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.

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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.*

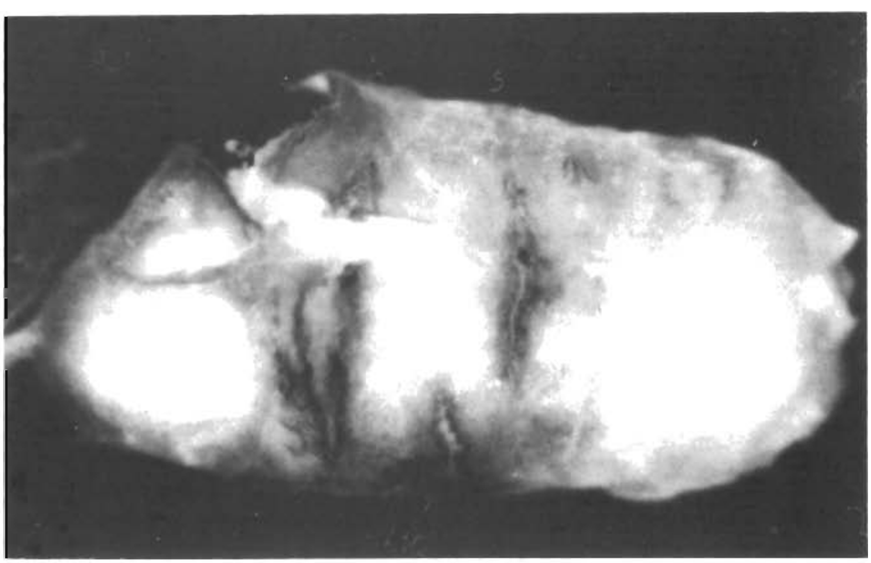

Fig. 2. Necrotic lesions on rice seed endosperm caused by *Aphelenchoides besseyi.*

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).

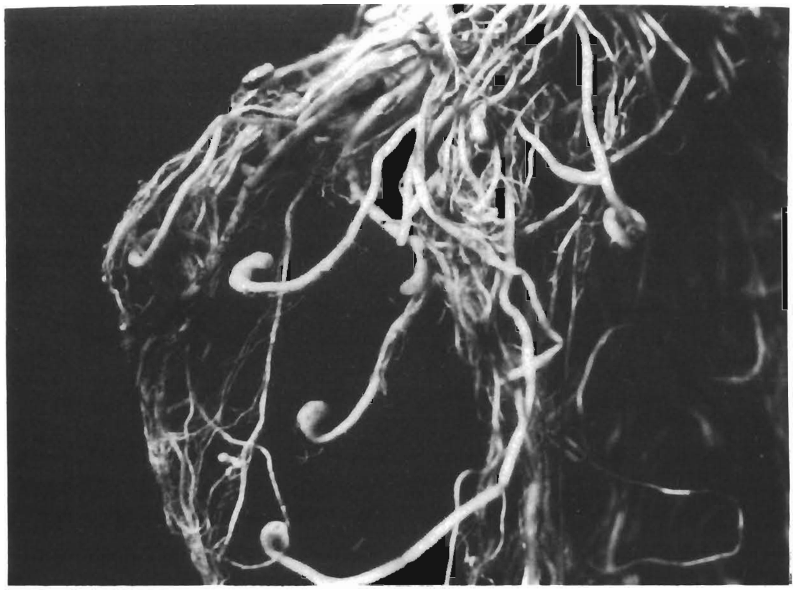

Fig. 7. Characteristic hooked, root tip galls on rice caused by *Meloidogyne graminicola*.

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

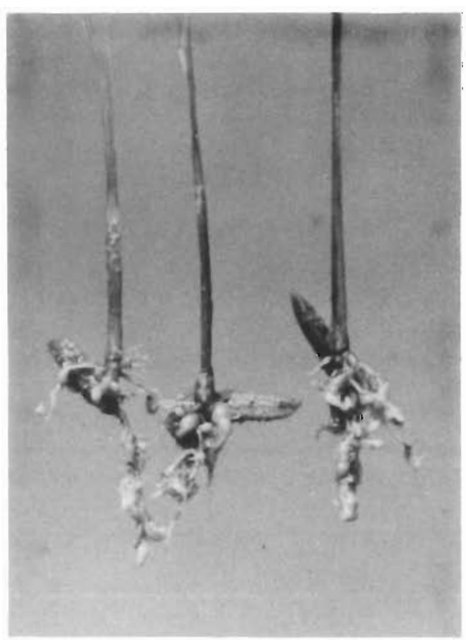

Fig. 8. *Meloidogyne graminicola* root galls on rice seedlings.

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.

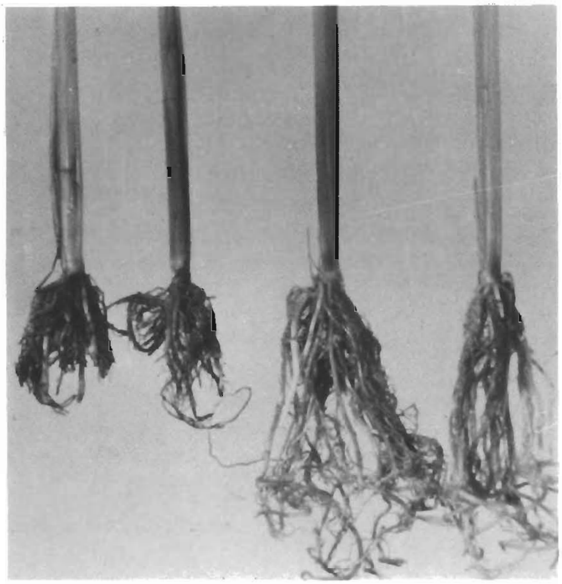

Fig. 11. Roots damaged by *Paralongidorus australis* compared to healthy rice roots (Photo. Graham Stirling).

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.

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