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.

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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

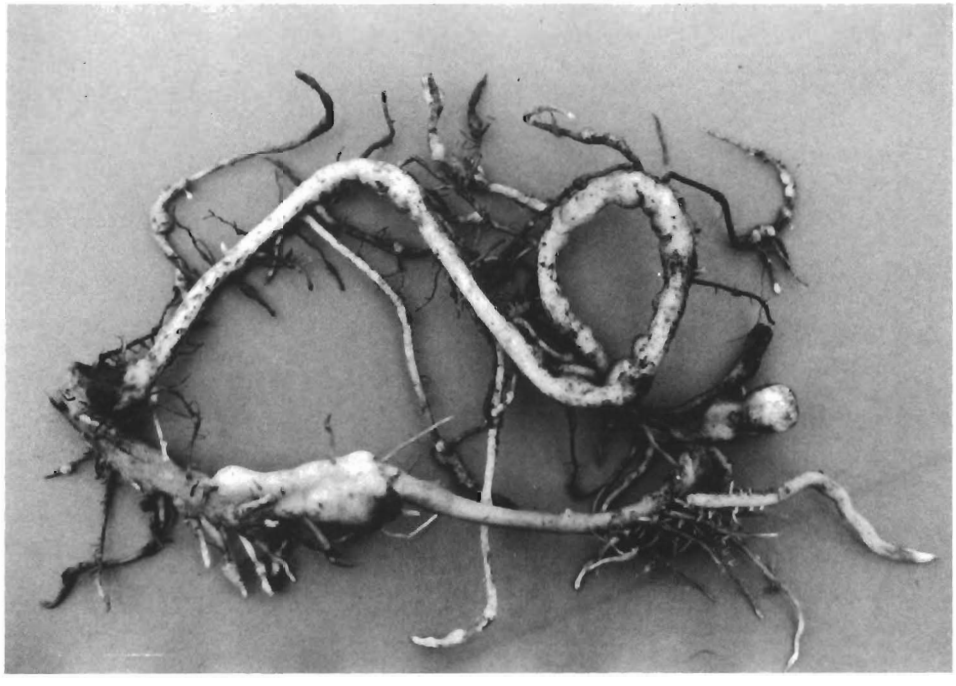

Fig. 1. Root galling caused by *Meloidogyne* sp. on a Cavendish AAA cultivar.

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.

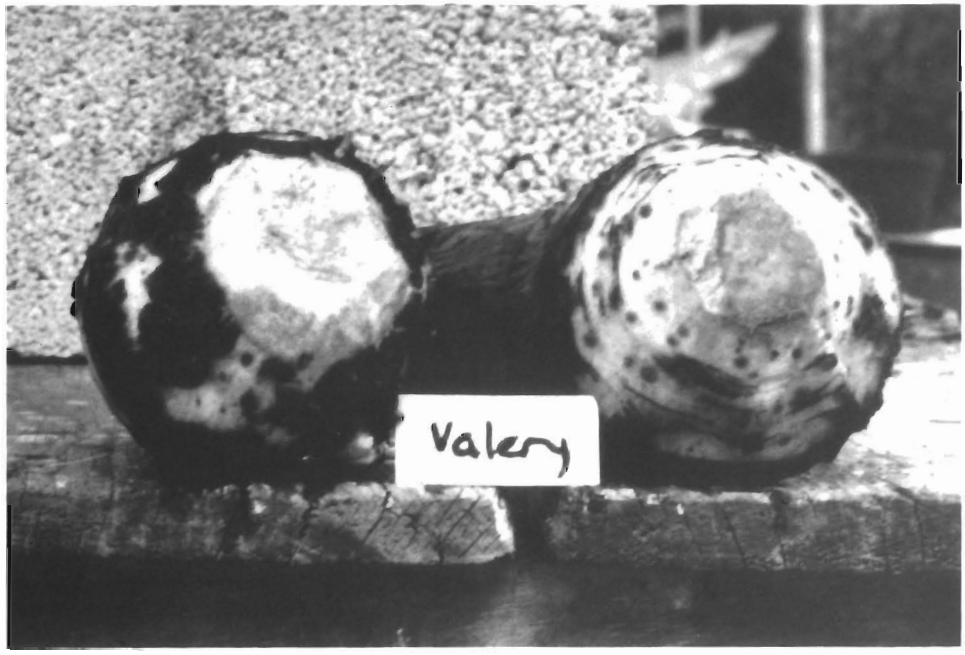

Fig. 4. Cavendish suckers cv Valery: left – heavily infected with *R. similis*; right – infection removed by paring.

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).

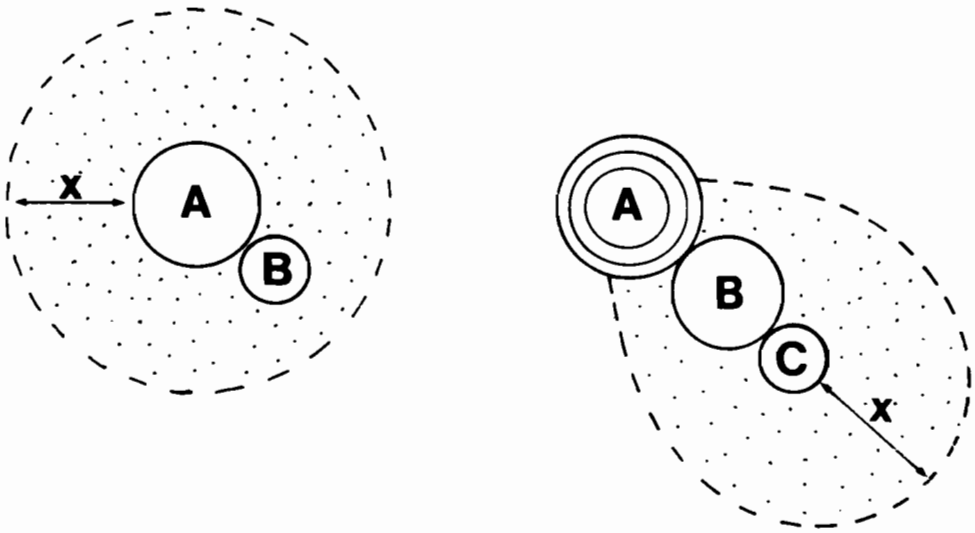

Fig. 6. Area of treatment when using granular nematicides on young plantation and on a ratooning crop.
A Mother plant
B Selected daughter sucker (1st ratoon)
C Selected daughter sucker (to produce second ratoon)
X Radius of treatment area 35–50 cm

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

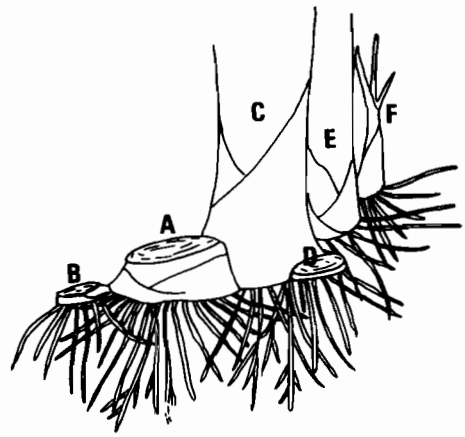

Fig. 7. The population levels of *Radopholus similis* (Rs) and *Helicotylenchus multicintus* (Hm) in the roots of the different components of a banana clump. From peaty soil, Niéky Valley, Ivory Coast (Quénéhervé unpubl.).

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.

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