guinea (Photo: J. Bridge). **F** *Helicotylenchus multicinctus*: banana roots with necrosis confined to outer cortex (Photo: J. Bridge).

PLATE 12. Nematode damage to sugarcane. **A** Increased vegetative growth and cover in sugarcane treated with the nematicides aldicarb (foreground) and DD (middle distance) compared to untreated cane (centre). **B** Roots of six-month old plant cane, cv NCo382, treated with aldicarb (right) compared to untreated cane (left). Note the almost complete absence of fine, lateral roots in the untreated cane. **C & D** Sett roots of cane damaged by nematodes: **C** six-week old cane showing well developed primary shoot and associated tillers detached from the central node of the mother sett. Note the stunted shoot growth on the adjacent node, enlarged in **D. E** Effect of soil fumigation on growth of cane: soil treated with Telone (right) compared to untreated soil (left).

PLATE 13. Symptoms of nematode damage to tobacco. **A** *Meloidogyne arenaria*: nematodes causing reduced growth of cv Coker 319, USA. **B** *Meloidogyne javanica*: susceptible and tolerant tobacco in field moderately infested with nematodes, Zimbabwe. **C** *Meloidogyne arenaria*: effect of *M. arenaria* (race 2) on *M. incognita* (races 1 & 3) resistant cv Speight G–28 and susceptible cv McNair 944 roots. **D** *Meloidogyne incognita*: root galls on susceptible tobacco cultivar. **E** Effect of various soil fungi on roots of tobacco infested with *Meloidogyne* (Photo: N.T. Powell). **F** Effect of soil fumigation in a tobacco field heavily infested with *Meloidogyne*, Zimbabwe. **G** Effect of ethoprophos application on growth of tobacco in a field badly infested with *Globodera tabacum solanacearum*, USA (Photo: D. Komus). **H** Effect of application of fenamiphos (left) on growth of tobacco in a field infested with *Meloidogyne arenaria* (Photo: N.T. Powell).

PLATE 14. Symptoms of nematode damage to pineapple. **A** Healthy pineapple plants. **B** Healthy root system of young pineapple. **C** *Meloidogyne javanica*: root tip galls. **D** *Rotylenchulus reniformis*: severe wilting of ratoon pineapple caused by the reniform nematode. **E** *Rotylenchulus reniformis*: damage to root system of young pineapple – nematodes with soil particles adhering to egg masses are visible on the roots. **F** Root system of a 14-month old pineapple grown in soil infested with *Rotylenchulus reniformis* and excavated perpendicular to the row using a needle board. Soil treated by preplant fumigation with 1, 3–D and subsequent applications (every three months) of fenamiphos by drip irrigation. Pointer indicates position of drip irrigation tube. Compared with G (Photo: R.C. Schneider). **G** Root system of a 14-month old pineapple grown in soil infested with *Rotylenchulus reniformis* and excavated perpendicular to the row using a needle board. Soil treated with applications (every three months) of fenamiphos by drip irrigation. Pointer indicates position of drip irrigation tube. Compare with **F** (Photo: R.C. Schneider).

PLATE 15. Symptoms of nematode damage to cotton. **A** Fusarium wilt and root-knot nematode (*Meloidogyne incognita*) damage to cotton in foreground, Tanzania (Photo: J. Bridge). **B** *Meloidogyne incognita*: damage to dry-land cotton in Texas; foreground fumigated with ethylene dibromide, rear is untreated. Cotton planted on a skip-row system to optimise use of limited soil moisture. **C** *Meloidogyne incognita*: cotton root systems infected with a damaging level of the root-knot nematode. Note small sized galls (arrowed) typical of root-knot on cotton. **D** *Meloidogyne incognita*: severe galling of cotton root system. **E** *Hoplolaimus columbus*: field damage to cotton, Georgia, USA (Photo: W. Powell). **F** *Xiphinema* sp.: field damage associated with the nematode in Zimbabwe.

PLATE 16. Symptoms of nematode damage to spices. **A** *Radopholus similis*: black pepper plant with yellows disease in Bangka, Indonesia. **B** *Radopholus similis*: black pepper on arecanut palms in India showing yellowing, defoliation and dieback symptoms due to slow wilt (yellows) disease. **C** *Radopholus similis*: patch of yellowed black pepper vines in Bangka, Indonesia. **D** *Radopholus similis*: later stage of yellows disease in black pepper, Bangka, Indonesia showing patch with dead and dying vines. **E** *Meloidogyne incognita*: young cardamom plant exhibiting symptoms of excessive root branching due to infection by the root-knot nematode. **F** *Meloidogyne* sp.: stunted and yellowed kava plants showing symptoms of severe root-knot damage in Tonga (Photo: P. Speijer).

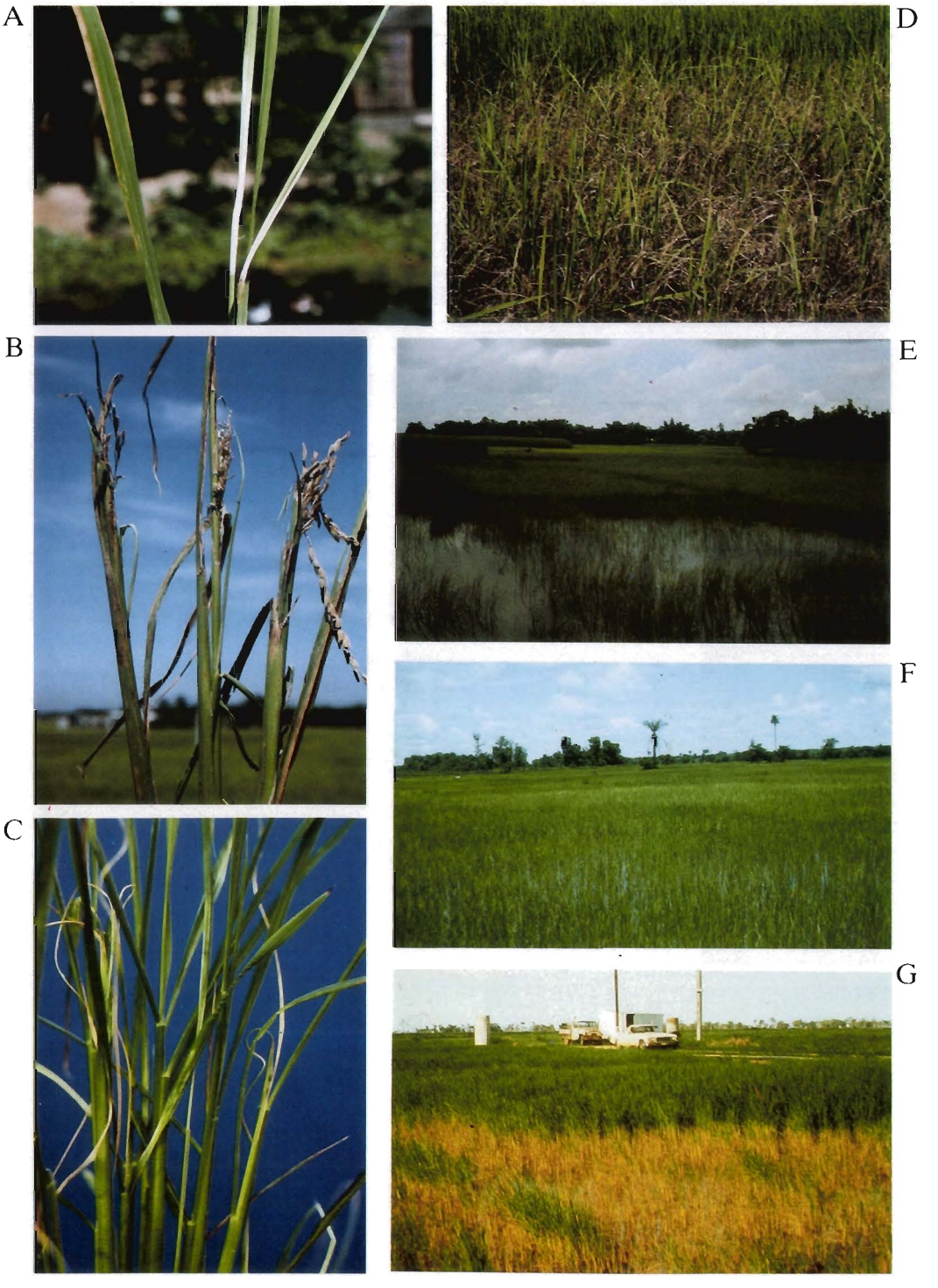

PLATE 1. Symptoms of nematode damage to rice.

