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Abstract. Botanical and economical backgrounds on dessert and non-dessert bananas, together with basic concepts for nematode management, are provided, including the geographic distribution of main banana nematode species in Asia, Oceania, Africa and Americas. Basic studies on the biology, damage, economic importance and control of nematodes are then discussed, with reference to the burrowing nematode *Radopholus similis*, the lesion nematodes *Pratylenchus* spp., root-knot nematodes *Meloidogyne* spp., and the spiral nematode *Helicotylenchus multicinctus*. The use of nematicides is reviewed and the research on alternatives to chemical control is discussed. Current nematode management strategies focus on the use of clean planting material, fallow and alternate croppings, application of mulching and fertilisers. Future and common strategies include best plant health measures, the identification of sources of resistance and plant defence mechanisms, including transgenic resistance. Other management strategies concern biological control through soil treatment with microbial antagonists, induction of in-planta suppressiveness and improvements in cultural practices. Tolerance to nematodes, use of new synthetic banana hybrids and their response to parasitism are also reviewed.

1. INTRODUCTION

Plant-parasitic nematodes are widespread and are among the most damaging pests of all banana varieties, causing not only severe crop losses in commercial banana plantations for export but also seriously limiting the production and viability of other banana types. Numerous reviews have already been written on the nematode problems in bananas (Wardlaw, 1961; Champion, 1963; Blake, 1969; Stover, 1972; Roman, 1978; Jones, 2000; Gowen & Quénéhervé, 1990; Gowen et al., 2005) and most of the knowledge of banana nematodes arose quite exclusively from their management on dessert bananas (*Musa* AAA Cavendish group) cultivated in large plantations for export.

A. Ciancio & K. G. Mukerji (eds.), *Integrated Management of Fruit Crops and Forest Nematodes*, 3-61.

In this chapter, we will try to widen these views by considering the different aspects of nematode management in respect both to the type of cultivated bananas and the geographic situation.

1.1. Botanical and Economical Backgrounds on Bananas

After rice, wheat and corn, bananas are the fourth most widely consumed food for humans and the majority of cultivated bananas are grown for local consumption in private gardens and smallholdings in mixed cropping systems. Bananas are cultivated in more than 130 countries and provide staple food and steady cash income to million people. Bananas, monocotyledons belonging to the *Musa* genus, are large herbaceous perennials with underground rhizomes (or corms) from which abundant roots and vegetative buds grow. The aerial part consists of leafy 'trunks' (or pseudostem), which eventually bear bunches.

Bananas can be divided into two main categories, the dessert bananas, mostly eaten fresh, and the non-dessert bananas, including cooking and brewing bananas. In general, pure stands of cooking and dessert types only occur where there is access to export or local markets or where bananas make a major contribution to the diet. From a pest management point of view, the division is even more precise and clearly opposes dessert bananas grown for export to all other banana types.

Most cultivated bananas within the genus *Musa* arose from the Eumusa section. The Eumusa group of species is the largest and most wide-ranging section of the genus and comprises some eleven species being found throughout South East Asia, from India to the Pacific Islands (Horry et al., 1997). Some other edible *Musa* varieties, including the Fe'i banana cultivars, are derived from wild species within the Australimusa section. However, most edible cultivars are derived from two ancestor species, *Musa acuminata* (A genome) and *Musa balbisiana* (B genome) (Simmonds & Shepherd, 1955).

Edible diploid and triploid *M. acuminata* cultivars were largely disseminated by humans (Simmonds, 1960) to native areas of *M. balbisiana*, resulting in natural hybridization and in the formation of hybrid progeny with the genome AB, AAB, and ABB. Consequently, a very diverse selection of *Musa* cultivars is thought to have arisen in South East Asia along with the earliest developments of agriculture many thousand years ago (Price, 1995). The number of different clones has been estimated to be 400-500 (Perrier & Tezenas du Montcel, 1990).

The main genomic groups and sub-groups with some important cultivars are summarized in Table 1, with their uses and geographical distribution (adapted from Simmonds, 1966). This wide genomic diversity, combined with a wide and worldwide human dispersal, have led to very different broad systems of banana cultivation and pest management, depending on local conditions (tropical or subtropical regions; native or introduced crops; productions for export, local market or subsistence; cultivated varieties for dessert, cooking or even brewing).

In 2003, the total world production was estimated at over 100 million metric tons, of which dessert bananas represented 56 %. Only 14 % of this world production is grown for commercial export, so the rest, over 86 %, comprises a wide

Table 1. Main genomic groups of banana with some important cultivars, their uses and geographical distribution (adapted from Simmonds, 1966).

Genome	*Sub-group*	*Cultivar*	*type*	*Distribution*
AA	sucrier	Pisang mas, Figue sucrée	sweet dessert	Worldwide
		Pisang lilin	dessert	Indonesia, Malaysia
		Pisang berangan, Lakatan	dessert	Indonesia, Malaysia, Philippines
AAA	Gros-Michel	Gros-Michel, Highgate	dessert	Wordlwide
	Cavendish	Dwarf Cavendish, Giant Cavendish, Robusta, Pisang masak hijau	dessert	Exporting countries wordlwide
	Red	Red, Green-red	dessert	Wordlwide
	Mutika Lujugira	Intundu, Mujuba	brewing-cooking	Central & East Africa, Colombia
	Matooke	Nshakara, Nyoya	cooking	East Africa
	Mbire	Mbire, Kisubi	brewing	East Africa
	Ibota	Yangambi Km5	dessert	Indonesia, Africa
AB	Ney poovan	Ney poovan, Safet velchi, Kunnan, Sukari, Lady's finger	dessert	India, East Africa
AAB	Plantain	French plantain, Horn plantain, False Horn	cooking	Central & West Africa, India, Latin America, Carribean
	Pisang kelat	Pisang kelat, Thiruvanthapuram	dessert	India, Malaysia
	Pisang raja	Pisang raja	cooking	Malaysia, Indonesia
	Mysore	Poovan, Mysore	dessert	India
	Chuoi Xiem	?	dessert	Asia
	Silk	Figue pomme, Maça, Silk	dessert	Wordlwide
	Pome	Prata	dessert	Asia, Australia, West Africa, Brasil
	Popoulou	Popoulou	cooking	Pacific
	Laknao	Laknao	cooking	Philippines
	Pisang nangka	Pisang nangka	cooking	Malaysia
ABB	Bluggoe	Bluggoe, Matavia, Poteau, Cacambou	cooking	Wordlwide
	Pelipita	Pelipita	cooking	Philippines, Latin America
	Pisang awak	Fougamou	dessert	India, Thailand, Philippines, East Africa
	Peyan	Peyan	cooking	Philippines, Thailand
	Saba	Saba	cooking	Philippines, Indonesia, Malaysia

Table 2. Estimates of banana production and Cavendish exportation (adapted from Lescot, 2004).

	Cooking bananas		*Dessert bananas*		*Total*	*Bananas for export*	
	AAB	*ABB*	*Cavendish*	*others*		*Cavendish*	*cooking*
North America	0	9 000	400	100	9 500	428 449	1
Central America	932 000	108 000	5 860 162	167 000	7 067 162	3 903 124	109 202
South America	5 424 570	299 400	10 729 070	5 010 060	21 463 100	6 346 533	207 195
Caribbean	873 096	563 152	1 310 097	222 024	2 968 369	549 667	17 801
East Africa	1 287 451	13 995 956	2 023 593	734 960	18 041 960	15 089	13
West -Central Africa	7 991 102	963 963	1 970 757	410 788	11 210 610	559 451	463
North Africa -Middle East	2	3 022	1 471 568	1 071	1 475 663	189 259	0
Asia	1 067 020	9 795 840	20 728 071	5 338 285	36 929 216	1 826 981	9
Oceania	1 130	688 200	269 705	85 350	1 044 385	1 282	0
Europe	1	5	440 191	5	440 202	393 878	73 868
Total	17 576 372	26 426 538	44 803 614	11 969 643	100 650 167	13 785 264	408 551

range of banana varieties and crop systems (Lescot, 2004). Table 2 (adapted from Lescot, 2004) illustrates both estimates of banana production and Cavendish export. It shows the importance of banana cultivation in the different parts of the world, from the most intensive production systems for export of Cavendish bananas to the subsistence production of brewing bananas for local consumption.

As a consequence, it is obvious that banana diseases and pest management are also very diverse and depend primarily on the local conditions of cultivation.

1.2. Integrated Nematode Management: Concept Definition and Applications

All definitions agree that Integrated Pest Management (IPM) is a general approach which first assesses the pest situation, evaluates the advantages and disadvantages of pest management options and then implements a system of complementary management actions used in combination to control pests, with an emphasis on methods that are least injurious to the environment and most specific to the particular pest. For example, nematode-resistant plant varieties, regular monitoring for nematodes, judicious use of pesticides, biological control, and good stand management practices may be used alone or in combination to control or prevent particular forms of nematode damage. IPM is a dynamic system that is adaptable to diverse management approaches. In these approaches, the pest management decisions are taken by the individual producer, business entity or government agency but are influenced by the diversity of public and private values.

Historically, some of the most important nematode management practices were scientifically sound very early for commercial bananas, but their practical application was difficult, due to the absence of certain techniques (e.g. in vitro culture) or basic biological knowledge (e.g. nematode survival and dispersal, transitional host plants). For example, early as the sixties, Loos and contemporaries laid the basis of nematode management measures for controlling the burrowing nematode on dessert bananas and already recommended planting clean seed material on uninfested land (Loos & Loos, 1960a).

Bananas are attacked by many species of plant parasitic nematodes but only a few cause damage of economic importance. Worldwide, the nematode species known to cause, in the broad sense, the most serious damage to bananas are the migratory endoparasites, *Radopholus similis*, the lesion nematodes *Pratylenchus coffeae* and *P. goodeyi*, the endoparasite *Helicotylenchus multicinctus* and the sedentary parasite *Meloidogyne* spp. In addition to these five major species, some other species have been reported to be associated with *Musa* spp. throughout the world. Depending on local conditions, the associated damage of any of these nematode species may be locally important where their densities are high.

As for any other pest or parasite, nematode relationships with bananas, including damage, depend on environmental conditions, susceptibility of the host and pathogenicity of the nematode considered. In the last 50 years, many efforts have been made in nematology to collect these basic biological data and to test new nematode management practices on bananas. These efforts were particularly important on dessert bananas for export but, thanks to some national and international research institutes and to the banana and plantain section (formerly INIBAP, International Network for the Improvement of Banana and Plantain) of Biodiversity International (formerly IPGRI, International Plant Genetic Resources Institute), these efforts are now very considerable on all the other banana types.

In this chapter, the different nematode management approaches will be reviewed as specific procedures on commercial dessert bananas, as regional options due to the specificity of the different cropping systems (e.g. Asia and Oceania, Africa, America and the Caribbean) and as shared strategies and future approaches common to these different banana cropping systems.

2. DESSERT BANANAS FOR EXPORT

The first exported bananas from Central America arrived on the west coast of the United States before 1870 and by 1905 almost 1 M tons had already been imported (USA: 740000 tons; Great Britain: 115000 tons) from Central America but also from Jamaica and the Canary Islands (Simmonds, 1960; Champion, 1963). At this time, the variety ‘Gros-Michel’, a triploid *Musa* AAA originating from Malaysia, was the favourite variety in all commercial banana plantations.

Following the spread of Panama disease (*Fusarium oxysporum* f. sp. *cubense*) in the seventies, all the commercial plantations changed over from the susceptible cultivar ‘Gros Michel’ to the resistant cultivars from the Cavendish subgroup, which are still cultivated (Jones, 2000). However, different authors in Central America (Leach, 1958; Whehunt et al., 1978), India (Rajendran et al., 1979) and West Africa (Mateille, 1992; 1993) had already noticed that the variety ‘Gros-Michel’ was less sensitive to *R. similis* than the newly introduced Cavendish varieties.

At present, the main producing countries of export bananas are localized in Central and South America (Guatemala, Costa Rica, Ecuador, Colombia) and in Southeast Asia (Philippines), where these Cavendish varieties are grown in intensive monoculture mostly for export (14.2 M tons in 2003). Ecuador alone accounts for more than one third of the international banana exports. However, the tonnages of these Cavendish bananas (a world production of more than 44.8 M tons in 2003) are even greater when grown for the local market in countries such as India, China, Brazil, Indonesia, Mexico and Egypt (Lescot, 2004).

Most of these bananas grown for export belong to the Cavendish subgroup and are cultivated in the humid tropics, with a uniform warm climate on flat lowlands with deep and well-drained soils.

2.1. Geographic Distribution of Associated Nematode Species

The nematode problem on commercial bananas was observed very early and soon received much attention from researchers in Latin America and the Caribbean, as dessert bananas were cultivated for export to North America and Europe from 1870 (Champion, 1963). Ashby (1915) in Jamaica was the first author to describe appropriately nematode symptoms in banana rhizomes as a ‘Black head disease of bananas’. The same year, Cobb completed the nematode description using soil samples taken earlier from around banana roots from Fiji, described as *Tylenchulus similis* (Cobb, 1893) and additional specimens from Hawaii and Jamaica. Following this early discovery, the burrowing nematode *Radopholus similis* was progressively observed in almost all dessert banana producing areas of the world: in the French West Indies, Jamaica and Trinidad (Mallamaire, 1939; Leach, 1958; Scotto la Massèse, 1968); in the large plantations of the United Fruit Company of Central America (Stover & Fielding, 1958; Holdeman, 1960); in Brazil (Carvalho, 1959); in Belize (Pinochet & Ventura, 1977); in West Africa (Mallamaire, 1939; Luc & Vilardebo, 1961), the Caribbean (Ayala & Roman, 1963; Decker & Casamayor, 1966; Stoyanov, 1967; Edmunds, 1968), Surinam (Maas, 1969), India (Nair et al., 1966) and Asia (Timm, 1965; O'Bannon, 1977).