PLATE 2. Symptoms of nematode damage to cereals.

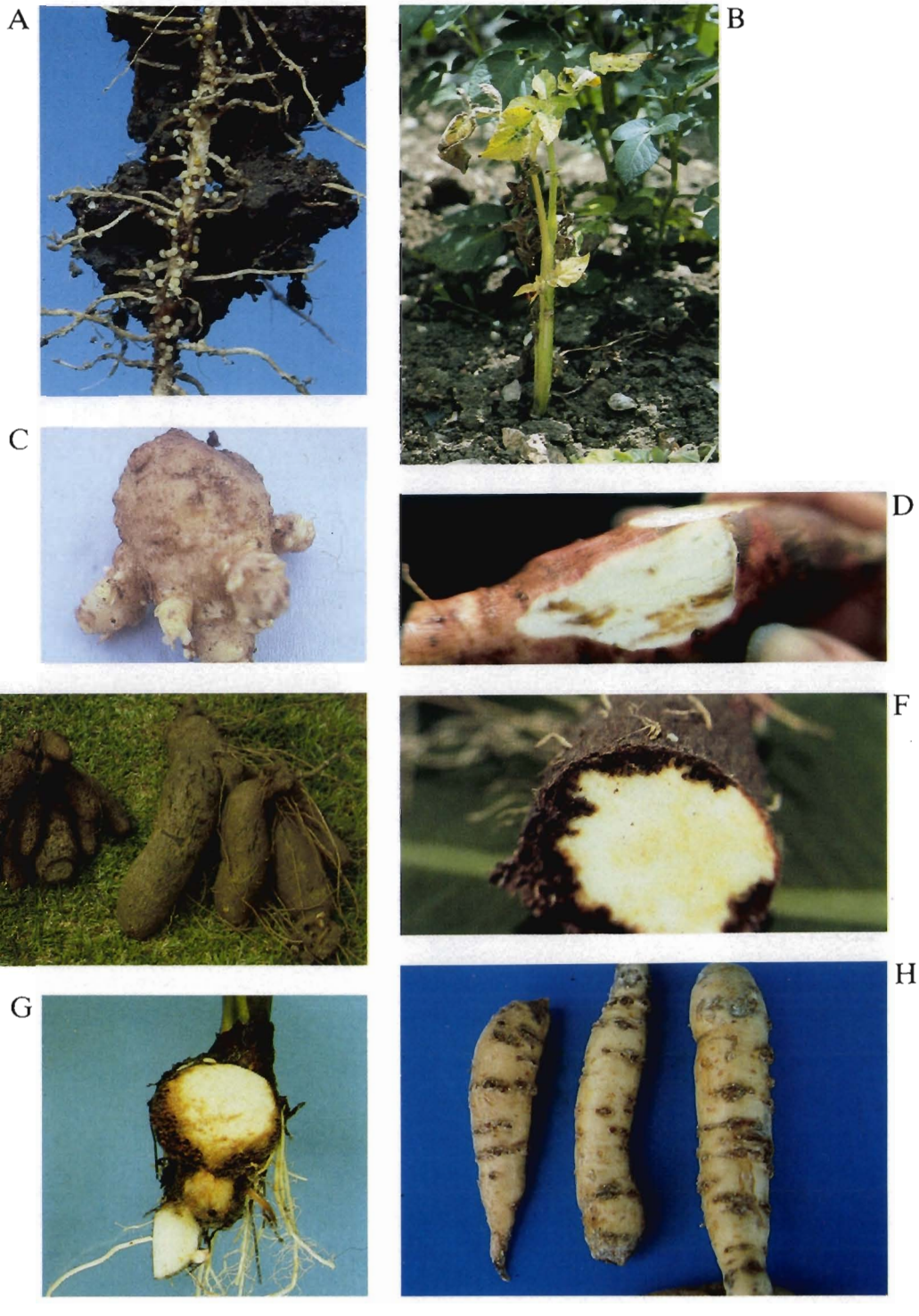

PLATE 3. Symptoms of nematode damage to root and tuber crops.

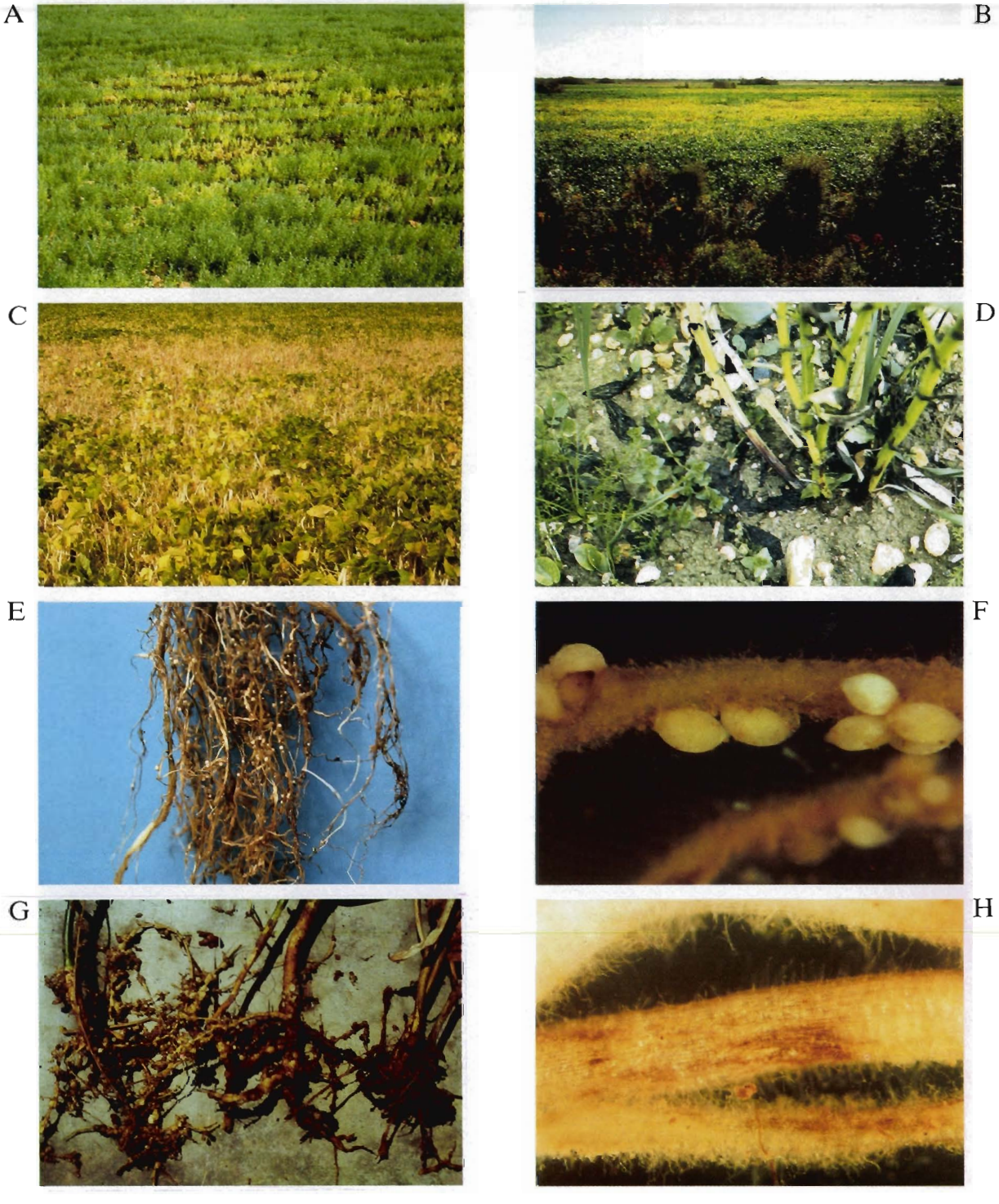

PLATE 4. Symptoms of nematode damage to food legumes.

PLATE 5. Symptoms of nematode damage to vegetables.

PLATE 6. Symptoms of nematode damage to peanut.

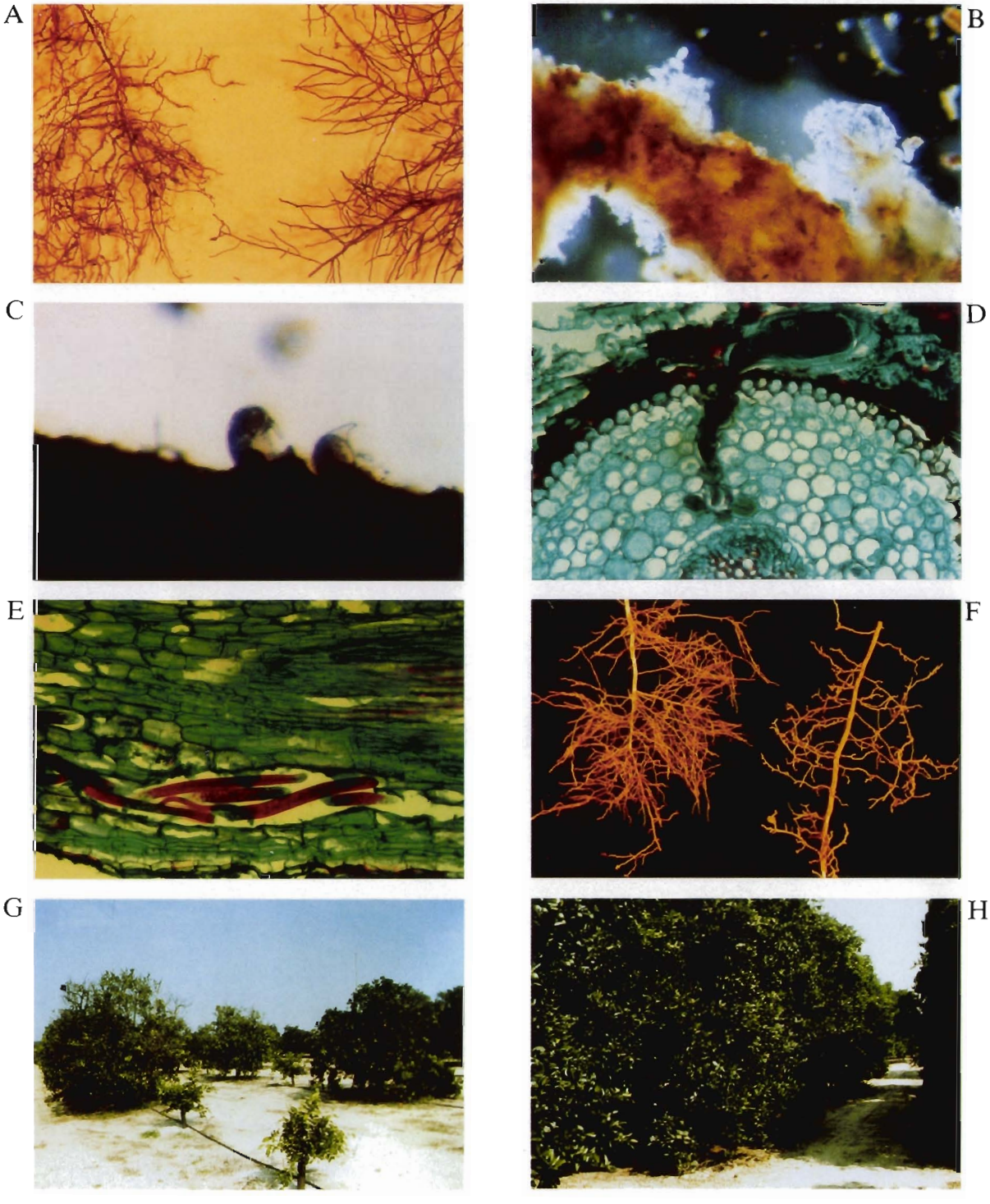

PLATE 7. Symptoms of nematode damage to citrus.

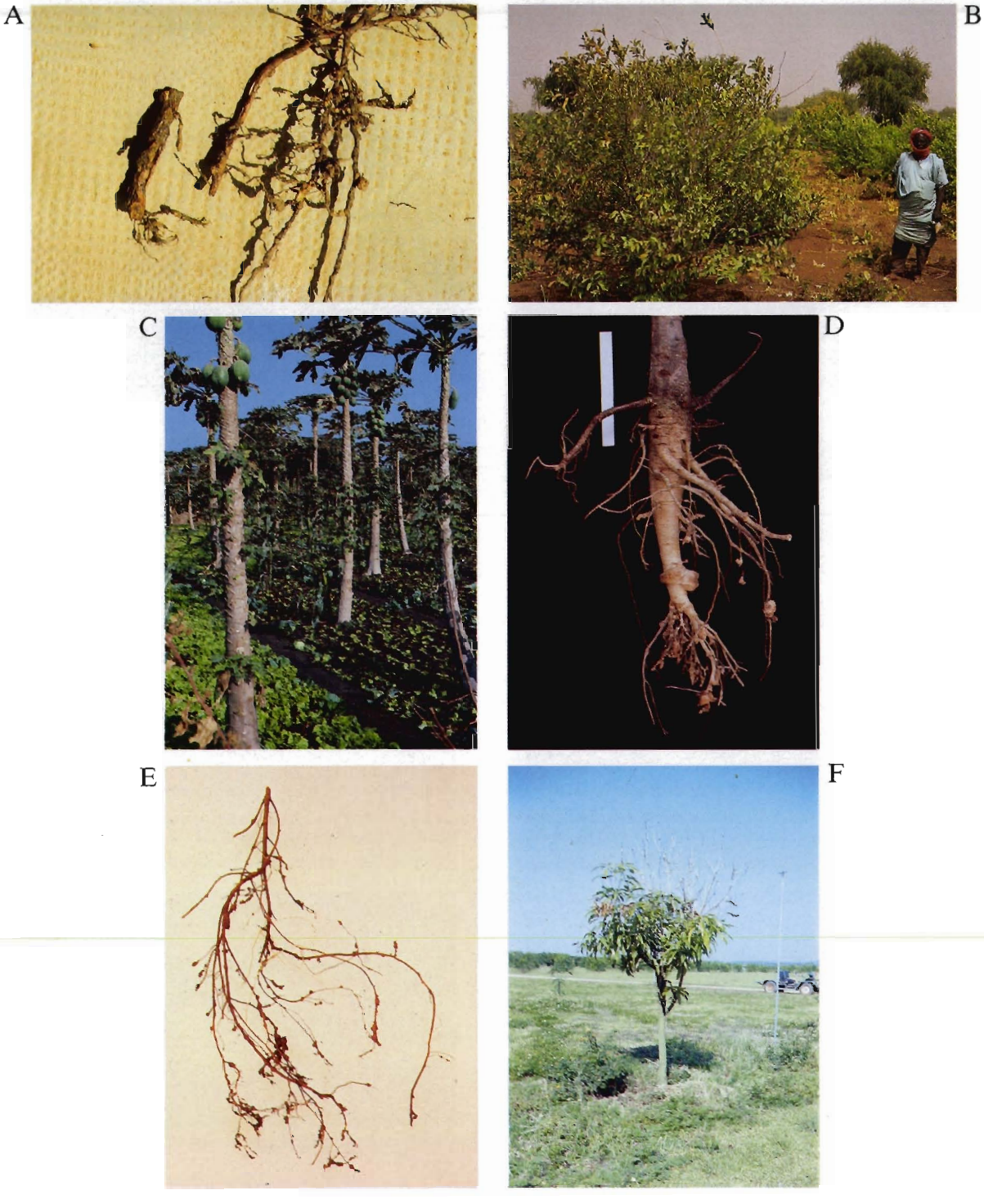

PLATE 8. Symptoms of nematode damage to tropical fruit trees.