Blake (1961) suggested that the burrowing nematode was first introduced into Australia in infested banana plants imported from Fiji between 1860 and 1910. In 1972, Stover advanced the explanation that the recent and widespread dissemination of *R. similis* began soon after the progressive replacement of the variety 'Gros Michel' by the Cavendish varieties. As an example, while already present in the Philippines, the occurrence of *R. similis* increased dramatically when large amounts of infested planting materials of giant Cavendish were imported from Central America in the early seventies (Boncato & Davide, 1980; Davide, 1992).

Recently, Marin et al. (1998a) reviewed the spread of bananas in Latin America and the Caribbean and its relationship to the occurrence of *R. similis*. Diseases caused by *R. similis* were also known as "spreading decline of citrus" in Florida, USA (Suit & DuCharme, 1953) and "yellows disease of pepper" in Bangka, Indonesia (van der Vetch, 1950). Throughout the world, *R. similis* has also been recovered from the roots of many other hosts, including important cultivated crops (tea, coffee, pepper), ornamentals and weeds (Gowen et al., 2005).

Besides the widespread occurrence of the burrowing nematode *R. similis*, some other nematode species are also able to cause economic damage on dessert bananas.

After *R. similis*, the spiral nematode *Helicotylenchus multicinctus* is probably the most damaging nematode on bananas. This species, originally described by Cobb in 1893 as *Tylenchus multicinctus*, has been frequently found in mixed populations with *R. similis* throughout the tropics and the subtropics on all varieties of bananas. Its geographical distribution follows almost exactly that of *R. similis* (McSorley & Parrado, 1986; Bridge, 1993) while its abundance depends both on the presence or absence of the burrowing nematode *R. similis* and on the soil organic matter content (Vilardebo & Guérout, 1976; Quénéhervé, 1988). Its economic importance has been acknowledged mostly in bananas growing in subtropical conditions, such as in Israel (Minz et al., 1960), South Africa (Jones, 1979) and Florida (McSorley & Parrado, 1986). *Helicotylenchus multicinctus* should be regarded as the main parasitic nematode on bananas in the absence of lesion nematodes (*Radopholus* and *Pratylenchus*) and where environmental conditions are suboptimal for the crop in relation to latitude, temperature and rainfall.

Among the lesion nematodes from the genus *Pratylenchus*, only *P. coffeae* and *P. goodeyi* are recognized as damaging species, and cause similar symptoms on bananas as the burrowing nematode. Zimmerman (1898) was the first to describe as *Tylenchus coffeae* the species infesting coffee plants in Java, whereas Cobb observed and described the species as *Tylenchus musicola* in roots of plantains in Grenada in 1919. Since then, *P. coffeae* has been recorded worldwide on bananas (Bridge, 1993). This nematode is a pan-tropical species and a major pest of economic crops such as coffee, banana and fruit trees, tuber crops and ornamentals (Luc et al., 2005). While the distribution of the burrowing nematodes was mostly associated with commercial plantations of Cavendish varieties, the distribution of the lesion nematode *P. coffeae* seems mostly associated with plantains, rather than Cavendish varieties.

Pratylenchus goodeyi was first observed in roots of dessert bananas in the Canary Islands by de Guiran & Vilardebo (1962) and later in Crete (Vovlas et al., 1994). Since then, this species has been observed on highland bananas in East Africa (Gichure & Ondieki, 1977; Walker et al., 1984; Bridge, 1988a) and Cameroon (Price & Bridge, 1995) in addition to its presence on *Ensete* in Ethiopia (Peregrine & Bridge, 1992). More recently, the species was also reported from subtropical areas of Australia (Stanton et al., 2001). The presence of *P. goodeyi* on bananas seems conditioned by the altitude and the latitude, presumably in relation to soil temperature (Price & Bridge, 1995).

All banana varieties are hosts of the root-knot nematodes belonging to the *Meloidogyne* genus, which attack many economically important crops and cause deformations and stunting of the roots. They were first reported to occur on bananas, in Egypt and Southeast Asia, by Delacroix (1901). In general, the root-knot nematodes are more likely to cause damage in subtropical conditions such as in Crete (Vovlas et al., 1994), Lebanon (Sikora & Schlosser, 1973), North Yemen (Sikora, 1979), South Africa (Jones & Milne, 1982) and Taiwan (Lin & Tsay, 1985) and in greenhouse production systems of Morocco (Janick & Ait-Oubalou, 1989) and the Canary Islands (Pinochet et al., 1998).

In tropical conditions, root-knot nematodes are more likely to be found in great numbers on Cavendish varieties in absence or near-absence of burrowing or lesion nematodes such as on sandy loam soils in the Philippines (Davide, 1980) or sandy soils of West Africa (Quénéhervé, 1988). Currently, in the French West Indies, they are reported in large numbers only on new Cavendish plantations established from tissue culture plants, after a fallow or a rotation period. In Asia, Boncato and Davide (1980) in the Philippines and Razak (1994) in Malaysia also reported large populations of root-knot nematodes on commercial Cavendish plantations.

Other species of minor incidence on dessert bananas include *Rotylenchulus reniformis*, *Hoplolaimus pararobustus*, *H. seinhorsti* and *Heterodera oryzicola*. In the islands of Madagascar and La Réunion, a nematode species, *Zygotylenchus taomasinae* has been found in association with *R. similis* in banana plantations (Vilardebo & Guérout, 1976).

2.2. Basic Studies on Nematode Biology

Outstanding studies on biology and life-cycle of the burrowing nematode *R. similis* and histological observations were first conducted by Blake in Australia (1961; 1966) and Loos while working at the United Fruit Co., in Honduras (Anonymous, 1957; Loos & Loos, 1960b). In these studies, the authors described how nematodes could invade, feed and reproduce in the cells of the cortex along the entire length of the roots and in the rhizome. Nematodes, while migrating in the cortical parenchyma but not in the stele, cause cavities which then coalesce to appear as necrotic tunnels. The migration and egg laying seem governed by nutritional and biochemical factors, as nematodes move in the parenchyma in search of healthy tissue, away from the necrosis (Blake, 1961). Loos (1962) was the first to describe the complete life-cycle from eggs to eggs in 20-25 days at a temperature range of 24-32°C, with the eggs hatching after 8-10 days and the completion of the juvenile stages in 10-13 days.

Increases of nematode populations in banana roots are thought to be the result of several factors (see: Gowen et al., 2005, for a review) but clearly the renewal of the root system following bursts of root growth is the main factor in the population build-up of *R. similis*. Any factor, endogenous or exogenous, which favours root emergence on banana plants, contributes to this increase (Quénéhervé, 1993a).

The existence of different biotypes of *R. similis* was first illustrated by the physiological differences in reproductive capabilities and morphological variations among *R. similis* populations. This hypothesis was extensively studied in Central America and the Caribbean (Edwards & Wehunt, 1971; Pinochet, 1979; Tarté et al., 1981; Kaplan & O'Bannon, 1985; Pinochet, 1987; Sarah et al., 1993; Fallas et al., 1995; Hahn et al., 1996; Marin et al., 1999). Different biotypes of *R. similis* are now widely recognised and certainly could explain the discrepancies observed worldwide in damage levels, in terms of yield losses, plantation longevity, transitional hosts and nematode management efficacy. Until recently, it was recognized that *R. similis* had two races, one non-pathogenic to citrus and another pathogenic either on citrus and banana, the former *R. citrophilus* (DuCharme & Birchfield, 1956). Recent research does not support the existence of a sibling species (Kaplan & Opperman, 1997; Valette et al., 1998). Nevertheless, these different biotypes of *R. similis* were also observed on other plants than bananas and led to inconsistent results in terms of the host status of some weeds (Edwards & Whehunt, 1971; Keetch, 1972; O'Bannon, 1977; Inomoto, 1994), and of very important rotation crops too (sugarcane, pineapple, forage crops e.g. *Bracharia* sp).

The interaction with other pathogens was studied since the increase in Panama disease (caused by *F. oxysporum* f. sp. *cubense*), in presence of the burrowing nematode was observed early on the cultivar 'Gros Michel' (Newhall, 1958). Soon after that, and beginning in the sixties, the cultivar 'Gros Michel' was completely replaced by banana varieties from the Cavendish subgroup following the spread of Panama Disease into every commercial plantation in Latin America and the Caribbean. Since then, many studies have described and assessed the pathogenic effects of fungi alone or in combination with nematodes on the *Musa* AAA, from the subgroup Cavendish (Brun & Laville, 1965; Stover, 1966; Booth & Stover, 1974; Pinochet & Stover, 1980; Loridat, 1989).

The presence of *R. similis* on hosts other than *Musa* was also investigated and Christie, in 1958, published the first list of putative hosts of *R. similis*, including cultivated crops and weeds. While this topic was extensively studied in Florida from a quarantine point of view (O'Bannon, 1977; Lehman, 1980; Esser et al., 1984), similar studies were gradually carried out in every banana producing country as a prerequisite for nematode management (Ayala & Roman, 1963; Keetch, 1972; Rivas & Roman, 1985; Zem, 1983). More recently, a study conducted in Martinique clearly shows how weeds could be significant reservoirs of plant parasitic nematodes, including *R. similis* and *P. coffeae* in banana fields (Quénéhervé et al., 2006).

The survival of *R. similis* in soils was studied in citrus soils in Florida (Tarjan, 1961) and banana soils in Honduras (Loos, 1961). These authors demonstrated that *R. similis*, which does not have a specialized survival strategy (e.g. quiescence, cryptobiosis), was not able to survive more than 6 months in the soil, in absence of host roots or pieces of live corms. The corms, used as seeds or planting materials, have been known to be a major means of dissemination of banana nematodes for many years in Latin America (Loos & Loos, 1960a), Australia (Blake, 1961) and Africa (Quénéhervé & Cadet, 1985b). In a study conducted in the Ivory Coast on the cultivar 'Poyo', most of the nematodes were localized in the outer part of the corm but a significant proportion (11 %) was found at depths ranging from 3 to 7 cm, well protected against any physical nematode control method (e.g. paring, heat-treatment) (Quénéhervé & Cadet, 1985a).

During the last decade, most of the studies on the biology of nematodes found on export bananas were mainly conducted in Costa Rica with the Corporación Bananera Nacional (CORBANA) (Araya et al., 1999; Araya & De Waele, 2004; Moens et al., 2006).

The biology of *R. similis* was extensively studied as the major nematode problem on export bananas, and relatively little information exists on the biology of the other nematode species. The biology of the lesion nematodes *Pratylenchus* spp. was mostly studied on non-export bananas and will be considered later. The spiral nematode, often encountered together with *R. similis* in dessert bananas, feeds on the outer cells of the root cortex and produces small, characteristic discoloured necrotic lesions (Luc & Vilardebo, 1961), but it is also able to complete its life-cycle within the cortical part of the root (Zuckerman & Strich-Harari, 1963). In contrast to *R. similis*, histological changes seem to be confined to parenchyma cells close to the epidermis (Orion et al., 1999).

The biology and life-cycle of root-knot nematodes are not documented on bananas but should not differ from those described for other hosts. In thick and fleshy primary roots, roots deformations and stunting can be very important, with many females and egg masses occurring within the same gall. In general, root-knot nematodes occur in banana roots in mixed populations of nematode genera and species (Pinochet, 1977; Cofcewicz et al., 2004a; 2004b; 2005) and their populations are greater on the distal part of the banana root system, as a reflection of the competition occurring with the other nematode species (Santor & Davide, 1982; Quénéhervé, 1990). Pinochet (1977) suggested that extensive colonization by *R. similis* might contribute to the inhibition of the *Meloidogyne* spp. development, by reducing the feeding sites and interrupting their life cycle in roots, near the rhizome.

For all these species, as with *R. similis*, survival occurs on infected corms or on tissue remaining from the previous crop, and infected planting material is also the primary means of dissemination (Quénéhervé & Cadet, 1985a, 1985b).

2.3. Damage and Economic Importance

The importance of nematodes as a widespread cause of banana losses was first reported in Jamaica by Leach (1958), who emphasized how destructive the burrowing nematode *R. similis* was for banana production, attributing to this pest the widely distributed disease know as "Black head toppling disease". Loos (Anonymous, 1957) was the first to describe root symptoms and associated damage with the presence of *R. similis* in banana roots, since "*the lesioning of the primary roots together with the girdling and death of those roots which anchor the plant to the ground make the plant prone to 'tip over' under wind pressure*".

Nematodes affect banana plant growth and yield by damaging the root system, and increases in population densities of some nematode species (e.g. burrowing and lesion nematodes) are most often associated with increased root necrosis, reduced root biomass and toppling of the plants. Bananas infected with plant-parasitic nematodes are therefore less able to take up water and nutrients, resulting in stunting, delayed maturation time and reduced bunch size. Depending on the nematode species mixture and on environmental factors, the damage can vary from a slight and hidden lengthening of the vegetative period to the most obvious symptom of attack by lesion nematodes, which is the toppling over of banana plants.

From a mechanistic approach, it is possible to define three successive levels of nematode damage (Quénéhervé, 1993a, 1993b):

1. A lengthening of the vegetative phase: the different phenological intervals (lag between planting and flowering, harvest and flowering of ratoons, harvest to harvest etc.) are lengthened without significant reduction in plant size, bunch weight, number of harvested bunches and total harvest. This minor damage is mostly ignored, except in commercial plantations, where the number of boxes is monitored such as in Central and Latin America.

2. A lengthening of the vegetative phase with a reduction in the total harvest: in this case there are two sub-levels according to the reduction in the number of harvestable bunches (bunches that are non-exportable because of poor quality or immature delayed fruits), in addition to the reduction in the average plant size and bunch weight. This type of damage is often observed in commercial plantations in West Africa.

3. A lengthening of the vegetative phase, with a reduction either in the total harvest and in the longevity of the plantation: this third level is the same as above but now it is irreversible, due to the destruction of plants which are uprooted or whose growth is too severely delayed. When infested with the highly pathogenic strain of the burrowing nematode and in absence of any nematode control, this third level of damage is observed almost worldwide on dessert bananas.

However, in some regions, irreversible damage due to uprooted plants bearing fruits can occur very early with gusty winds. The probability of observing this type of damage with *R. similis* is highest in the Caribbean and Central America, as compared to other continental banana producing areas of the world.