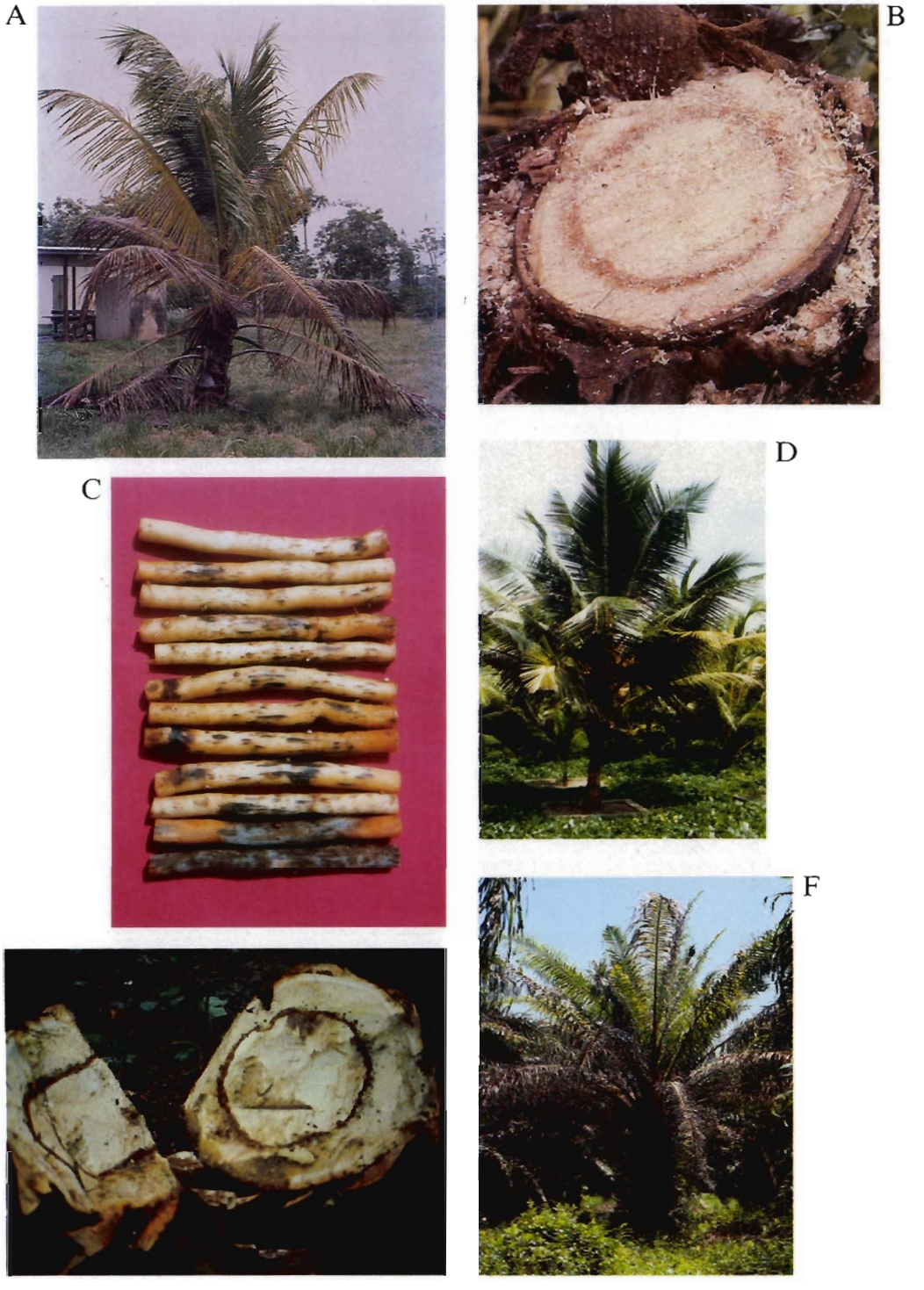

PLATE 9. Symptoms of nematode damage to palms.

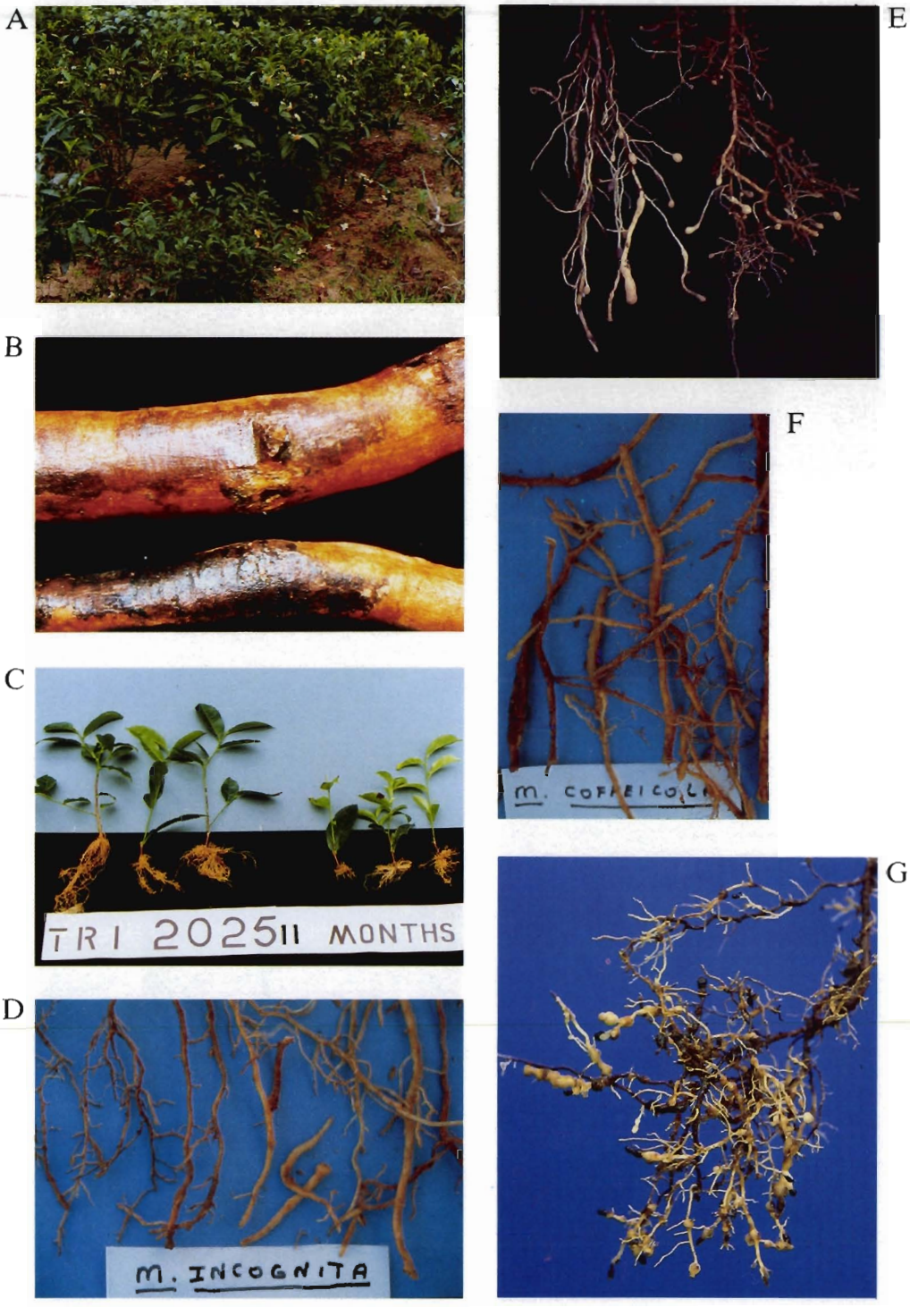

PLATE 10. Symptoms of nematode damage to tea and coffee.

PLATE 11. Symptoms of nematode damage to bananas.

PLATE 12. Symptoms of nematode damage to sugarcane.

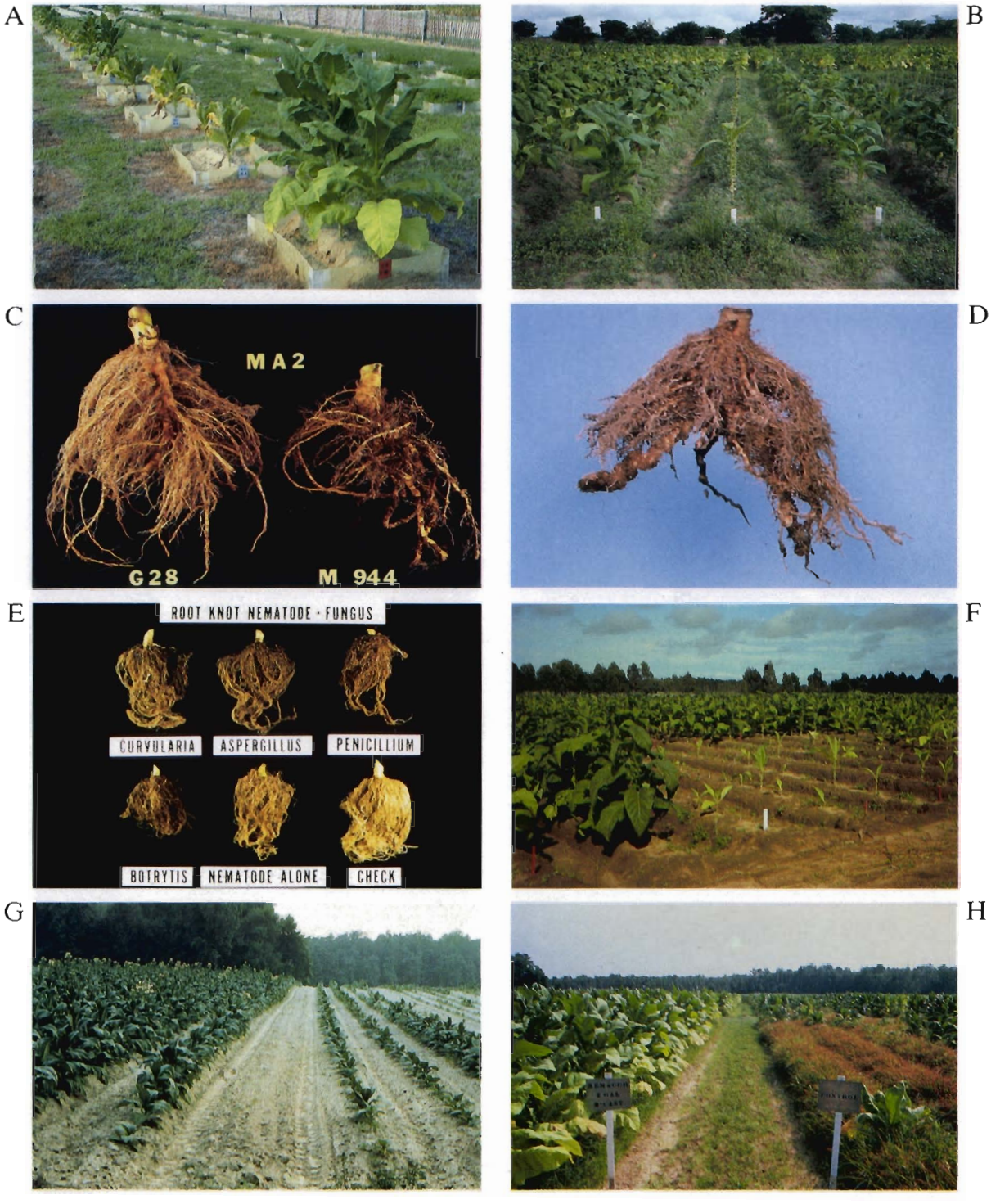

PLATE 13. Symptoms of nematode damage to tobacco.

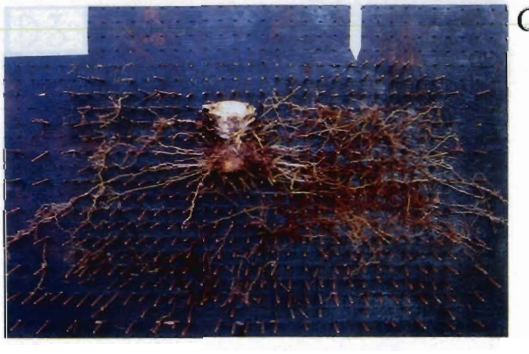

PLATE 14. Symptoms of nematode damage to pineapple.

PLATE 15. Symptoms of nematode damage to cotton.

PLATE 16. Symptoms of nematode damage to spices.

APPENDICES

Appendix A. Nematicides

Peter S. GOOCH

CAB International, Wallingford, Oxon OX10 8DE UK.

A list is given here that includes most of the chemicals in use in the 1980s for the control of plant parasitic nematodes by nematicidal, nematostatic or nematorepellent action. Some of these chemicals may also be used to control insects, weeds or other plant pests or diseases, but insecticides, fungicides or herbicides which may also be active against nematodes are not included.

Entries are arranged by common name followed by the preferred chemical name, then other names or codes which may vary from country to country, and finally by the type of formulation of the chemical.

For information on the usage of a particular nematicide refer to the index of this book or to standard reference works such as the Pesticide Manual produced by the British Crop Protection Council.

Fumigants

Basamid see dazomet

1, 3-dichloropropene
1, 3-D; DCP; Telone
Liquid formulation

carbathion see metham sodium

chloropicrin
trichloronitromethane; nitrochloroform
Liquid formulation

dazomet
3, 5-dimethyl, 1, 3, 5-thiadiazine–2-thione
Basamid; Mylone
Dust formulation

DBCP see dibromochloropropane

D-D see dichloropropane-dichloropropene

***dibromochloropropane**
1, 2-dibromo–3-chloropropane
DBCP; Fumazone; Nemagon
Liquid formulation

***dichloropropene-dichloropropane**
D-D; Telone
Liquid formulation

Dowfume see methyl bromide

EDB see ethylene dibromide

***ethylene dibromide**

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1, 2-dibromethane
EDB; Terrafume
Liquid formulations

Fumazone see dibromochlororopropane

metham sodium
monosodium methyldithiocarbamate
carbathion; Vapam
Liquid formulation

***methyl bromide**

bromomethane
Dowfume MC;
Gas formulation

methyl isothiocyanate

isothiocyanatomethane
Trapex
Liquid formulation

Mylone see dazomet

Nemagon see dibromochloropropane

Telone see dichloropropene-dichloropropane and 1, 3-dichloropropene

Telone II see 1, 3-dichloropropene

Terrafume see ethylene dibromide

Trapex see methyl isothiocyanate

Vapam see metham sodium

Non-Fumigants

Organophosphates

Acconem see Fosthietan

Counter see terbufos

Dazanit see fensulfothion

Diamidafos

phenyl *N N'*-dimethyl-phosphorodiamidate
Nellite

dichlofenthion

O-(2, 4-dichlorophenyl) *O,O*-diethyl phosophorothioate
Hexanema

Ebufos

S,S-di-*sec*-butyl *O*-ethyl phosphorodithioate
Rugby
Granular formulations

ethoprop see ethoprophos

Ethoprophos

O-ethyl *S, S*-'-diporpyl phosphorodithioate
Mocap
Granular and liquid formulations

fenamiphos

ethyl 4-methylthio-*m*-tolyl isopropylphosphoramidate
Nemacur
Granular and liquid formulations

fensulfothion

O, O-diethyl-*O*–4-methylsulfinylphenylphosphorothioate
Terrracur
Granular and liquid formulations

Fosthietan
diethyl 1, 3-dithietan–2-ylidenephosphoramidate
Acconem; Nem-a-tak; geofos

geofos see Fosthietan

Hexanema see dichlofenthion

Isazofos
O–5-chloro–1-isopropyl–1*H*–1,2, 4-triazol–3-yl *O, O*-diethyl phosophorothioate
Miral
Granular and liquid formulations

Miral see isazofos

Mocap see Ethoprophos

Nellite see Diamidafos

Nem-a-tak see Fosthietan

Nemacur see fenomiphos

Nemafos see thionazin

Phenamiphos see fenamiphos

phorate
O, O-diethyl *S*-ethylthiomethylphosphorodithioate
Thimet
Granular and liquid formulations

Rugby see ebufos

terbufos
S-tert-butylthiomethyl *O, O*-diethylphosphorodithioate
Counter
Granular formulations

Terracur see fensulfothion

Thimet see phorate

thionazin
O, O-diethyl *O*-pyrazin–2-yl phosphorothioate
Nempahos; Zinophos
Granular and liquid formulations

Zinophos see thionazin

Carbamates

aldicarb
2-methyl–2-(methylthio) propionaldehyde *O*-(methylcarbamoyl)-oxime
Temik
Granular formulations

Aldoxycarb
2-methyl–2-methylpropionaldehyde *O*-methylcarbamoyloxime
Standak
Flowable formulation

carbofuran
2, 3-dihydro–2, 2-dimethylbenzofuran–7-yl methylcarbamate
Curaterr; Furadan
Granular and flowable formulations

cloethocarb
2-(2-chloro–1-methoxyethoxy)phenyl methylcarbamate
Lance
Granular formulation
Curaterr see carbofuran
Furadan see carbofuran
Furadon see carbofuran
Lance see cloethocarb
oxamyl
S-methyl *N'*, *N'*-dimethyl-N-[(methyl-carbamoyl)oxy]–1-thio-oxamimidate
Vydate
Granular and liquid formulations
Standak see aldoxycarb
Temik see aldicarb
Vydate see oxamyl

*The manufacture and/or use of these compounds has been banned in certain countries and they are no longer generally available but may be obtainable locally under other brand names.

Off-patent compounds may be available under brand names not listed in this index. The omission of other product names or formulations does not imply that they might not be suitable as nematicides.

Nematicides should only be used with strict adherence to the safety precautions recommended by the manufacturer. Many nematicides are toxic to human beings and livestock and should always be treated with respect.

Appendix B. Nematode Genera and Species Cited

Michel LUC

All genera and species of plant parasitic nematodes cited in the book are listed alphabetically below.

They are followed by their "authorities" i.e. the name(s) of the author(s) of the original description, in some cases followed by the name(s) of the author(s) having given the more recent valid taxonomic name. In such cases, the original authorities are placed between brackets. Both authorities are followed by the year of the publication of their respective works.