After the replacement of cv. 'Gros Michel' by more nematode-susceptible Cavendish cultivars, crop losses were estimated on the basis of the yield improvement after nematicide treatments in the different producing countries. These reported yield responses varied greatly from 15 to 275% (Gowen & Quénéhervé, 1990). These differences may be due to the several biotic and abiotic factors affecting the nematode population dynamics that were extensively studied such as the soil type (Stover & Fielding, 1958; Ayala & Roman, 1963; Guérout, 1975; Davide, 1980; McSorley & Parrado, 1981; Quénéhervé, 1988), the nematode species and biotype (cf. above), the host plant physiology (Guérout, 1972; Jaramillo & Figueroa, 1974; Hugon et al., 1984; Mateille et al., 1984; Quénéhervé, 1993a) and the climate (Jimenez, 1972; Jaramillo & Figueroa, 1974, 1976 ; Vilardebo, 1976; Marcelino et al., 1978; Hutton, 1978; McSorley & Parrado, 1981 ; Badra & Caveness, 1983; Davide & Marasigan, 1985; Hugon et al., 1984; Quénéhervé, 1989a; 1989b).

Besides *R. similis*, some other species have been shown to cause damage to dessert bananas for export. In the Canary Islands on sandy and loamy soils, root-knot nematodes can cause yield reductions of over 20 %, while the lesion nematode *P. goodeyi*, widespread at altitudes above 300-500 m, causes serious root damage in the three major banana producing Canary Islands, with 16 % yield reduction (Rodriguez, in: Pinochet et al., 1998). In the Philippines, yield reductions based on bunch weights ranging from 26.4 % to 57.1 % were observed after inoculation with the root-knot nematode *M. incognita* (Davide & Marasigan, 1985). In greenhouse experiments, significant reductions in plant growth (Jonathan et al., 2000) and alteration of the concentration of macro- and micronutrients in leaves (Cofcewicz et al., 2004) were observed after inoculation with root-knot nematodes. In Israel and Cyprus, yield reductions ranging from 18 % (Minz et al., 1960) to 30 % (Phillis: in Gowen & Quénéhervé, 1990) have been observed with *H. multicinctus*.

Due to the almost constant superiority in numbers of the burrowing nematodes on Cavendish bananas, the assessment of yield losses due to other nematode species has always been neglected and certainly underestimated, such as for *H. multicinctus* (Moens et al., 2006). In recent experiments conducted in Costa Rica on cv. 'Grande Naine' (*Musa* AAA), *H. multicinctus* reduced the mean root weight by 13 % compared to uninoculated plants, *M. incognita* increased the mean root weight by 6.7 % and *P. coffeae* did not significantly decrease the mean root weight. In a microplot experiment, only plants infected with *R. similis* showed a significant root weight reduction of 66 %, after 12-15 months.

Damage is assessed by choosing an appropriate nematode extraction technique (Gowen & Edmunds, 1973; Whyte & Gowen, 1974; Vilardebo, 1974; Quimi & Villacis, 1977; Escobar & Rodriguez-Kabana, 1980; Araya, 2002) and type and place for root sampling (Quénéhervé & Cadet, 1986; Araya et al., 1999; Moens et al., 2001) or a standardized sampling method for pesticide or resistance screening trials (Vilardebo, 1974; Carlier et al., 2002). Obviously, the choice of any assessment method depends both on objectives (research or laboratory routine diagnosis) and laboratory facilities. In the absence of laboratory facilities, the visual assessment of damage is also possible by recording the incidence of banana plant uprooting per hectare and per month (Tarté & Pinochet, 1981). This technique is still currently used in large plantations where uprooted banana plants are monitored weekly. As an example, in Costa Rica the incidence of uprooted plants can reach 5.5 $\% \cdot ha^{-1} \cdot week^{-1}$ without treatments, while this percentage is lowered to 0.3-0.5 % with nematicide applications (G. Fallas, pers. comm.). Techniques of visual assessment of necrosis on roots and rhizomes were also developed in America (Stover, 1972; Tarté & Pinochet, 1981), Africa (Bridge, 1988a; Bridge & Gowen, 1993; Speijer & Gold, 1996) and Australia (Broadley, 1979). These methods (percentage of necrotic roots) combined with nematode countings are applied in most of the banana nematode monitoring programmes in Latin America (Araya, 2002) and Australia (Stanton et al., 2001).

2.4. Nematode Control: The Golden Age of Nematicides (1960-1990)

The early investigations on the control of nematodes in banana soils were conducted in Africa and Australia (Blake, 1961) with two fumigant nematicides (D-D, dichloropropane-dichloropropene; EDB, ethylene dibromide), which gave a 30-40 % yield increase (Vilardebo, 1959; Champion, 1963). Very soon, these fumigants were replaced by DBCP (1,2-dibromo-3-chloropropane) because it was the only fumigant nematicide which was not phytotoxic and could therefore be applied prior to planting, or onto established crops, to control *R. similis* (Luc & Vilardebo, 1961).

In Central America and as early as the sixties, Loos and contemporaries laid the basis of the nematode management measures for controlling the burrowing nematode on bananas, and already recommended planting clean seed plants on uninfested land (Anonymous, 1957; Loos & Loos, 1960a). This objective was tentatively first achieved using physical (paring, heat treatment) and chemical (dipping in a nematicide) methods, in order to clean the planting material. This use of DBCP was recommended in the Windward Islands (Edmunds, 1968), while some phytotoxicity after dipping with DBCP was observed in Honduras, leading to its replacement by heat treatment (Hildreth, 1962).

Between 1960 and 1978, the fumigant nematicide DBCP was used extensively on commercial bananas in Africa, Latin America and the Caribbean, and treatments were normally applied twice a year using hand-held injectors in which the fumigant was injected around individual plants. Wehunt and Edwards (1968) reported yield increases in Central America varying from 14 to 86 %. In parallel, research efforts were concentrated on the evaluation of the newly released non-fumigant nematicides (organophosphates and carbamates), mostly systemic, used as seed treatment (Vilardebo & Robin, 1969; Coates, 1971; Guérout, 1975) or as soil treatment after planting (Vilardebo, 1970; Guérout, 1970; Gowen, 1975; 1979; Figueroa & Mora, 1977).

At present, the application of non-fumigant nematicides still remains the most used nematode control worldwide on dessert bananas for export, with granular or liquid nematicides applied through the sure-fill system and hand-held applicators to ensure safe application. In most countries, governments require all nematicides to be used only where banana plantation companies exercise close supervision of workers handling and applying the chemicals.

In the past these treatments were mostly applied at fixed times of the year, but now they are applied on the basis of nematode incidence, of banana plant uprooting and/or nematode counts in the roots, in an effort aiming at minimizing nematicide applications. It is interesting to note that no universal threshold level in terms of nematodes per unit of roots has been suggested. For *R. similis*, this threshold level can vary from place to place: from 1000 per 100 g of roots in the Ivory Coast (Guérout, 1972) and Martinique; from 4000 to 6000 in plantations of Costa Rica (Fallas pers. com); from 10000 in the Philippines (Davide, 1992) and the Windward Islands (Gowen, pers. com.) and from 20000 in Honduras and Panama (Pinochet, 1987) as a response to regional differences in *R. similis* pathogenicity.

2.5. Research of an Alternative to Chemical Control

During recent decades there have been many changes in the management of banana nematodes in large commercial plantations (e.g., loss of important non-fumigant nematicides and homologation of one new nematicide only; absence of a still effective nematicide alternative, e.g. biological control; increased concerns related to nematicide applications for environmental quality (product, soil, water) and human health). These problems were very important in the frequently replanted crop systems of the Caribbean, compared to the large plantations of Latin America or Asia (Philippines) where bananas are grown continuously without replanting. As a consequence, the search for an alternative to chemical treatments has been quite intense in the Caribbean.

Efforts were concentrated on replanting practices, using tissue culture plants on cleaned soils. The concept was proposed very early (Loos & Loos, 1960a) but its application only became feasible since the availability of disease-free tissue culture plants, through the meristem culture technique. Since that period, hot-water treatment, following peeling away of all lesions from the corms, became a standard practice in many parts of Central America and the Caribbean (Stover, 1972) with inconsistent results. As an example, four years after the establishment of new plantations in Belize with heat-treated seeds imported from Honduras in areas where bananas had never been grown before, the infestation rate by *R. similis* was already 43.1 % (Pinochet & Ventura, 1977).

In the meantime, many cultural practices were tried in Latin America and Caribbean regions in order to free the soil from *R. similis*. These practices included:

- flood fallowing in Surinam and the Ivory Coast, prior to replanting (Maas, 1969; Sarah et al., 1983)
- dry- or bare-fallow (Loos, 1961; Edwards, 1963; Salas et al., 1976)
- weed fallow (Chabrier & Quénéhervé, 2003)
- cultivated fallow with Pangola grass (Stoyanov, 1967; Roman et al., 1978) and Sudan grass (Ternisien & Melin, 1989)
- rotation with other crops such as sugarcane (Loos, 1960; Stoyanov, 1967), cassava (Zem & Alves, 1983) or pineapple (Sarah, 1989)

Nevertheless, these efficient rotation crops are still rarely practised because of the high cost of planting and maintaining the rotation crop along with the inability to develop marketable rotation crops. Following these studies, some improvements in the fallow setting-up were made to ensure the elimination of the burrowing nematode from the soil. This was achieved by a previous individual chemical destruction of each plant before the mechanical destruction of the banana plantation (Chabrier & Quénéhervé, 2003). In the French West Indies, the use of these practices not only extended the longevity of the plantations, but also drastically reduced (by 63 % from 1996 to 2004) the application of nematicides (Chabrier et al., 2005).

2.6. Future Prospects

For more than fifty years, many (and probably the most important) advances in the knowledge and management of banana nematodes were obtained in Latin America, the Caribbean and in West Africa, beginning in the labs of the United Fruit Co. in La Lima, Honduras, in the field of the Banana Board of Jamaica at Bodles, as well as in Guinea and the Ivory Coast. Currently, most of outstanding research on nematodes of banana for export is now conducted in Costa Rica and in the French Antilles, with new challenges. The golden age of nematode control with nematicides is definitely behind us. There is a global tendency to replace the former nematode control by a wider view of 'sustainable nematode management' (Sikora et al., 2005). This trend will certainly increase under the pressure of consumers and commercial firms in order to improve quality and diversity of dessert bananas for export. The breeding of new dessert banana varieties, not only resistant to Black Sigatoka but also to burrowing and lesion nematodes, is certainly the next step.

3. NEMATODES ON BANANAS IN ASIA AND OCEANIA

3.1. Introduction

Given their size and diversity, Asia and Oceania are more a cultural concept incorporating a number of regions and peoples than homogeneous, physical entities. Asia can be divided into different sub-regions in which some of the major banana producing countries are found, such as South Asia (India subcontinent), Southeast Asia (mainland and archipelago) and Eastern Asia with China. Oceania is a geographical region consisting of numerous islands including Australia. It is traditionally divided into the Australasian, Melanesian, Micronesian and Polynesian archipelagos. Southeast Asia is considered to be the centre of origin of *Musa* species and of domestication of the edible banana (Jones, 2000) and Melanesia is the centre of origin of the burrowing nematode *R. similis*, the most detrimental plant-parasitic nematode associated with bananas worldwide. Paradoxically, Asia was also, until recently, the world region where the least number of studies had been made on banana nematodes. This was mainly because very few countries grew bananas for export until recently. In 2004, banana production in Asia and Oceania was estimated at 38 M tons (95 % of non-export bananas) produced in more than 35 countries with some countries such as India (the largest banana producer in the world, at 16.4 M tons), China (5.8 M tons), the Philippines (ranked fifth among the world's major export banana countries, with 1.7 M tons out of 5.5 M tons) and Indonesia (3.8 M tons) being the most important producing countries for dessert bananas, Cavendish and others, in the world (Lescot, 2004).

In Asia, banana is an indigenous crop to many countries, especially from Southeast Asia, planted everywhere for thousands of years by smallholder farmers while wild species are commonly found in the primary and secondary forests. As a centre of origin of *Musa*, the genomic diversity of cultivated bananas is very wide (*Musa* genome AA, AAA, AB, AAB, ABB). There is also a wide diversity of banana lines in Oceania, especially in Papua New Guinea, the Solomon Islands and Vanuatu (*Musa* genome AA, AAA, AAB and Fe'i group of the Australimusa section). These bananas are very important in terms of nutrition, cultural significance and traditional use in medicine. Until recently, the edible cultivars were mostly grown as a subsistence crop to provide small incomes and to contribute to the nutrition of the population. However, in recent decades, four distinct production systems can be roughly distinguished (Valmayor, 1990):

- a backyard production system characterized by a wide diversity of banana cultivars and very minimal inputs.
- a mixed-cropping production system in which bananas are intercropped with annual crops (taro, ginger, sweet potato, bean, corn, etc.) or perennials plants (rubber, Durian trees , coconut, arecanut, etc.).
- a commercial smallholder monoculture production system with some minimal management practices (fertilizing, weeding, etc.).
- a corporate farm production system strictly intended for the export market of dessert Cavendish bananas.

Since the development of the market economy in Asia, banana production for domestic consumption and export is also considered as a new opportunity in terms of economic value and often ranks now in the top ten of the total fruit production of these countries.

3.2. Nematode Species

Until recently, there was a general lack of information on the nematode species associated with local banana cultivars in Asia as there was no public or private priority in terms of funding for research and development in comparison with export crops (e.g. rubber, oil palm, cocoa, coffee).

Paradoxically, it was very early that Cobb (1893) completed the first description of the burrowing nematode described as *Tylenchulus similis*, from specimens found in soil around banana roots from Fiji in Melanesia. Following this early discovery in Oceania, banana nematodes including *R. similis* have only been reported lately from bananas in Australia (Blake, 1972), Samoa (Orton Williams, 1980), Tonga (Kirby et al., 1980), Papua New Guinea (Bridge & Page, 1984) and the Solomon Islands (Bridge, 1988b).

In South Asia, the occurrence of *R. similis* on bananas was first reported from the Kerala district in India (Nair et al., 1966) and from Sri Lanka (Gnanapragasam et al., 1991). In fact, extensive surveys in India revealed that the root lesion nematode *P. coffeae* was the predominant species and ranked first in prominence and importance. This species was followed by the root knot nematode, the spiral nematode and the burrowing nematode. Subsequently, the burrowing nematode was reported from almost all banana-growing states including isolated pockets like the Andaman Island (Khan, 1999; Sundararaju et al., 2005). In Bangladesh, the main nematode species reported on banana is *R. similis* (Mian, 1986).

In Southeast Asia, the detection of *R. similis* on bananas also occurred lately after its previous detection on other crops (Table 3): in the Philippines (Timm, 1965; Boncato & Davide, 1980), Malaysia (Larter & Allen, 1953; O'Bannon, 1977; Winoto & Sauer, 1982), Thailand (Timm, 1965; Prachasaisoradej et al., 1994) and Indonesia (O'Bannon, 1977; Hadisoeganda, 1994). In the Philippines, all species except *R. similis* were generally associated with native banana cultivars (Davide & Gargantiel, 1974) while *R. similis* was found widely associated with the Cavendish bananas. Often crops, which are good hosts of *R. similis* but also of *P. coffeae* and *Meloidogyne* spp., including banana, ginger, turmeric, betel vine, coconut and arecanut were intercropped with pepper, as in India (Koshy et al., 2005).

In Eastern Asia, *R. similis* has not yet been detected until now on bananas from Vietnam and China. In Vietnam, all the common species associated with banana were identified on both wild and cultivated bananas. The most frequently species found were *Helicotylenchus dihystera*, *Meloidogyne incognita* and *Rotylenchulus reniformis*, while the lesion nematode *P. coffeae* and the spiral nematode *H. multicinctus* were also found rather infrequently (Chau et al., 1997). However, indigenous populations of *R. similis* were recently reported from coffee in two Vietnam provinces (Nguyet et al., 2003). In China, with the notable exception of *R. similis*, the banana root-knot nematodes *M. javanica* and *M. arenaria* occur in sandy fields in Hainan and Fujian provinces, as well as *Rotylenchulus reniformis* and *Helicotylenchus* spp. (Linbing et al., 2004).

The lesion nematode *P. coffeae*, was first reported on abaca in the Philippines (Taylor & Loegering, 1953). It was reported to cause damage to young bananas in Malaysia (Winoto, 1976) in combined infestation with *Meloidogyne incognita*.

Beside these common species, Charles and Venkitesan (1984) first reported the occurrence of a cyst nematode, *Heterodera oryzicola*, on banana (Musa AAB) in the state of Kerala, India, where this nematode is also one of the major pests on rice.

Among the *Meloidogyne* species, *Meloidogyne graminicola*, one of the major pests of rice in the Philippines and other Asian countries (Bridge et al., 1990) can also be found associated in large numbers with some common banana cultivars in the Philippines like Saba, Latundan and Lakatan (Reversat & Soriano, 2002).

Table 3. Early detections of **Radopholus similis** *on banana and on some other crops.*

	America	*Caribbean*	*Africa*	*South Asia*	*Southern Asia*	*Pacific*
Anthurium						Hawaii (Sher, 1954)
Arecanut				India (Kumar et al., 1971)		
Avocado	Florida (DuCharme & Suit, 1953)			India (Jasy & Koshy, 1992)		
Banana	Panama (Newhall, 1958)	Jamaica (Ashby, 1915)	Guinea (Mallamaire, 1939)	India (Nair et al., 1966)	Malaysia (Larter & Allen, 1953)	Fiji (Cobb, 1893)
Betel Vine				India (Koshy & Sosamma, 1975)		
Black Pepper					Indonesia (Van der Vetch, 1950)	
Citrus	Florida (Suit & DuCharme, 1953)					
Coconut				Sri Lanka (Ekanayake, 1964)		
Coffee					Indonesia (Zimmermann, 1898)	
Date Palm				India (Lal & Mathur, 1986)		
Faba Bean				India (Sosamma & Koshy, 1977)		
Food Legumes				India (Sikora et al., 2005)		
Ginger	Florida (Hart, 1956)					Fiji (Butler & Vilsoni, 1975
Kava						Fiji (Kirby et al., 1980)
Persimmon	Florida (McSorley, 1981)					
Sugarcane						Hawaii (Cobb, 1909)
Swam Taro						Guam (Jackson, 1987)
Sweet Potato				India (Koshy & Jasy, 1991)		
Tamarind				India (Sosamma & Koshy, 1977)		
Taro						Fiji (Kirby et al., 1980)
Tea					Indonesia (Zimmermann, 1898)	
Turmeric				India (Sosamma et al., 1979)		
Yam						Fiji (Butler & Vilsoni, 1975)

3.3. Importance and Damage Potential

Limited information is available on the nematode damage to native bananas from Asia and Oceania since most studies were carried out on the Cavendish banana. However, despite favourable environmental conditions for banana production, the average yield is often very low.

In South Asia, nematodes constitute one of the major limiting factors to banana production in India, with reported yield reductions up to 41 % for *R. similis* (Nair, 1979), 44 % for *P. coffeae* (Sundararaju & Cannayane, 2003), 34 % for *H. multicinctus* (Rajendran & Sivakumar, 1996), 20-56 % for the cyst nematode *H. oryzicola* (Charles & Venkitesan, 1993) and 31 % for *M. incognita* (Jonathan & Rajendran, 2000).

In the Philippines, most of the studies to evaluate the pathogenic capabilities of nematodes commonly associated with banana were conducted on dessert Cavendish banana (Davide & Marasigan, 1985). In Vietnam, *Meloidogyne* spp. seems to have an adverse effect on the growth of native banana cultivars, while the effect of *P. coffeae* on Musa plant growth is unclear (Van den Berg et al., 2002).

3.4. Nematode Management

In Asia, and particularly Oceania, the banana cultivation is basically a smallholder enterprise of small size and, except in home gardens where bananas benefit from the regular application of animal manure and household refuse, these banana-cropping systems receive little or no inputs. In general, management practices that include nematode control are used less extensively in commercial smallholder plantations than on corporate farms, which rely almost exclusively on the use of chemicals to control nematodes on export Cavendish bananas.

In the Philippines, the government has decreed that all nematicides in the country should be for institutional use only, where plantation companies exercise close supervision of labourers handling and applying the chemicals. Alternative control measures were also conducted to explore the potential of botanical nematicides and of biological control agents against the nematodes (Villanueva, 2004).

The use of suckers or rhizomes as seed stock is the main practice among smallholders in Asia and Oceania. Due to this practice, the spread of pests such as nematodes is difficult to control and/or eliminate and often production becomes poorer from one cycle to the next, while nematode populations build up over the years.

However, in China, more than 100 commercial laboratories produce millions of tissue-cultured plants for most banana plantations. Eighty to ninety percent of tissue culture plants are used for new plantings. Some of these tissue-cultured plants, issued with a certification ISO-9001, are even exported to other countries (Linbing et al., 2004).

The burrowing nematode is the most important nematode on bananas in Australia. Current management options mostly include a rotation, application of the registered nematicides, fallow and the use of clean planting material. The prospect of a financial return from fallows has raised enormous interest in the use of fallows (Rhodes grass, Digitgrass) for management of the burrowing nematode.

3.5. Future Prospects

One important fact to consider is that the centre of origin of the burrowing nematode is undoubtedly located in the Pacific Rim islands and that the nematode has already been reported from many primary crops other than bananas. This information is crucial in terms of nematode management and future prospects.

In most countries of Asia and Oceania, growers are not aware of the prime importance of the quality of planting material. Suckers are mostly collected from old banana fields without knowing their disease status. Some nematode species can cause extensive root damage on native banana. In general, infested plants exhibit stunted growth, premature defoliation and carry small bunches and fruits. In addition, nematodes can cause decay and death of the proximal parts of the roots and the plants are prone to toppling over, specially when bearing bunches or during windy weather, because of inadequate anchorage. There is definitely a need for the provision of pest-free banana seeds from local extension or research services to ensure that all material used for planting by the farmer is free of nematodes. Everywhere there is also an increase in growers wanting to evaluate new varieties to explore potential new markets. In Australia, the banana industry faces a changing consumer focus with more emphasis on environmental protection and sustainability while pressure from pests and diseases still increases. Current and future research into pests and diseases, as well as industry development, all rely on the use of disease-free banana varieties.

4. NEMATODES ON BANANAS IN AFRICA

4.1. The Nematode Problem

The first evidence of *Musa* on the African continent comes from the discovery of ancient banana phytoliths, distinctive microscopic silica bodies that accumulate in plant cells. According to new phytolith evidence from Uganda, it appears that humans may have brought bananas to eastern Africa during the fourth millennium BC (Lejju et al., 2006). Now, it is commonly assumed that not only Arab traders but also traders from India and from the Indonesian peninsula brought diverse banana clones to the east coast of Africa and Madagascar and then across the continent to the west coast (Simmonds, 1966).

Nowadays, and after this early introduction on the African continent, approximately one-third of the total world production of bananas (98 % of non-export bananas, 29.3 M tons in 2004) is produced in sub-Saharan Africa (Lescot, 2004). These bananas, particularly important in the humid forest and mid-altitude regions, are produced mostly for subsistence purposes by smallholder farmers *i)* under systems of shifting cultivation in West and Central Africa, *ii)* in permanent farming systems in East Africa where they are often grown in association with coffee or cocoa tree crops or *iii)* everywhere as backyard/garden crops. Generally, these production systems are characterized by no or very low inputs.

While less diverse than in Asia, a relative range of genetic diversity of bananas is observed in Africa, with different types specifically adapted to different sub-regions. In West and Central Africa, cultivars of the plantain subgroup *Musa* AAB (False Horn, French Horn) predominate in the humid lowlands while in East Africa, endemic highland bananas (*Musa* AAA) and diverse brewing cultivars (*Musa* ABB) predominate (Table 4).

Over recent years, banana yield and plantation longevity have been gradually declining in sub-Saharan Africa. Many pests, diseases and abiotic constraints (declining soil fertility, high soil acidity) were observed on bananas in Africa and not only affected production but also led to an increased frequency of land clearing. Currently, among the diseases, one of the major constraints to banana production is black leaf streak (or black Sigatoka) caused by the fungus *Mycosphaerella fijiensis*. All traditional banana cultivars of West and Central Africa are very susceptible and this particular disease causes severe leaf necrosis, increasing gradually with the age of the plantation, leading to 33-76% yield losses (Carlier et al., 2000). Major pests include the banana weevil *Cosmopolites sordidus* and nematodes: *H. multicinctus*, *Meloidogyne* spp., *R. similis*, *P. goodeyi* and *P. coffeae*. These species affect the root system functionality at two levels: anchorage and ability to take up and transport water and nutrients.

The first studies dealing with the nematode associated with bananas in sub-Saharan Africa were very scarce and preliminary (Luc & de Guiran, 1960; Luc & Vilardebo, 1961). Since then, several extensive surveys provided reference data on species occurrence and densities for the different countries (Speijer & Fogain, 1999).

4.2. Nematode Species Occurrence

In sub-Saharan Africa, the most commonly occurring nematode species on bananas is *H. multicinctus*, which is found in 70-100% of samples (Table 4), while declining at altitudes above 1500 meters above sea level in East Africa (Speijer & Fogain, 1999). As already mentioned for Cavendish bananas, this nematode species is always found in mixed populations, often with root-knot nematodes, and its abundance depends primarily on the presence and abundance of other nematode species, particularly the burrowing and lesion nematode species.

Whereas the geographical distribution of *R. similis* follows closely the distribution of dessert bananas cultivated for export (e.g. Cavendish), the distribution of this species on other banana types in Africa differs widely from place to place. In West Africa, the occurrence of *R. similis* has increased on plantain types in recent decades from nil (Caveness, 1967; Fademi & Bayero, 1993) to 46 % in Nigeria (Speijer et al., 2001) whereas it remains absent in Gambia (Merny et al., 1974); from 2-9 % in the mid-west to 43-52 % in the south east of Ivory Coast (Adiko, 1988; Adiko & N'Guessan, 2001) and at least by 39 % in Cameroon (Bridge et al., 1995).

Table 4. Occurrence (%) of the different banana nematode species in Africa

Region	*Musa group*	*Hm*	*Rs*	*Pc*	*Pg*	*Msp*	*Hp*	*Reference*
Ivory Coast (mid-west)	AAB	99	9	2	0	98	1	Adiko, 1988
Ivory Coast (mid-west)	AAB	100	2	2	0	93	0	Adiko & N'Guessan, 2001
Ivory Coast (southeast)	AAB	99	52	7	0	93	3	Adiko, 1988
Ivory Coast (southeast)	AAB	96	43	35	0	90	19	Adiko & N'Guessan, 2001
Ghana	AAB	98	32	66	0	56	0	Speijer & Fogain, 1999
Cameroon	AAB	38	39	5	33	36	44	Bridge et al, 1995
Nigeria	AAB	100	0	68	0	+	+	Fademi & Bayero, 1993
Nigeria (southern)	AAB	100	46	49	0	68	64	Speijer et al., 2001
Kenya	EAHB	75	42	8	62	17	0	Seshu Reddy et al.,1997
Kenya	ABB	62	20	25	55	50	0	Seshu Reddy et al.,1997
Rwanda	EAHB	60	40	0	80	0	0	Bagabe et al., 1997
Rwanda	ABB	40	40	0	60	20	0	Bagabe et al., 1997
South Africa & Swaziland	AAA & ABB	93	9	3	0	94	0	Daneel et al., 2003
Uganda (central)	AAA & ABB	88	71	0	47	35	0	Speijer & de Waele, 2001
Uganda (central)	ABB	88	76	0	52	82	0	Speijer & de Waele, 2001
Uganda (southeast)	EAHB	83	54	8	96	54	12	Kashaija et al., 1994
Tanzania	EAHB	100	50	0	100	80	0	Speijer & Bosch, 1996
Zanzibar	mixed	100	75	68	0	42	0	Rajab et al., 1999

Hm: *Helicotylenchus multicinctus*; **Rs**: *Radopholus similis*; **Pc**: *Pratylenchus coffeae*; **Pg**: *Pratylenchus goodeyi*; **Msp**: *Meloidogyne* sp.; **Hp**: *Hoplolaimus pararobustus*; + = presence.