The most common synonyms are also alphabetically listed as "cf", and referred to "=" below the valid name.

For each genus, the group and the family to which it pertains are given.

Groups are indicated as follows:

T = Tylenchina
A = Aphelenchina
Do = Dorylaimina
Di = Diphtherophorina

Achlysiella Hunt, Bridge & Machon, 1989
T. Pratylenchidae
Achlysiella williamsi (Siddiqi, 1964) Hunt, Bridge & Machon, 1989
= *Radopholus williamsi* Siddiqi, 1964

Anguina Scopoli, 1777
T. Anguinidae
Anguina agrostis (Steinbuch, 1799) Filipjev, 1936
Anguina tritici (Steinbuch, 1799) Chitwood, 1935

Aorolaimus Sher, 1963
= *Peltamigratus* Sher, 1964
T. Hoplolaimidae
Aorolaimus holdemani (Sher, 1964) Fortuner, 1987
= *Peltamigratus holdemani* Sher, 1964
Aorolaimus luci (Sher, 1964) Fortuner, 1987
= *Peltamigratus luci* Sher, 1964

Aphasmatylenchus Sher, 1965
T. Hoplolaimidae
Aphasmatylenchus straturatus Germani, 1970

Aphelenchoides Fischer, 1894
A. Aphelenchoididae
Aphelenchoides arachidis Bos, 1977

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Aphelenchoides besseyi Christie, 1942
= *A. oryzae* Yokoo, 1948
Aphelenchoides bicaudatus (Imamura, 1931) Filipjev & Schuurmans Stekhoven, 1941
Aphelenchoides fragariae (Ritzema – Bos, 1890) Christie, 1932
Aphelenchoides ritzemabosi (Schwartz, 1911) Steiner & Buhrer, 1932

Basirolaimus
cf. *Hoplolaimus*

Belonolaimus Steiner, 1949
= *Ibipora* Monteiro & Lordello, 1977
T. Belonolaimidae
Belonolaimus euthychilus Rau, 1963
Belonolaimus gracilis Steiner, 1949
Belonolaimus longicaudatus Rau, 1958
Belonolaimus maritimus Rau, 1963
Belonolaimus nortoni Rau, 1963

Cactodera Krall & Krall, 1978
T. Heteroderidae
Cactodera amaranthi (Stoyanov, 1972) Krall & Krall, 1978

Caloosia Siddiqi & Goodey, 1964
T. Criconematidae
Caloosia heterocephala
cf. *C. paxi*
Caloosia nudata (Colbran, 1963) Brzeski, 1974
= *Hemicycliophora nudata* Colbran, 1963
Caloosia paradoxa (Luc, 1958) Brzeski, 1974
= *Hemicycliophora paradoxa* Luc, 1958
Caloosia paxi Mathur, Khan, Nand & Prasad, 1969
= *C. heterocephala* Rao & Mohandas, 1976

Cephalenchus Goodey, 1962
T. Tylenchidae
Cephalenchus emarginatus (Cobb, 1893) Geraert, 1968
Cephalenchus hexalineatus (Geraert, 1962) Geraert & Goodey, 1964

Criconema Hofmänner & Menzel, 1914
T. Criconematidae
Criconema crassianulatum (de Guiran, 1963) Raski & Luc, 1985

Criconemella De Grisse & Loof, 1965
T. Criconematidae
= *Macroposthonia* de Man, 1880 (*gen. dub.*)
= *Criconemoides* Loof & De Grisse, 1967 (*gen. dub.*)
Criconemella axestis (Fassuliotis & Williamson, 1959) Luc & Raski, 1981
Criconemella curvata (Raski, 1952) Luc & Raski, 1981
Criconemella ferniae (Luc, 1959) Raski & Luc, 1981
= *Criconemoides obtusicaudatus* Heyns, 1962
Criconemella onoenis (Luc, 1959) Luc & Raski, 1981

= *Macroposthonia onoensis* (Luc, 1959) De Grisse & Loof, 1965
Criconemella ornata (Raski, 1958) Luc & Raski, 1981
= *Macroposthonia ornata* (Raski, 1958) De Grisse & Loof, 1965
Criconemella palustris (Luc, 1970) Raski & Luc, 1981
Criconemella pseudohercyniensis (De Grisse & Koen, 1964) Raski & Luc, 1981
Criconemella rustica (Micoletzky, 1915) Luc & Raski, 1981
Criconemella sphaerocephala (Taylor, 1936) Luc & Raski, 1981
= *Macroposthonia sphaerocephala* (Taylor, 1936) De Grisse & Loof, 1965
Criconemella xenoplax (Raski, 1962) Luc & Raski, 1981
= *Macroposthonia xenoplax* (Raski, 1952) De Grisse & Loof, 1965

Criconemoides
cf. *Criconemella*

Crossonema
cf. *Ogma*
Crossonema taylatum
cf. *Ogma taylatum*

Discocriconemella De Grisse & Loof, 1965
T. Criconematidae
Discocriconemella limitanea (Luc, 1959) De Grisse & Loof, 1965

Ditylenchus Filipjev, 1936
T. Anguinidae
Ditylenchus angustus (Butler, 1913) Filipjev, 1936
Ditylenchus destructor Thorne, 1945
Ditylenchus dipsaci (Kühn, 1857) Filipjev, 1936
Ditylenchus myceliophagus Goodey, 1958
Ditylenchus procerus (Bally & Reydon, 1931) Filipjev, 1936

Dolichodorus Cobb, 1914
T. Dolichodoridae
Dolichodorus heterocephalus Cobb, 1914
Dolichodorus minor Loof & Sharma, 1975

Globodera Skarbilovich, 1959
T. Heteroderidae
Globodera pallida (Stone, 1973) Behrens, 1975
Globodera rostochiensis (Wollenweber, 1923) Behrens, 1975
Globodera tabacum (Lownsbery & Lownsbery, 1954) Behrens, 1975
= *G. tabacum tabacum* (Lownsbery & Lownsbery, 1954) Behrens, 1975
Globodera tabacum solanacearum (Miller & Gray, 1972) Behrens, 1975
= *G. solanacearum* (Miller & Gray, 1972) Behrens, 1975
Globodera virginiae (Miller & Gray, 1968) Behrens, 1975
= *G. tabacum virginiae* (Miller & Gray, 1968) Behrens, 1975

Gracilacus Raski, 1962
T. Tylenchulidae
Gracilacus peratica Raski, 1962

Helicotylenchus Steiner, 1945
= *Rotylenchoides* Whitehead, 1958
T. Hoplolaimidae
Helicotylenchus abunaamai Siddiqi, 1972
Helicotylenchus affinis (Luc, 1960) Fortuner, 1984
= *Rotylenchoides affinis* Luc, 1960
Helicotylenchus brevis (Whitehead, 1958) Fortuner, 1984
= *Rotylenchoides brevis* Whitehead, 1958
Helicotylenchus cavenessi Sher, 1966
Helicotylenchus digonicus Perry *in* Perry, Darling & Thorne, 1959
Helicotylenchus dihystera (Cobb, 1893) Sher, 1961
Helicotylenchus erythrinae (Zimmerman, 1904) Golden, 1956
Helicotylenchus indicus Siddiqi, 1963
Helicotylenchus intermedius (Luc, 1960) Siddiqi & Husain, 1964
= *Rotylenchoides intermedius* Luc, 1960
Helicotylenchus microcephalus Sher, 1966
Helicotylenchus mucronatus Siddiqi, 1963
Helicotylenchus multicinctus (Cobb, 1893) Golden, 1956
Helicotylenchus oleae Inserra, Vovlas & Golden, 1979
Helicotylenchus pseudorobustus (Steiner, 1914) Golden, 1956
Helicotylenchus sharafati Mulk & Jairajpuri, 1975

Hemicriconemoides Chitwood & Birchfeld, 1957
T. Criconematidae
Hemicriconemoides chitwoodi Esser, 1960
Hemicriconemoides cocophillus (Loos, 1949) Chitwood & Birchfield, 1957
Hemicriconemoides gaddi (Loof, 1949) Chitwood & Birchfield, 1957
Hemicriconemoides kanayaensis Nakasono & Ichinohe, 1961
Hemicriconemoides mangiferae Siddiqi, 1961
Hemicriconemoides snoeki Van Doorselaere & Samsoen, 1982

Hemicycliophora de Man, 1921
T. Criconematidae
Hemicycliophora arenaria Raski, 1958
Hemicycliophora chathami Yeates, 1978
Hemicycliophora nudata
cf. *Caloosia nudata*
Hemicycliophora parvana Tarjan, 1952
Hemicycliophora penetrans Thorne, 1955
Hemicycliophora thienemanni (Schneider, 1925) Loos, 1948
Hemicycliophora typica de Man, 1921