Radopholus similis is also present in Ghana, but its occurrence is mainly localised in the western region (Brentu et al., 2004). In East Africa, the occurrence of *R. similis*, absent from the region prior to the 1960s (Price, 2006), seems now to be greater, ranging from 42 to 76 % (Table 4) while declining rapidly at altitudes above 1400 meters above sea level. In South Africa, its occurrence is still fairly limited (9 %) in home garden bananas (Daneel et al., 2003).

The lesion nematode *P. coffeae* occurs widely throughout the tropics and is a significant pest of some primary crops (e.g. yams and tubers). The species is only found in pockets on bananas in Ivory Coast, Ghana, Nigeria, Kenya and Zanzibar (Speijer & Fogain, 1999). It was first reported on bananas from Ghana (Addoh, 1971) while being absent from plantains in Nigeria (Caveness, 1967). In 1988, it was reported in the Ivory Coast only near the Ghana border both on bananas (Fargette & Quénéhervé, 1988) and plantains (Adiko, 1988). There is no doubt that the occurrence of this species on bananas and plantains is now increasing as illustrated by the 35 % occurrence in the south-east of the Ivory Coast in 2001 (Table 4).

Pratylenchus goodeyi is regarded as a species indigenous to Africa (Table 4), where it is recognized as an important pest of highland bananas in East Africa (Gichure & Ondieki, 1977; Bridge, 1988a; Speijer & Fogain, 1999) and in Cameroon (Bridge et al., 1995). This nematode species is also a major pest of bananas in the Canary Islands (de Guiran & Vilardebo, 1962) and has been found in Egypt (Oteifa, 1962) and in Crete (Machon & Hunt, 1985). The distribution of *P. goodeyi* is closely linked to altitude and temperature, since *P. goodeyi* is rarely observed below 800 meters above sea level and its occurrence in western Africa is restricted to the highlands of Cameroon (Price & Bridge, 1995).

Meloidogyne spp. occur widely throughout the tropics on bananas and also are significant pests of numerous crops (Luc et al., 2005). In Africa, they mostly occur on banana roots together with other nematode species and are likely to be found in great numbers in absence (or limited density) of the burrowing or lesion nematodes (Table 3) due to competition phenomena (Quénéhervé, 1990).

Hoplolaimus pararobustus also shows a distribution in pockets (Table 4) with an considerable occurrence in Nigeria and Cameroon and an increasing occurrence in the south-eastern Ivory Coast, from 3 to 19 % (Adiko & N'Guessan, 2001). While scarcely present in 1961 in the Ivory Coast, the occurrence of this species was already over 80 % on dessert bananas in 1988, presumably after the introduction of infested Cavendish material from Cameroon (Fargette & Quénéhervé, 1988).

All these studies show that the nematode problem is changing rapidly, mainly with the increasing occurrence of the burrowing and lesion nematodes, in areas and on banana varieties formerly free of these pests (Price, 2006). During the last fifty years, the increasing occurrence of *R. similis* was mainly due to the dissemination and exchange of infested planting materials (e.g. dessert Cavendish bananas inter-planted with other banana varieties), locally facilitated by the improved means of communication (roads and trucks) among the different banana production areas and between countries, during the establishment of new commercial plantations from place to place with infested planting materials (Sarah, 1989; Marin et al., 1998).

The situation is presumably similar with the increasing distribution of *P. coffeae* and *H. pararobustus* through infested planting materials. In fact, all these nematode species can infest banana corms deeply and in abundance, reaching a depth of more than 7 cm (Quénéhervé & Cadet, 1985a). Therefore they are totally protected during transport and against some of the primary nematode management procedures, such as root removal and surface paring of corms.

4.3. Importance and Potential Damage

It is always difficult to partition the damage according to species or species mixtures. In the 1980s, only *H. multicinctus* and *Meloidogyne* spp. were considered important pests of plantains in Nigeria (Caveness & Badra, 1980) and Ivory Coast (Adiko, 1988), and yield increases ranging from 61 to 98 % were observed after nematicide treatments of established plantains infested with these nematode species (Caveness & Badra, 1980; Badra & Caveness, 1983). In East Africa, production losses ranging from 15 to 50 % have been associated with *R. similis* and *H. multicinctus* attack on East African Highland bananas (EAHB)(Speijer et al., 1999; Speijer & De Waele, 2001). Results of path analysis showed that *H. multicinctus* was also a severe constraint, second in importance to *R. similis* in terms of root death and necrosis (Ssango et al., 2004). Recently, its own importance has been assessed in micro-plot evaluations and greenhouse experiments and indicates low (26 %) to zero effect on vegetative growth and yield loss (Brentu et al., 2004; Adiko, 2005). Nevertheless, these experimental results, although consistent with some field observations and trials (Barekye et al., 2000), need to be confirmed with different *Musa* cultivars and in different experimental conditions.

The pathogenicity of *H. pararobustus*, often present in low densities in the roots, to either plantain or banana has not yet been observed (Price, 1994b). Plant toppling can be considered as the major loss factor for banana production, and is mostly associated with the presence of the burrowing nematode *R. similis* or the lesion nematodes *P. coffeae* and *P. goodeyi*.

In Ghana, a total production loss of 70 % (associated toppling incidence 60 %) was observed after inoculation of plantains with the lesion nematode *P. coffeae* (Brentu et al., 2004). Plantain yield losses ranging from 25-64 % for the first crop to 50-90 % for the successive crop cycles were reported from Ghana (Udzu, in: Coyne et al., 2005). In a field experiment in Cameroon, the total production losses in the first and second cycles were 60 and 51 % respectively (associated toppling incidence of 18 and 53 %) (Fogain, 2000).

In Tanzania, *P. goodeyi* has been associated with plant toppling of highland bananas (Bridge, 1988a) and has been implicated as a cause of the cultivar shifts from indigenous highland bananas to newly introduced ‘Pisang awak’ and ‘Gros Michel’ cultivars (Speijer & Bosch, 1996). As mentioned by Speijer et al. (1999), when plant toppling occurred on a mat, the chance for this mat to produce a harvestable bunch in the following cycle is highly reduced, thus diminishing the plantation longevity.

4.4. Current Nematode Management

Integrated pest management (IPM) strategies offer the most suitable and efficient means by which small-scale farmers can control pest and disease attack. IPM strategies are also environment friendly, and should provide a highly desirable alternative to pesticide application in highly populated areas. In general, three main types of nematode management are envisaged. These include prevention with the use of clean planting material, cultural control with a particular focus on soil fertility treatments, and host plant resistance. During recent years in Africa, the combined efforts of regional research networks such as IITA (International Institute for Tropical Agriculture) and CARBAP (Centre Africain de Recherche sur le Bananier et le Plantain) has led to the development and adoption of user-friendly techniques in terms of nematode management to the benefit of banana and plantain growers.

4.4.1. Clean Planting Material

Farmers depend on natural regeneration of plants for the supply of planting materials. However, poor soil fertility, combined with high nematode and weevil infestation, not only slow down this natural regeneration in numbers but also lead to the production of suckers of poor health and quality. The most sophisticated way to obtain nematode-free planting materials is by using plants micropagated in vitro. However this method will certainly be restricted, for a long time yet, to only certain banana clones and to high value crops, such as commercial bananas. Nevertheless, other methods of propagating banana plants have been improved during the last decade.

The use of in vivo seedbed techniques increases the rate of banana multiplication in the field, but it carries the risk of multiplying contaminated materials. In Cameroon, CARBAP has developed a new detached corm technique for in vivo mass multiplication easily usable by growers. This technique allows the activation of latent buds and the quick production of large quantities of healthy planting material, at least free of nematodes and black weevils, in soil-less culture conditions (Kwa, 2003). Thanks to CARBAP and IITA, this detached corm technique has been instrumental in the recent increase of banana production and hybrid dissemination process both in Cameroon and Nigeria (Tenkouano et al., 2006).

In the absence of nematode-free planting material, paring is certainly the first and easiest prophylactic measure to apply. Complete root removal followed by a severe paring to discard all the necrotic and discoloured areas of the corms should be done before any use of planted materials infested with either nematodes or black weevils. This sanitation method can be combined with sun exposure: the storage of peeled rhizome for 2 weeks prior to planting (Quénéhervé & Cadet, 1985b) can complete this elimination of surface-living nematodes. However, neither paring nor sun exposure will completely eliminate nematodes from the deepest infested layers of the corms, and these physical methods cannot be applied to small suckers in order to avoid loss of regrowth and vigor.

Other physical methods include the hot water treatment of planting materials. Mallamaire (1939) was the first to suggest immersing banana suckers in water at

65°C for 5 minutes to eliminate *R. similis*. The hot water treatment technique was then improved (Blake, 1961) and widely recommended (55° C for 25 minutes) to farmers (Colbran, 1967) in Australia and Central America with minor adjustments. Nevertheless, its application to commercial bananas in Africa was not considered to be as feasible and successful as treatment with nematicides (Melin & Vilardebo, 1973). If its application on commercial bananas seemed difficult and uneconomic, its application to other banana types was absolutely unrealistic and scarcely applied. However the technique has been drastically simplified recently in East and West Africa (immersion in boiling water, 30 seconds) using local materials to treat infested suckers and has led to significant improvements in yield (Tenkouano et al., 2006).

4.4.2. Cultivated Fallow and Alternate Cropping

Unlike the situation in Asia, the fact that *R. similis* was rarely found on other primary crops in large numbers outside banana roots suggests that some management strategies (e.g. crop rotation) should be tried for better control. However, these management strategies are still rarely adopted since available land is scarce and farmers are usually reluctant to grow other crops than banana. Many studies were conducted in Cameroon and West Africa: natural fallow followed by a 3-4 month groundnut crop was recommended (Sarah, 1989) but only if the natural fallow lasted for a long time. As a substitute for natural fallow the spontaneous weed *Chromolaena odorata* was also used as a cover crop to eliminate *R. similis* from the soil before the replanting of dessert bananas (Sarah, 1989). In Cameroon, alternate cropping with maize and groundnut showed heavy infestation with *R. similis* in the following plantain crop (Price, 1994). Further studies with alternating crops demonstrated that maize and okra maintained a high level of nematode infestation and that groundnut and soya beans were similar to natural fallow, while only sweet potato and amaranth crops were able to suppress *R. similis* for almost 18 months. In terms of plantain yields over two experiments during two cycles and compared to a permanent plantain crop, this strategy of alternate cropping allowed significant yield increases of 57-96 % with sweet potato or amaranths, of 33-47 % with maize or okra, while increases were 38-42 % under natural fallow (Achard, personal communication). Similarly, sweet potato and Irish potato were also found to be non-hosts of *P. goodeyi* while intercropped with highland bananas (Price, 1994). A study conducted in Uganda with some plants reported as antagonistic or suppressive to nematodes (*Canavalia ensiformis*, *Mucuna pruriens*, *Tephrosia vogelli*) and cultivated as legume intercrops do not show significant advantages in banana production and no benefit in terms of nematode control or spatial distribution of banana roots and nematodes (Kashaija et al., 2004).

4.4.3. Mulching and Fertilisers

As mulching improves soil physical structure and therefore soil fertility, nematode damage to roots appears to restrict the growth potential of bananas. A study carried out in Nigeria suggested that mulching might mitigate the impact of nematodes on bananas only when applied to low fertility systems (McIntyre et al., 2000). In Uganda on highland bananas, the presence of nematodes reduced the average production by 32 % without mulch and by 30 % with mulch, but the average yield increase with mulch was over 65 % (Speijer et al., 1999). In a recent experiment in Nigeria, only the mulched plants, with a low level of infestation, reached harvest (71 % of dead plants in the highly infested non-mulched plants compared to only 1 % in the lightly infested mulched plant in the first cycle) (Coyne et al., 2005b).

Promising results were obtained with the use of *Tithonia diversifolia*, a shrub of the family Asteraceae, easily recognisable and widely distributed along farm boundaries in the humid and subhumid tropics of Central America and Africa. Its use as mulch led to a significant decrease in nematode damage and improved yield (Coyne et al., 2005a). All these studies confirmed the highly damaging nature of nematodes to banana production in Africa and the importance of the systematic evaluation of different organic mulches to improve banana plant vigor and longevity.

Recent studies indicate that nematode infestations need to be controlled before fertilizer use becomes profitable in terms of banana fruit yields (Smithson et al., 2001).

4.5. Future Prospect

Almost everywhere in Africa, except in permanent highland banana production systems, bananas are still established after a slash and burn preparation of the land and are seldom maintained for more than one cycle of production. Bananas are shifting from the status of a perennial crop to that of an annual crop. The reasons for abandoning the crop before it ratoons are numerous and comprise biotic (pests and diseases) and abiotic constraints (declining soil fertility, high soil acidity). During recent decades, population pressure in Africa has also led to a shortening of the fallow periods and increased the need for banana planting material, which is often the vector of pests and diseases. With this social and environmental situation, is prevention a lost cause?

In theory, IPM strategies offer the most suitable and efficient means by which small-scale farmers can control pest and disease attack. IPM strategies should also be environment friendly, and should provide a highly desirable alternative to pesticide application in heavily populated areas. Fortunately, the use of pesticides has never been a realistic nematode control method for smallholders in Africa. At present, nematode management includes the use of clean planting material, the establishment of nematode-free nurseries, crop rotation with a particular focus on soil fertility treatments and the development of host plant resistance. In recent years, the efforts of international research networks such as IITA and CARBAP has led to the development and adoption of user-friendly techniques to mitigate nematode damage and other problems, for the benefit of banana and plantain growers in Africa.

As we have seen, the recent spread of banana nematodes such as *R. similis* still increases and the efficiency of intra-continent domestic quarantine seems totally inadequate. Only the massive distribution of pest-free tissue culture plants can prevent the further spread of nematode species and allow the distribution of new dessert banana and plantain hybrids resistant to Black Sigatoka but also resistant or tolerant to nematodes and other pests and diseases. All these improvements will only be possible through the coordination of strong regional and international research networks.