Heterodera Schmidt, 1871
T. Heteroderidae
Heterodera avenae Wollenweber, 1924
Heterodera cajani Koshy, 1967
= *H. vigni* Edward & Misra, 1968
Heterodera ciceri Vovlas, Greco & di Vito, 1985
Heterodera cruciferae Franklin, 1945
Heterodera delvii Jairajpuri, Khan, Setty & Govindu, 1979
Heterodera elachista Ohshima, 1974

Heterodera fici Kirjanova, 1954
Heterodera gambiensis Merny & Netscher, 1976
Heterodera glycines Ichinohe, 1952
Heterodera goettingiana Liebscher, 1892
Heterodera graminis Stynes, 1971
Heterodera latipons Franklin, 1969
Heterodera lespedezae Golden & Cobb, 1963
Heterodera mediterranea Vovlas, Inserra & Stone, 1981
Heterodera oryzae Luc & Berdon Brizuela, 1961
Heterodera oryzicola Rao & Jayaprakash, 1978
Heterodera punctata
cf. *Punctodera punctata*
Heterodera sacchari Luc & Merny, 1963
Heterodera schachtii A. Schmidt, 1871
Heterodera sorghi Jain, Sethi, Swarup & Srivastava, 1982
Heterodera trifolii Goffart, 1932
Heterodera vigni
cf. *H. cajani*
Heterodera zeae Koshy, Swarup & Sethi, 1971

Hirschmanniella Luc & Goodey, 1964
T. Pratylenchidae
Hirschmanniella belli Sher, 1968
Hirschmanniella caudacrena
cf. *H. mexicana*
Hirschmanniella diversa Sher, 1968
Hirschmanniella gracilis (de Man, 1880) Luc & Goodey, 1964
Hirschmanniella imamuri Sher, 1968
Hirschmanniella magna Siddiqi, 1966
Hirschmanniella mexicana (Chitwood, 1961) Sher, 1968
= *H. caudacrena* Sher, 1968
Hirschmanniella miticausa Bridge, Mortimer & Jackson, 1984
Hirschmanniella mucronata (Das, 1960) Luc & Goodey, 1964
Hirschmanniella oryzae (van Breda de Haan, 1902) Luc & Goodey, 1964
= *H. nana* Siddiqi, 1966
Hirschmanniella shamimi Ahmad, 1972
Hirschmanniella spinicaudata (Schuurmans Stekhoven, 1944) Luc & Goodey, 1964
Hirschmanniella truncata Razjivin, Fernandez, Ortega, Quincosa, 1981

Hoplolaimus von Daday, 1905
= *Basirolaimus* Shamsi, 1979
T. Hoplolaimidae
Hoplolaimus aegypti Shafiee & Koura, 1970
Hoplolaimus columbus Sher, 1963
Hoplolaimus dimorphicus Mulk & Jairajpuri, 1975
Hoplolaimus galeatus (Cobb, 1913) Filipjev & Schuurmans Stekhoven, 1941
Hoplolaimus indicus Sher, 1963
Hoplolaimus pararobustus (Schuurmans Stekhoven & Teunissen, 1938) Sher, 1963
Hoplolaimus seinhorsti Luc, 1958

Hypsoperine
cf. *Meloidogyne*

Ibipora
cf. *Belonolaimus*

Longidorus (Micoletzky, 1922) Thorne & Swanger, 1936
Do. Longidoridae
Longidorus africanus Merny, 1966
Longidorus elongatus (de Man, 1876) Thorne & Swanger, 1936
Longidorus fursti Heyns, Coomans, Hutsebaut & Swart, 1987
Longidorus laevicapitatus Williams, 1959
Longidorus leptocephalus Hooper, 1961
Longidorus pisi Edward, Misra & Singh, 1964
= *Longidorus siddiqii* Aboul-Eid, 1970
Longidorus vineacola Sturhan & Weischer, 1964

Macroposthonia
cf. *Criconemella*

Meloidogyne Goeldi, 1892
= *Hypsoperine* Sledge & Golden, 1964
T. Heteroderidae
Meloidogyne acrita
cf. *M. incognita*
Meloidogyne acronea Coetzee, 1956
Meloidogyne africana Whitehead, 1960
Meloidogyne arenaria (Neal, 1889) Chitwood, 1949
Meloidogyne artiellia Franklin, 1961
Meloidogyne brevicauda Loos, 1953
Meloidogyne chitwoodi Golden, O'Bannon, Santo & Finley, 1980
Meloidogyne coffeicola Lordello & Zamith, 1960
Meloidogyne cruciani Garcia-Martinez, Taylor & Smart, 1982
Meloidogyne decalineata Whitehead, 1958
Meloidogyne enterolobii Yang & Eisenback, 1983
Meloidogyne ethiopica Whitehead, 1968
Meloidogyne exigua Goeldi, 1892
Meloidogyne fujianensis Pan, 1985
Meloidogyne grahami Golden & Slana, 1978
Meloidogyne graminicola Golden & Birchfield, 1965
Meloidogyne hapla Chitwood, 1949
Meloidogyne hispanica Hirschmann, 1986
Meloidogyne incognita (Kofoid & White, 1919) Chitwood, 1949
= *M. incognita acrita* Chitwood, 1949
= *M. acrita* Chitwood, 1949
Meloidogyne inornata Lordello, 1956
Meloidogyne javanica (Treub, 1885) Chitwood, 1949
Meloidogyne kikuyensis De Grisse, 1961
Meloidogyne mayaguensis Rammah & Hirschmann, 1988
Meloidogyne megadora Whitehead, 1958
Meloidogyne microcephala Cliff & Hirschmann, 1984

Meloidogyne naasi Franklin, 1965
Meloidogyne oryzae Maas, Sanders & Dede, 1978
Meloidogyne oteifae Elmiligy, 1968
Meloidogyne platani Hirschmann, 1982
Meloidogyne salasi Lopez, 1984
Meloidogyne thamesi Chitwood *in* Chitwood, Specht & Havis, 1952
= *M. arenaria thamesi* Chitwood *in* Chitwood, Specht & Havis, 1952

Merlinius Siddiqi, 1970
T. Belonolaimidae
Merlinius brevidens (Allen, 1955) Siddiqi, 1970
Merlinius cylindricus (Ivanova, 1962) Siddiqi, 1970

Monotrichodorus
cf. *Trichodorus*

Nacobbus Thorne & Allen, 1944
T. Pratylenchidae
Nacobbus aberrans (Thorne, 1935) Thorne & Allen, 1944
Nacobbus dorsalis Thorne & Allen, 1944

Ogma Southern, 1914
T. Criconematidae
= *Crossonema* Khan, Chawla & Saha, 1976
Ogma decalineatum (Chitwood, 1957) Andrássy, 1979
Ogma rhombosquamatum (Mehta & Raski, 1971) Andrássy, 1979
Ogma taylatum (Khan, Chawla & Saha, 1976) Siddiqi, 1986
= *Crossonema taylatum* Khan, Chawla & Saha, 1976

Paralongidorus Siddiqi, Hooper & Khan, 1963
= *Siddiqia* Khan, Chawla & Saha, 1968
Do. Longidoridae
Paralongidorus australis Stirling & McCulloch, 1985
Paralongidorus citri (Siddiqi, 1959) Siddiqi, Hooper & Khan, 1963
Paralongidorus natalensis (Jacobs & Heyns, 1982) Luc & Doucet, 1984
Paralongidorus oryzae Verma, 1973

Paratrichodorus Siddiqi, 1974
Di. Trichodoridae
Paratrichodorus anemones (Loof, 1965) Siddiqi, 1974
Paratrichodorus christiei
cf. *P. minor*
Paratrichodorus lobatus (Colbran, 1965) Siddiqi, 1974
Paratrichodorus minor (Colbran, 1956) Siddiqi, 1974
= *P. christiei* (Allen, 1957) Siddiqi, 1974
Paratrichodorus mirzai (Siddiqi, 1960) Siddiqi, 1974
Paratrichodorus pachydermus (Seinhorst, 1954) Siddiqi, 1974
Paratrichodorus porosus (Allen, 1957) Siddiqi, 1974

Paratylenchus Micoletzky, 1922
T. Tylenchulidae

Paratylenchus besoekianus Bally & Reydon, 1931
Paratylenchus curvitatus van der Linde, 1938 (*sp. inquirenda*)
Paratylenchus hamatus Thorne & Allen, 1950

Peltamigratus
cf. *Aorolaimus*

Pratylenchoides Winslow, 1958
T. Pratylenchidae

Pratylenchus Filipjev, 1936
T. Pratylenchidae
Pratylenchus alleni Ferris, 1981
Pratylenchus andinus Lordello, Zamith & Boock, 1961
Pratylenchus barkati Das & Sultana, 1979
Pratylenchus brachyurus (Godfrey, 1929) Filipjev & Schuurmans Steckhoven, 1941
Pratylenchus coffeae (Zimmermann, 1898) Filipjev & Schuurmans Steckhoven, 1941
Pratylenchus crenatus Loof, 1960
Pratylenchus dasi Fortuner, 1985
Pratylenchus delattrei Luc, 1958
Pratylenchus exilis Das & Sultana, 1979
Pratylenchus fallax Seinhorst, 1968
Pratylenchus flakkensis Seinhorst, 1968
Pratylenchus hexincisus Taylor & Jenkins, 1957
Pratylenchus goodeyi Sher & Allen, 1953
Pratylenchus indicus Das, 1960 (*sp. inquirenda*)
Pratylenchus loosi Loof, 1960
Pratylenchus minyus
cf. *P. neglectus*
Pratylenchus neglectus (Rensch, 1924) Filipjev & Schuurmans Stekhoven, 1941
= *P. minyus* Sher & Allen, 1953
Pratylenchus penetrans (Cobb, 1917) Filipjev & Schuurmans Stekhoven, 1941
Pratylenchus pratensis (de Man, 1880) Filipjev, 1936
Pratylenchus scribneri Steiner, 1943
Pratylenchus sefaensis Fortuner, 1974
Pratylenchus singhi Das & Sultana, 1979
Pratylenchus sudanensis Loof & Yassin, 1971
Pratylenchus thornei Sher & Allen, 1953
Pratylenchus vulnus Allen & Jensen, 1951
Pratylenchus zeae Graham, 1951

Punctodera Mulvey & Stone, 1976
T. Heteroderidae
Punctodera chalcoensis Stone, Sosa-Moss & Mulvey, 1976
Punctodera punctata (Thorne, 1928) Mulvey & Stone, 1976
= *Heterodera punctata* Thorne, 1928

Radopholus Thorne, 1949
T. Pratylenchidae
Radopholus citrophilus Huettel, Dickson & Kaplan, 1984
= *Radopholus similis citrophilus*

Radopholus inaequalis Sauer, 1958
Radopholus rotundisemenus Sher, 1968
Radopholus similis Cobb, 1913
= *Radopholus similis similis*
Radopholus vangundyi Sher, 1968
Radopholus williamsi
cf. *Achlysiella williamsi*

Rhadinaphelenchus Goodey, 1960
T. Aphelenchoididae
Rhadinaphelenchus cocophilus (Cobb, 1919) Goodey, 1960

Rotylenchoides
cf. *Helicotylenchus*
Rotylenchoides intermedius
cf. *Helicotylenchus intermedius*

Rotylenchulus Linford & Oliveira, 1940
T. Hoplolaimidae
Rotylenchulus borealis Loof & Oostenbrink, 1962
Rotylenchulus macrodoratus Dasgupta, Raski & Sher, 1968
Rotylenchulus macrosoma Dasgupta, Raski & Sher, 1968
Rotylenchulus parvus (Williams, 1960) Sher, 1961
Rotylenchulus reniformis Linford & Oliveira, 1940

Rotylenchus Filipjev, 1936
T. Hoplolaimidae
Rotylenchus buxophilus Golden, 1956
Rotylenchus caudaphasmidius Sher, 1965
Rotylenchus microstriatus Siddiqi & Corbett, 1983

Scutellonema Andrássy, 1958
T. Hoplolaimidae
Scutellonema africanum Smit, 1971
Scutellonema brachyurus (Steiner, 1938) Andrássy, 1958
Scutellonema bradys (Steiner & Le Hew, 1933) Andrássy, 1958
= *Scutellonema blaberum* (Steiner, 1937) Andrássy, 1958
Scutellonema cavenessi Sher, 1964
Scutellonema clathricaudatum Whitehead, 1959
Scutellonema magniphasma Sher, 1965
Scutellonema siamense Timm, 1965

Senegalonema Germani, Luc & Baldwin, 1984
T. Hoplolaimidae

Siddiqia
cf. *Paralongidorus*

Tetylenchus Filipjev, 1936 (*gen. dubium*)
T. Belonolaimidae

Thecavermiculatus Robbins, 1978
T. Heteroderidae
Thecavermiculatus andinus Golden, Franco, Jatala & Astogaza, 1983

Trichodorus Cobb, 1913
= *Monotrichodorus* Andrássy, 1976
Di. Trichodoridae
Trichodorus borneoensis Hooper, 1962
Trichodorus monohystera Allen, 1957
= *Monotrichodorus monohystera* (Allen, 1957) Andrássy, 1976
Trichodorus primitivus (de Man, 1880) Micoletzky, 1922
Trichodorus similis Seinhorst, 1963
Trichodorus viruliferus Hooper, 1963

Trophotylenchulus Raski, 1957
T. Tylenchulidae
Trophotylenchulus obscurus (Colbran, 1961) Cohn & Kaplan, 1983
Trophotylenchulus piperis Mohandas, Ravana & Raski, 1985
Trophotylenchulus saltensis Hashim, 1984

Trophurus Loof, 1956
T. Belonolaimidae
Trophurus imperialis Loof, 1956

Tylenchorhynchus Cobb, 1913
T. Belonolaimidae
Tylenchorhynchus acutus Allen, 1955
Tylenchorhynchus annulatus (Cassidy, 1930) Golden, 1971
= *T. martini* Fielding, 1956
Tylenchorhynchus brassicae Siddiqi, 1961
Tylenchorhynchus brevilineatus Williams, 1960
= *T. indicus* Siddiqi, 1961
Tylenchorhynchus capitatus Allen, 1955
Tylenchorhynchus clarus Allen, 1955
Tylenchorhynchus claytoni Steiner, 1937
Tylenchorhynchus crassicaudatus Williams, 1960
Tylenchorhynchus elegans Siddiqi, 1961
Tylenchorhynchus indicus
cf. *T. brevilineatus*
Tylenchorhynchus martini
cf. *T. annulatus*
Tylenchorhynchus mashhoodi Siddiqi & Basir, 1959
Tylenchorhynchus nudus Allen, 1955
Tylenchorhynchus obtusus (Siddiqi, 1978) Fortuner & Luc, 1987
Tylenchorhynchus vulgaris Upadhyay, Swarup & Sethi, 1972

Tylenchulus Cobb, 1913
T. Tylenchulidae
Tylenchulus graminis Inserra, Vovlas, O'Bannon & Esser, 1988
Tylenchulus palustris Inserra, Vovlas, O'Bannon & Esser, 1988
Tylenchulus semipenetrans Cobb, 1913

Tylenchus Bastian, 1865
T. Tylenchidae

Xiphinema Cobb, 1913
Do. Longidoridae
Xiphinema americanum Cobb, 1913
Xiphinema attorodorum Luc, 1961
Xiphinema basilgoodeyi Coomans, 1964
Xiphinema bergeri Luc, 1973
Xiphinema brevicolle Lordello & da Costa, 1961
Xiphinema cavenessi Luc, 1973
Xiphinema diversicaudatum (Micoletzky, 1927) Thorne, 1939
Xiphinema ebriense Luc, 1958
Xiphinema elongatum Schuurmans Stekhoven & Teunissen, 1938
Xiphinema heynsi Siddiqi, 1979
Xiphinema ifacolum Luc, 1961
Xiphinema imitator Heyns, 1965
Xiphinema index Thorne & Allen, 1950
Xiphinema insigne Loos, 1949
Xiphinema krugi Lordello, 1955
= *X. denoudeni* Loof & Maas, 1972
Xiphinema mammatum Siddiqi, 1979
Xiphinema neobasiri Siddiqi, 1979
Xiphinema nigeriense Luc, 1961
Xiphinema oryzae Bos & Loof, 1985
Xiphinema pachtaicum (Tulaganov, 1938) Kirjanova, 1951
= *X. mediterraneum* Martelli & Lamberti, 1967
Xiphinema paritaliae Loof & Sharma, 1979
Xiphinema radicicola Goodey, 1936
Xiphinema savanicola Luc & Southey, 1981
Xiphinema seredouense Luc, 1975

Zygotylenchus Siddiqi, 1963
T. Pratylenchidae
Zygotylenchus guevarai (Tobar Jiménez, 1963) Braun & Loof, 1968

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