5. NEMATODES ON BANANA IN AMERICA

5.1. The Nematode Problem

Marin et al. (1998) wrote an in-depth review of the different hypotheses for the dissemination of bananas in Latin America and the Caribbean. According to their findings and although no exact dates can be assigned to their introduction, it is likely that bananas were introduced early in the 1500s to the New World in Hispaniola island (now the Dominican Republic) by the Portuguese settlers via the Cap Verde and Canary Islands. From the sixteenth to the nineteenth centuries, European traders carried bananas all over tropical America. According to Simmonds (1960), the first bananas identified in the New World were the ‘Silk Fig’ (Figue Pomme, *Musa* AAB) and the ‘French plantain’ (*Musa* AAB), which were present in the West Indies in the seventeenth century. Some very important dessert banana clones such as ‘Gros Michel’ and cultivars of Cavendish (*Musa* AAA) were introduced directly from Asia into Martinique island in the nineteenth century and then distributed widely in Central America and the Caribbean islands, before being adopted by the banana trade (Simmonds, 1960).

After this late introduction into Latin America and the Caribbean, approximately one-third of the total world production of bananas (63.3 % of non-export bananas, 31.5 M tons in 2004) is now produced in the Americas in more than 33 countries (Lescot, 2004). The leading banana-producing countries are Brazil, Ecuador and Colombia with 6.5, 5.9 and 5.2 M tons, respectively, being produced in 2003.

Depending on the country, banana production is dominated by different banana types (Table 1). In Ecuador, 77 % is dessert bananas for export from the Cavendish subgroup. In Brazil, bananas are mostly cultivated for the local market (96.3%) and comprise different types such as the ‘Silk Fig’ (Figue Pomme, *Musa* AAB), the ‘Figue sucrée’ (*Musa* AA), and the ‘Prata’ (Pome, AAB). In Colombia, besides the Cavendish bananas for export, other bananas such as the cultivar “Gros Michel” and cultivars of the plantain subgroup *Musa* AAB (French Horn, False Horn) are particularly important in mid-altitude regions, where they are often grown in association with other crops such as coffee. Cooking bananas such as ‘Bluggoe’ in Cuba and ‘Pelipita’ (*Musa* ABB) are also very important in Latin America and the Caribbean.

As in other banana producing areas, many pests, diseases and abiotic constraints (declining soil fertility, high soil acidity) are observed on bananas in Latin America and the Caribbean. At present, besides the major world constraint to banana production, the 'black leaf streak' or 'black Sigatoka', other pests include the banana weevil *C. sordidus*, and the nematodes *H. multicinctus*, *Meloidogyne* spp., *R. similis* and *P. coffeae*.

5.2. The Nematode Species Occurrence

In Latin America and the Caribbean, nematode surveys on non-export bananas were very scarce and detailed studies on their relative abundance are lacking (Table 5). In areas free of *R. similis*, the main nematode species reported belong to the *Pratylenchus*, *Meloidogyne* and *Helicotylenchus* genera (Stover, 1972) beside other minor species (Roman, 1978).

As reported previously, the rapid spread of the burrowing nematode *R. similis* is closely linked to the dissemination of dessert bananas cultivated for export. Its introduction into Latin America is believed to have occurred with infested plants of 'Gros Michel', originally introduced into Martinique from Southeast Asia early in the 1800s and then transferred to Jamaica in about 1835. From Jamaica, this cultivar 'Gros Michel' and associated nematodes were exported to Cuba, Colombia (1892) and Surinam (1904) and then widely distributed in Central America and the Caribbean for the banana trade (Marin et al., 1998). Although infestations were present, the symptoms associated with *R. similis* on the banana roots and corms were not described until 1957 (Anonymous, 1957; Loos & Loos, 1960b).

Table 5. Occurrence (%) of banana nematode species on plantains in America.

Region	*Musa group*	*Hm**	*Rs*	*Pc*	*Msp*	*Reference*
Venezuela	mixed	75	0	19	56	Torrealba, 1969
Venezuela	mixed	31	14	20	12	Yepez et al., 1972
Costa Rica	AAB	58	71	65	50	Araya & Cheves, 1997
French Guiana	AAB	29	14	50	64	Quénéhervé (not publ.)

*Hm: *Helicotylenchus multicinctus*; Rs: *Radopholus similis*; Pc: *Pratylenchus coffeae*; Msp: *Meloidogyne* sp.

As soon as banana and plantain production became business-related, the crops were mostly cultivated intensively in lowland areas and the presence of *R. similis* on plantains usually arose through the proximity of dessert bananas or through infested soil or planting materials. In Puerto Rico, Ayala and Roman (1963) found *R. similis* widely distributed on bananas and plantains. Loof (1964) first recorded the presence of *Radopholus* sp. in Venezuela on *Musa* sp. and Yepez et al. (1972) suggested its introduction into Venezuela occurred circa 1966, with infested planting material from Honduras.

In Honduras, *R. similis*, while very frequent on dessert banana, was reported to occur less frequently on plantains, unlike the lesion nematode *P. coffeae* which was the most important nematode species found associated with root and rhizome injury on plantains but also on coffee and citrus (Wehunt & Edwards, 1968; Pinochet & Ventura, 1980).

In southern Florida, the most prevalent species on bananas is the spiral nematode *H. multicinctus* while *R. similis* is very infrequent (McSorley, 1979).

The root lesion nematode *P. coffeae* was first observed on roots of plantains in Grenada and described by Cobb in 1919. As reported by Stover (1972), this species was frequently found associated with root injury in plantains (*Musa* AAB, ABB) in Central America. Histopathological studies by Pinochet (1978) showed that the destruction of the cortical parenchyma of plantain roots by *P. coffeae*, leading to large cavities eroded and detached from the vascular tissues, was similar to the effects described by Blake (1961; 1966) for *R. similis*, with typical cell discoloration followed by the dark necrotic lesions on the roots that appeared 6 days after nematode inoculations.

Besides this lesion nematode, root-knot nematodes are also encountered on bananas and plantains in Central America (Pinochet, 1977) and Brazil (Zem & Alves, 1978) in mixed populations. Cofcewicz et al. (2004b) in a study of different banana producing areas of Brazil (*Musa* AAA, AAB) provided an outline of the diversity of root-knot nematodes parasitizing *Musa*, showing the prevalence of *M. javanica* (61.7 %), *M. incognita* (32.2 %) and *M. arenaria* (4.3 %). A similar study conducted in the Caribbean indicated the prevalence of *M. arenaria* (61.9 %) followed by *M. incognita* (34.3 %) (Cofcewicz et al., 2005).

The spiral nematode, *H. multicinctus*, was first recorded as damaging to plantains in Cuba (Stoyanov, 1967). The nematode attacks and feeds on the outer cells of the root cortex and produces small necrotic lesions (Luc & Vilardebo, 1961).

The reniform nematode *R. reniformis* has also been reported to be pathogenic to plantains in Puerto Rico (Roman, 1978).

5.3. Importance and Damage Potential

Yield decline of plantains caused by the lesion nematode *P. coffeae* was first described from Cuba (Stoyanov, 1967) and Trinidad (Ogier & Merry, 1970). In Honduras, Stover (1972) observed a 455 % increase in uprooted plants of 'Horn plantain' (Musa AAB) in *R. similis*-infested plots and a 62 % increase in uprooted plants in *P. coffeae*-infested plots compared to nematode-free plots, with no effect on fruit weight in a three-year experiment. Depending on the presence of *R. similis* and on the soil fertility, the plantation longevity varied from more than 10 years to only 2-3 years in the Dominican Republic.

In the same conditions of poor soil fertility and with *P. coffeae*, plantation longevity of plantains rarely exceeds 2-3 years in French Guiana (Queneherve, unpublished).

The fungi associated with nematode lesions on plantains are the same as those found on dessert bananas (Pinochet & Stover, 1980). Conversely, bananas such as the cultivar 'Gros Michel' and cultivars of the plantain subgroup *Musa* AAB (French Horn, False Horn) growing in association with other crops such as coffee in the mid-altitude regions of Colombia, and highland bananas called 'Guineo' do not suffer from nematode problems (Grisales & Lescot, 1993; Price, 1999).

The pathogenicity of different *Meloidogyne* species was studied on different banana cultivars (triploids AAA-group, triploids AAB-group and tetraploid AAAB-group) in Brazil and it was found that all species partially affected plant growth and altered the concentration of macro- and micronutrients in leaves (Cofcewicz et al., 2004).

5.4. Nematode Management

In Latin America and the Caribbean, except on dessert bananas for export, very little research has been done on banana nematode management. When nematode control was practised, usual recommendations followed those already made for dessert bananas. Roman (1978) reviewed the different experiments with nematicides in Latin America and the Caribbean.

After chemical treatment, large yield improvements were observed in Jamaica with 119 % over one cycle (Hutton & Chung, 1973) and in Puerto Rico, with yield increases of 207-275 % over three years on plantains cv 'Maricongo' (*Musa* AAB) (Roman et al., 1977). Since that time, when chemicals were applied in commercial plantains, most changes simply concerned new chemicals, following those used on dessert bananas.

In the Dominican Republic, some field experiments were done on possible crops to rotate with plantains to control banana nematodes. These studies showed that *i)* the burrowing nematode *R. similis* was recovered from continuous plantings of beans and corn after 6 months, but not from sorghum, tobacco, cassava, Pangola grass, sugarcane or grapefruit, *ii)* the lesion nematode *Pratylenchus* sp. was suppressed under cassava and *iii)* *Meloidogyne* sp. was suppressed by Pangola grass (Smith & Thames, 1969).

In Brazil, Bringel and Silva (2000) showed the antagonistic properties of some rotation crops (*Crotalaria juncea*, *C. spectabilis*, *Mucuna nivea*, *M. atterima*) towards the spiral nematode *H. multicinctus*.

5.5. Future Prospects

America and the Caribbean, while now producing almost one third of the total world production of bananas, were the latest continent and islands where bananas and their associated nematodes were introduced. This could explain the relatively narrow host range of the burrowing nematode *R. similis* and spiral nematode *H. multicinctus* on primary crops other than bananas (Table 3). As a result, IPM strategies including the use of clean planting material, the establishment of nematode-free nurseries and appropriate rotation crops should be successful in the eradication of *R. similis*, as already observed in some former contaminated areas. On the other hand, the research on nematode resistance will have to focus on the lesion nematode

P. coffeae, as this nematode is already replacing *R. similis* in terms of damage and occurrence on non-export bananas in Latin America and the Caribbean.

6. FUTURE AND COMMON STRATEGIES

As illustrated above, except for some geographical areas, the current options for nematode control on dessert bananas for export are still quite limited to a better use of pesticides through practical improvements (e.g., chemical formulation and dosage, application procedure, decision of nematicide application after nematode and/or damage monitoring). On non-export bananas, the range of options for nematode management is more directed towards prophylactic methods and regional improvements in cultural practices (e.g. crop rotation, fallowing) than on chemical treatments. Nevertheless in the future, nematode management for bananas should converge towards similar plant health measures and IPM options, such as the use of resistant or tolerant varieties, the distribution of clean plants obtained by tissue culture as well as the development of biological control methods in order to limit the use of pesticides.

6.1. Plant Health Measures

According to the International Plant Protection Convention (IPPC), phytosanitary measures include any legislation, regulation or official procedure whose purpose is to prevent the introduction and/or spread of plant pests and to be applied to regulated pests. Among the different nematode species encountered on banana, the burrowing nematode, *R. similis*, is qualified as a 'quarantine pest' in more than 55 countries, mostly because the occurrence of a physiological race of *R. similis* able to infest and damage citrus in Florida has prompted a worldwide ban of this nematode especially in citrus-growing countries (Hockland et al., 2006). In some countries, specific restrictions are imposed against other endoparasitic root lesion nematodes (*P. coffeae*, *P. goodeyi*). However, the dissemination of *R. similis* and other banana nematodes first occurred very early in Asia and has continued since. Beginning in the sixteenth century, early travellers, traders and more recently, research scientists, disseminated these nematodes with infested plant materials all over the world, such as in Asia (Khan, 1999), in Africa (Price, 2006) and America (Marin et al., 1998).

Radopholus similis is a polyphagous species that will feed and reproduce in the roots of more than 400 plant species in most of the tropical and subtropical areas of the world. As illustrated in table 2, this species has been found associated with many primary crops mostly in Asia and the Pacific. After its early discovery on banana in Fiji by Nathan A. Cobb (1893), *R. similis* was found associated with coffee and tea plants in Indonesia (Zimmerman, 1898). Its presence as a potential pest of tea has been confirmed since then in Sri Lanka, India, China, Zimbabwe and South Africa (Gnanapragasam & Mohotti, 2005). In the Pacific, *R. similis* was also observed in Fiji on sugarcane (Cobb, 1915), on yam and ginger (Butler & Vilsoni, 1975), on taro (Kirby et al., 1980) and on swamp taro in Guam (Jackson, 1987). Currently the presence of *R. similis*, causing dry rot of yam tubers, seems only restricted to Papua New Guinea, New Caledonia, Fiji and Solomon Islands (Bridge et al., 2005). According to Williams (1969), *R. similis* was recorded from sugarcane from Hawaii, Louisiana and Florida (USA), Cuba, India, the Philippines and Australia. However, this species is no longer considered as a pest of sugarcane (Cadet & Spaull, 2005) although some records of *R. similis* on sugarcane could suggest the existence of a biotype or 'sugarcane race'. Similar observations were made by Godfrey (1931) with records of a 'citrus race' of *R. similis* able to attack pineapple in Florida, while this species is also not considered as a pest of pineapple worldwide (Sipes et al., 2005).

The first and major evidence of plant damage was observed when *R. similis* was responsible of the loss of 22 million pepper vines within 20 years in Bangka Island, Indonesia, due to the 'pepper yellows disease' (Van der Vecht, 1950), a severe disease of pepper (*Piper nigrum*) subsequently reported from Malaysia, Thailand, India and Sri Lanka (Koshy et al., 2005). In India but also in some other countries of Asia, many plant species, used as live standards for pepper vines (coconut, arecanut) or intercropped with pepper (banana, ginger, turmeric, betel vine, food legume) were also recognised as primary hosts for *R. similis* (Table 2). This fact, in addition to its dissemination through infested banana plants (Khan, 1999), is certainly of major importance in the widespread dissemination of *R. similis* in India and Southeast Asia.

At the same time in Florida, Suit and DuCharme (1953) identified *R. similis* as the causal agent of the very severe "spreading decline of citrus" and differentiated this 'citrus race', able to parasitize banana from the distinct but more widespread 'banana race' for which citrus is not a host (DuCharme & Birchfield, 1956). On ornamentals, *R. similis* was first reported to occur on anthurium by Sher (1954) in Hawaii and is one of the major pests of *Anthurium andreanum*, characterised by root necrosis, stunting of plants and chlorosis. This important disease known as "anthurium decline" was mostly reported from Hawaii (Aragaki et al., 1984) and from the Caribbean (Bala & Hosein, 1996; Quénéhervé et al., 1997). The nematode is well known as a pest of foliage ornamentals belonging to the Araceae, Marantaceae and Zingiberaceae. Sixteen palms including coconuts are already reported as hosts of the burrowing nematode. Among them arecanut or betel nut (*Areca catechu*) growing in India and southeast Asia is highly infested with *R. similis*, particularly when intercropped with banana, black pepper, cardamon, coconut and cocoa (Griffith et al., 2005). Other hosts include weeds, acting either as transitional or primary hosts. All these records illustrate the importance of the quarantine regulations concerning not only *R. similis* but also other banana nematodes liable to become major pests on some other important crops.

In accordance with the principles of the IPPC, most of the countries around the world have developed their own plant health and quarantine regulations and now the international movement of soil and infested plants (e.g. banana planting materials, black pepper cuttings, anthurium cuttings) should be totally banned. Therefore, these basic principles of exclusion still seem always difficult to apply at the borders of many countries from Asia, Africa and America and there is no domestic quarantine to limit the dissemination of infested banana planting materials within some large countries (e.g. Brazil, Colombia, Ivory Coast, Nigeria, Uganda, India) or archipelagos (e.g. Indonesia, Polynesia). In order to avoid the new introduction or dissemination of banana nematodes or other pests, only pest-free tissue culture should be now authorized for transfer among and within countries. In parallel, prophylactic measures should be taken in the research stations to ensure the establishment of nematode-free nurseries, before any further distribution to farmers within the country.

6.2. The Search for Sources of Resistance to Nematodes

Due to increasing concern about environment contamination by pesticides, the search for both plant resistance and/or tolerance to plant-parasitic nematodes of bananas is now a major challenge, with many research teams involved. Currently, screening for nematode resistance is an ongoing process, particularly as newly-developed banana hybrids become available. The *Musa* germplasm screening, while formerly restricted to searching for resistance against *R. similis*, is also developed for some other nematode species (*P. coffeae*, *P. goodeyi*, *Meloidogyne* spp., *H. multicinctus*).

Historically, the first search for possible sources of resistance was conducted in the 1960s: the 'Banana Breeding Scheme' in Jamaica at Bodles produced a series of tetraploid banana hybrids bred specifically for desirable factors such as disease resistance or fruit characteristics (dessert banana). Among these, the cultivar 'Bodles Altafort' (Osborne, 1962) that was obtained from a cross between cultivars 'Gros Michel' and 'Pisang lilin' was promising against some diseases, but further results indicated different degrees of susceptibility to nematodes rather than true resistance (Gowen, 1976). Following this early work, the most significant contribution in this field was made in Honduras at the FHIA on the field screening of numerous cultivars and the first discovery of nematode resistance in the diploids *Musa* AA from the 'Pisang jary buaya' group (Wehunt et al., 1978).

In recent decades, different procedures and guidelines for the screening of *Musa* germplasm have been set up (Pinochet, 1988b; Sarah et al., 1992; Speijer & De Waele, 1997; Marin et al., 2000; Elsen et al., 2002; Quénéhervé et al., 2006). In parallel, several successive results of resistance screenings were published: in Asia (Davide & Marasigan, 1985; Van den Bergh et al., 2002; Elsen et al., 2002; Nguyet et al., 2002; Krishnamoorthy & Kumar, 2005), Europe (Pinochet et al., 1998), Latin America and the Caribbean (Binks & Gowen, 1996; Costa et al., 1998; Marin et al., 2000; Moens et *al*., 2003; Viaene et al., 2003; Moens et al., 2005), Africa (Price, 1994b; Fogain & Gowen, 1997; Fogain, 1996; Stoffelen et al., 2000) and Australia (Stanton, 1999), in search for different sources of resistance to nematodes. As mentioned by Gowen et al. (2005), inconsistencies in the results may be due to the highly variable environmental conditions and biological materials (plants and nematodes).

Some authors (Mateille, 1990; Stanton, 1999) also indicated that results of screening studies done on young tissue culture plants might not be consistent with studies with older plants. It is reasonable to think that results of early resistance screenings can only be indicative of a tendency that should be confirmed through multi-site field experiments.

6.2.1. Resistance to the Burrowing Nematode R. similis

The first resistance source to *R. similis* was found in the diploid ‘Pisang jari buaya’, accession III-116 (Wehunt et al., 1978). In spite of many breeding difficulties (e.g. male sterility and low female fertility, difference between accessions from different geographical origins), this source of resistance was used to create the resistant diploid ‘SH-3142’ (Pinochet & Rowe, 1979), that led by successive crossing to the cultivar ‘Goldfinger’ (tetraploid SH-3481 or FHIA-01) but also to other interesting tetraploid cultivars (Pinochet, 1988; Rowe & Rosales, 1994).

From a practical and breeding standpoint, Pinochet and Rowe (1979) already mentioned that the synthetic diploid ‘SH-3142’ was not only more resistant than its parents but was also pollen fertile and produced several seeds per bunch. Following this work, some discrepancies were observed in the field on the level of resistance to *R. similis* of the tetraploid cultivars (Stanton, 1994; Binks & Gowen, 1996, Marin et al., 1998b). This fact, among other undesirable traits (e.g. consumer acceptance, susceptibility to *P. coffeae*), limited the commercial development of these cultivars and confirmed that the resistance, if any, will be certainly difficult to handle directly in a breeding programme (Pinochet, 1988a). Beside this first source of resistance, the cultivar ‘Yangambi Km5’ (*Musa* AAA group Ibota) was reported to be partially resistant to *R. similis* (Sarah et al., 1992; Fallas & Marban-Mendoza, 1994; Price, 1994b; Fogain & Gowen, 1998).

Hahn et al. (1996), indicated that cultivar ‘Yangambi Km5’, although not totally resistant to *R. similis*, was able to tolerate nematode parasitism. In fact, the damage caused by *R. similis* on the banana root system (% of root necrosis) was always lower on this cultivar than on susceptible cultivars, by 5 % to 85 % (Fogain & Gowen, 1997), or 10.5-19 % to 48-56 % (Dochez et al., 2006). Other sources of potential resistance to *R. similis* were found in two other diploids, the cultivars ‘Paka’ (*Musa* AA) and ‘Kunnan’ (*Musa* AB) (Collingborn & Gowen, 1997). In a recent study, Dochez et al. (2006) found ten new potential sources of resistance to *R. similis* within *Musa* diploids (AA) and triploids (AAA, ABB) from Papua New Guinea, Malaysia and the Philippines.

6.2.2. Resistance to the Lesion Nematode Pratylenchus *spp.*

Besides its resistance to *R. similis*, the cultivar ‘Yangambi Km5’ (*Musa* AAA group Ibota) was also reported to be partially resistant to *P. goodeyi* (Fogain & Gowen, 1998; Pinochet et al., 1998) and to *P. coffeae* (Collingborn & Gowen, 1998). This is a remarkable feature since most frequently, resistance is found to be effective to a single nematode species. Unfortunately, due to some breeding incompatibilities, this cultivar is not really used in banana breeding programs. Similarly, cultivars ‘Paka’ and ‘Kunnan’ were also found resistant to *P. coffeae* (Collingborn & Gowen, 1997). In field trials conducted in Cameroon, Price (1994b) reported some triploid cultivars

'Banane Cochon' (AAA), 'Gros Michel' (AAA) and 'Big Ebanga' (AAB) to be partially resistant while most of the plantain cultivars (AAB and ABB) and cultivar 'Pisang jari buaya' were equally susceptible to *P. goodeyi.*

6.2.3. Resistance to the Root-Knot Nematode Meloidogyne *spp.*

Very little information is available on the existence of sources of resistance or tolerance to root-knot nematodes in *Musa*, although some screening studies were carried out in Indonesia (Hadisoeganda, 1994), Brazil, (Costa et al., 1998), the Canary Islands (Pinochet et al., 1998) and Vietnam (Stoffelen et al., 2000a; 2000b; Van den Bergh et al., 2002).

In the Philippines, Davide and Marasigan (1985) found nine cultivars assigned as 'resistant' to *M. incognita*. However, although these cultivars showed gall indices and root nematode densities lower than the control, their real host status needs to be confirmed using standardized procedures (Speijer & De Waele, 1997; Quénéhervé et al., 2006).

6.2.4. Resistance to the Spiral Nematode Helicotylenchus multicinctus

In Costa Rica, Moens et al., (2005) were the first to assess the host response of *Musa* cultivars to *H. multicinctus* and found a resistance response in the cultivar 'Tjau lagada'.

6.3. Tolerance to Nematodes

The existence of 'tolerance' or varietal susceptibility of cultivated bananas to nematodes was first observed by the response of the cv. 'Gros Michel' which apparently was less susceptible to nematode damage than Cavendish cultivars (Leach, 1958; Stover, 1972). In 1978, Wehunt et al., confirmed these observations and also showed that moderate susceptibility to high level of resistance to *R. similis* might be found in wild diploids and diploid cultivars. Gowen (1976) was the first to mention that tetraploid cultivars bred in Jamaica exhibited better vigor and were less susceptible to nematodes than others.

Many workers (Price, 1994; Fogain, 1996) observed a higher susceptibility of plantains to nematodes than Cavendish cultivars. Swennen et al., (1986) related this higher susceptibility to the quality of their root systems, which are less vigorous than those of *Musa* AAA. Similar observations were made with FHIA tetraploids (Rowe & Rosales, 1994). The results of the numerous nematode screenings (see above) among *Musa* germplasm definitely confirmed this huge varietal susceptibility.

The rapid development of the meristem culture technique has revolutionized banana propagation (Israeli et al., 1995) and commercial tissue culture laboratories (France, Israel, Republic of South Africa, Taiwan, Costa Rica, etc…) produce millions of banana plantlets throughout the world. Since the work of Champion (1963) and Stover (1972) it is widely accepted that varieties from the Cavendish subgroup were highly and equally susceptible to nematodes.

At present several different clones of Cavendish are widely distributed, sometimes under the same name ('Grande Naine', 'William', 'Poyo', 'Americani', 'Dwarf Cavendish'), while exhibiting slight phenotypic differences depending on their geographic origin but without any data on pest susceptibility.

In 1990, scientists from CIRAD, while working in collaboration with a tissue culture laboratory, selected within the 'Grande Naine' bananas from Martinique, Guadeloupe, but also from Africa (Ivory Coast, Cameroon) some peculiar plants based on several interesting criteria locally defined (dwarfism, hardiness, vigor, drought or cold tolerance, productivity, bunch conformation, finger size etc.). As a result, several clones of 'Grande Naine' were selected and evaluated against nematodes in greenhouse and field experiments.

A natural mutant of 'Grande Naine' cv. 'MA13' demonstrated significantly lower susceptibilities to *R. similis* and *P. coffeae* in addition to its good horticultural characteristics (Quénéhervé, unpublished).

As most of the banana-producing countries are now trying to reduce their use of pesticides for the sake of environmental and human safety, it is important to select the best clones to cultivate in terms of resistance to pests and parasites. As illustrated in nematode population dynamics studies (Quénéhervé, 1993a) and in modelling studies (Tixier et al., 2005), any plant or environmental characteristic which reduces the multiplication rate of nematodes, is a step forwards a global reduction use of nematicides.

6.4. New Synthetic Banana Hybrids and Their Response to Nematodes

In most banana growing parts of the world, different *Musa* breeding programs are developed to create new synthetic hybrids primarily resistant to Sigatoka leaf spot diseases, such as in Africa (IITA; CARBAP), Latin America (FHIA; Embrapa), the Caribbean (CIRAD) and Asia (Tamil Nadu Agricuture University). As soon as these new hybrids are released, they are evaluated for their reaction to the burrowing nematode *R. similis* and other nematode species.

In Honduras, different bred genotypes were evaluated in pot tests for resistance and tolerance to *R. similis* (Viaene et al., 2003). These tests confirmed once again the resistance status of the synthetic hybrid FHIA-01 to *R. similis* and the resistance of the male parents (diploids 'SH-3142', SH-3362, SH-3648, SH-3723) and female parents (Calcutta 4, Prata Enana) used in the *Musa* improvement programme of FHIA. The same synthetic hybrid FHIA-01 was already reported as tolerant to *P. goodeyi* (Pinochet et al., 1998). This hybrid has been already distributed for experiments in many countries (Honduras, Costa Rica, Cuba, Ecuador, Brasil, Nigeria, Australia, South Africa, Taiwan, Canary Islands).

In Uganda, IITA is developing a breeding program for the production of new hybrids of highland bananas (EAHB), and those which have the resistant 'Pisang jari buya' cultivar in their pedigree are very promising in terms of resistance to *R. similis* (Dochez et al., 2000).

In Nigeria, the hybrid 'Pita-14' is currently distributed to farmers (Coyne et al., 2005a).

In India, at the Tamil Nadu Agricultural University, recent results (Krishnamoorthy & Kumar, 2005) indicate the breeding of some resistant and tolerant diploids to *R. similis* that could be used in their future breeding programs.

In the Caribbean, CIRAD is currently releasing new synthetic hybrids of dessert bananas (*Musa* AAA), resistant to Sigatoka leaf spot diseases and highly tolerant to nematodes (*R. similis* and *P. coffeae*). All these synthetic hybrids, originally bred for the resistance to Sigatoka disease from a common pool of resistant parents, often share also a better tolerance to nematode than current cultivars.

Unfortunately, banana streak disease, caused by several distinct badnavirus species, has severely hindered international *Musa* breeding programmes, as new hybrids were frequently infected with this virus, curtailing any further exploitation. This infection is thought to arise from viral DNA integrated into the nuclear genome of *Musa balbisiana* (B genome) of the wild species, contributing to many of the cultivars currently grown (Geering et al., 2005).

6.5. Resistance Mechanisms and Plant Defence

It is more and more recognized that plant defence responses to plant-parasitic nematodes have the potential to become part of the management strategies to increase plant productivity and that both constitutive and induced defence mechanisms can be observed in plants (Giebel, 1982; Veech, 1982). Within the plant metabolism, the phenylpropanoid pathway that produces different phenolic compounds (e.g. tannins, anthocyans) is involved in the plant's defence against abiotic and biotic factors (Treutter, 2006).

On bananas, Mateille (1994) first suggested that the compatibility to *R. similis* of a susceptible cultivar 'Poyo' was due to a high polyphenol oxidase (PPO) activity, while the relative incompatibility of a less susceptible cultivar 'Gros Michel' was due to a higher peroxidase activity. He also found higher numbers of cells with phenolic contents in the cv 'Gros Michel' compared to the susceptible cv. 'Poyo' using histochemical studies (Mateille, 1994b). In subsequent studies, these results (e.g. callose and phenol accumulation) were confirmed on susceptible 'Poyo' and partially resistant 'Yangambi km5' cultivars (Valette et al., 1997).

On the other hand, the resistant cv 'Pisang jari buaya', in which fewer preformed phenolic cells were found but larger numbers of cells with lignified walls, suggested a different resistance mechanism (Fogain & Gowen, 1996). The production of phenyphenalenone phytoalexins (Binks et al., 1997) and of proanthocyanidins (Collingborn et al., 2000) after infection with nematodes or fungi (Luis, 1998) were also reported. Wuyts et al., (2003) tried to elucidate the biochemical basis for nematode resistance in bananas and concluded that after nematode infection, *i)* constitutive lignification and induced cell wall strengthening were similar in susceptible and resistant cultivars, *ii)* cells containing flavonols increased in the central cylinders of resistant cultivars.

In a recent study, Wuyts et al., (2006) confirmed through in vitro bioassays the effect of several phenylpropanoid compounds on chemotaxis, motility and hatching of migratory and sedentary nematode species. In this study, several flavonols and lignin-related compounds were found repellent to *R. similis*.

At present the mechanisms by which constitutive or induced root cell compounds are active against plant-parasitic nematodes are still largely unknown. However this research should benefit from the discovery of new sources of resistance in the *Musa* germplasm, in order to find biochemical links among resistance mechanisms against nematodes.

The use of elicitors of plant defence leading to systemic acquired resistance (SAR) is in its infancy (Sticher et al., 1997) but promising results should also arise in the coming years, as already shown in pineapple (Chinnasri et al., 2006).

6.6. Transgenic Resistance

Until recently, the only way to obtain nematode-tolerant or resistant cultivars was through conventional plant breeding, while the prospects for genetically engineered nematode-resistant banana cultivars were already understood (De Waele et al., 1994). A decade later, Atkinson et al. (2004) successfully transformed Cavendish bananas using *Agrobacterium tumefaciens* in order to express a protein engineered rice cystatin (OcI deltaD86) of value for control of plant parasitic nematodes. When ingested by nematodes, this protein, a cystein proteinase inhibitor, impairs digestion of dietary protein and then reduces the multiplication of nematodes. That was already demonstrated on sedentary endoparasites such as *M. incognita*, *Globodera pallida*, *Heterodera schachtii* and *R. reniformis* (Urwin et al., 1997; 2000; 2001).

This first work on transformed Cavendish bananas showed that eight of 115 lines were able to reduce *R. similis* multiplication and expressed detectable levels of cystatin in their roots, with one of these promising lines providing a resistance level of 70 ± 10 % (Atkinson et al., 2004).

While still controversial among banana consumers, this type of partial resistance, induced through transgenic transformation, will certainly be deployed in the future alongside conventional banana breeding (Tripathi, 2003), due to its enormous potential. It is also noteworthy that the cystatin used in this work has already been donated on a royalty-free basis to resource poor small banana farmers in Africa (Atkinson et al., 2001).

As mentioned by the FAO (Anonymous, 2001), the most compelling reason for adopting genetic transformation in bananas is to reduce the use of fungicides and insecticides. It is for these constraints that genetic constructs are already recognized and attempts at their incorporation in Cavendish (and other bananas) are advanced but protected under commercial secrecy agreements.

6.7. Biological Control

Biological control of plant-parasitic nematodes has long been considered as an alternative to chemicals, especially because of the environmental and health concerns associated with these chemicals. Plant-parasitic nematodes have many natural enemies in the soil and early research on biological control focused mainly on microorganisms which are predacious (e.g. trapping fungi) and parasitic (e.g. *Pasteuria penetrans*) towards sedentary endoparasites (e.g., *Meloidogyne* spp.). Among all groups of plant-parasitic nematodes, migratory endoparasites such as *R. similis* and *Pratylenchus* spp. are the most difficult to control with natural enemies (Stirling, 1991).

As an alternative to chemicals, these biocontrol agents were first applied as soil treatments but the industrial attempts were all unsuccessful. Ongoing research is now directed to biocontrol agents able to induce *in planta* suppressiveness (Sikora & Pocasangre, 2005). These biocontrol agents should be able to colonize permanently either the rhizosphere or the roots and to induce direct or indirect nematode control or to promote the natural plant defence against plant-parasitic nematodes. The currently potential biocontrol agents include parasitic fungi, rhizobacteria, mycorrhizae and endophytic fungi.

6.7.1. Soil Treatment with Antagonistic Microorganisms

An isolate of a parasitic fungus *Paecilomyces lilacinus* (Pl251) originating from the Philippines was the first to be developed commercially (Tandigan & Davide, 1986; Davide, 1988) and used against banana nematodes. This same strain of parasitic fungi (Pl251) is now sold in many countries under several trade names as water dispersible granules made up of 10^{10} viable spores of *P. lilacinus* per gram, but published data on its long-term efficacy on banana nematodes under field conditions are still lacking.

Recent experiments conducted in Martinique, in fields heavily infested with *R. similis*, *P. coffeae* and *M. arenaria*, failed to show any effect either on nematode populations or banana yields (Chabrier, personal communication). On the other hand in Cuba, in a recently established banana plantation with low initial nematode populations, the preventative use of *P. lilacinus* on tissue culture led to good nematode control and increased the yield by 25 % (Fernandez et al., 2005).

In Cuba, the application on banana fields on a large scale of a particular strain of *Bacillus thuringiensis* (Bt var. Kurstaki, strain LBT-3) gave an average nematode reduction of 87 % two months after treatments (Fernandez et al., 2005). The trapping fungi *Arthrobotrys* sp. have also been found promising on plantain in a laboratory experiment (Lopez et al., 2000). Under controlled conditions the use of the strain of *Corynebacterium paurometabolum* (C-924) led to 85 % *R. similis* reduction and in the field, yields of treated plants were significantly higher than those of the control plants, with increases of 106 % for the bacteria and 66 % for the nematicide treatment (Fernandez et *al*, 2005).

6.7.2. Induction of In Planta *Suppressiveness*

Among the rhizobacteria, the fluorescent *Pseudomonas* spp. constitute a major group, certain strains of which have been demonstrated to act positively on plants either by promoting their growth or by inhibiting root pathogens (Kloepper et al., 1980). An experimental study on bananas showed promising results in terms of reduction of root invasion and repulsion of *R. similis* (Aalten et al., 1998).

Arbuscular mycorrhizal fungi (AMF), which are obligate symbionts, increase the plant's capacity to take up water and mineral nutrients (e.g. soluble phosphates) from the soil, especially under poor fertility conditions (Jaizme-Vega, 1999). The inoculation of banana plants with AMF has shown positive growth responses in the early vegetative stage (Declerck et al., 1994; Rodriguez-Romero et al., 2005). The studies on the interaction with plant-parasitic nematodes showed both a suppressive effect in the nematode population build-up and nematode damage in the presence of AMF on bananas (Umesh et al., 1988; Jaizme-Vega & Pinochet, 1997; Jaizme-Vega et al., 1997; Pinochet et al., 1997, Fogain & Njifenjou, 2003). From the different studies, it is clear that if the migratory nematodes can be harmed by the presence of AMF, the development of AMF can also be harmed by migratory nematodes (Elsen et al., 2003).

Since both plant-parasitic nematodes and AMF colonize the root tissues, the competition for food resources should be considered, either directly due to root necrosis or indirectly due to structural and physiological root alteration. The possibility of in-vitro mass production of AMF (Declerck et al., 1996) may allow massive inoculation of young plantlets in nurseries.

Most plants harbour endophytic fungi (e.g. *Fusarium* and *Trichoderma* spp.) that live part of their life cycle inside the plant, without producing disease symptoms, and can even develop mutualistic relationships with the plant acting as antagonists to various pests and diseases (Sikora, 1992).

Among the naturally occurring avirulent endophytic fungi on bananas, avirulent strains of *F. oxysporum* are the most promising and many studies have shown nematode control through induced systemic resistance (Vu et al., 2006) in greenhouse trials in Africa (Dubois et al., 2004; Paparu et al., 2006) and Latin America (Pocasangre et al., 2000; Zum Felde et al., 2004). Secondary metabolites produced by these *F. oxysporum* strains were strongly inhibitory to the movement and hatching of *R. similis* in a recent study (Athman et al., 2006). The use of these avirulent fungal endophytes is very promising, especially if these endophytes are able to persist over cropping cycles after inoculation.

More data on parameters associated with the use of these new biocontrol agents and their mode of action are necessary to understand the mechanisms underlying the incidence of these different microorganisms on the different nematode species on bananas. Nevertheless from a practical standpoint, due to the promotion of tissue culture derived plants, not only in the commercial banana industry but also for smallholders through regional banana networks, this new approach in nematode management should be easily applicable to any banana production systems.

At least, endophytes and/or AMF and/or rhizobacteria should be artificially inoculated into tissue culture plants to give a better start to the banana plantation and increase host tolerance to pests and diseases. However, these biological products will certainly have to follow the same biosafety and homologation procedures as chemical products.

6.8. Cultural Practice Improvements

Most of the listed cultural practices were already described above as regional strategies and they will only be briefly summarized below.

The priority is in the use of clean banana seeds. The revolution observed with the distribution of millions of dessert banana plantlets following the rapid development of the meristem culture technique (Israeli et al., 1995) is still limited to commercial dessert bananas. In parallel, new hybrids of non-export bananas are introduced into farmers' fields in on-farm demonstration plots by the different research institutes in Africa (FHIA, IITA, CARBAP) with funding from several development investors. The challenge is now to ensure permanent access to clean banana plantlets and new hybrids to farmers worldwide via public or non-governmental public extension service.

The use of rotation crops and fallowing should be encouraged whenever possible. Replanting on highly infested soils is worthless. The use of plants that are antagonistic or detrimental to the development of plant parasitic nematodes is currently gaining most interest from research institutes, especially in areas where these plants are readily available and accessible. However, even if these plants are inexpensive and provide a valuable nematode management option, their adoption and usefulness will mainly depend on their economic or agronomic value (e.g. vs soil fertility) and if the farmers can derive some benefit from their presence beyond nematode management.

Treatments with nematicides, as part of nematode management strategies in some cropping systems (e.g. commercial dessert bananas), needs to be applied more rationally. Their intensive use in the past led to different drawbacks, e.g. soil and water contamination, loss of efficacy through microbial biodegradation. They should only be applied as control means of last resort on the basis of nematode incidence (percentage of uprooted plants) and/or numbers of nematodes in roots, in an effort to minimize nematicide applications. In older banana fields with plants at various developmental stages, the treatment could be applied individually after harvest *i)* to improve efficacy by application at the ideal time and *ii)* to minimize the risk of leaching and acute pollution (Quénéhervé et al., 1991; Quénéhervé, 1993a). However, the adoption of this practice will mainly depend of the willingness of the banana companies, often reluctant to modify any cultural procedures involving workers.

Recently, the model SIMBA-NEM (Tixier et al., 2006) has been designed to simulate the population dynamics of *R. similis* and *P. coffeae* on *Musa* spp. This model, able to predict long-term nematode population size for a range of conditions, is already a very helpful tool for designing sustainable and more environment-friendly banana cropping systems (e. g. optimization of the effect of nematicide applications on commercial bananas).

7. CONCLUSION

Banana farmers, from subsistence farming to commercial production, are typically faced with a multitude of problems. Nematode problems on bananas are widespread and can severely affect crop productivity and longevity. The different approaches to nematode management (e.g. cultural practices, use of nematicide, plant resistance and biological control) have all their interests, depending on the banana cropping systems. Until recently, commercial banana growers producing fruits for the international banana trade relied almost exclusively on the regular application of nematicides as pre- or post-plant treatments in the planting holes or around the established plants. However, the golden age of chemical control with nematicides is definitely behind us for many well-understood reasons in terms of environmental security and human health. The hierarchy and range of management tactics are now widened and differ greatly between export and non-export banana and in the different parts of the world.

In Asia and Oceania, centres of origin of both *Musa* spp. and burrowing nematode *R. similis*, the huge potential of diversity among wild and cultivated bananas has yet to be explored in order to select cultivars that can be grown without nematode control and still yield enough to be economic despite nematode damage.

In Africa, America and the Caribbean, cultural practices that include pest avoidance through international and domestic quarantine should slow down the dissemination, not only of the burrowing nematode but also of the lesion nematodes.

In export banana, very soon the application of diverse cultural practices including systematic use of pest-free vitroplants, fallows, rotation crops and biological control (e.g. in planta suppressivness) should totally replace the chemical control of nematodes, to respond to the new requirements in terms of quality and safety of the international banana trade.

Definitely host resistance, which is an environment friendly management tactic that has much potential, needs to be more effectively used and the development of disease-resistant and high yielding banana hybrids should constitute the most significant scientific achievement of the near future. This is particularly true in Africa in terms of food security impact .

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