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PREFACE

This series originated during a visit of prof. K. G. Mukerji to the CNR Plant Protection Institute at Bari, Italy, in November 2005. Both editors convened to produce a series of five volumes focusing, in a multi-disciplinary approach, on recent advances and achievements in the practice of crop protection and integrated pest and disease management.

This fourth Volume deals with management of nematodes parasitic of tree crops, and includes a section on tropical fruit crops and commodities, as well as a second section on tree crops from more temperate areas. The latter also includes a chapter updating the current knowledge about the pine wood nematode, *Bursaphelenchus xylophilus*. Volume 4 flanks Volume 2 of this IMPD series, which focused on management of vegetable and grain crops nematodes.

Nematodes are a very successful, diversified and specialised animal group, present in nature in any ecological niche. Among nematode species, only a reduced number feeds on plants, of which a few species cause severe economic impacts on crop productions. Plant parasitic nematodes represent an important concern for a broad range of agricultural productions and systems, worldwide. This statement explains the attention devoted in last decades to nematodes, and the research and technical efforts invested for their control. As for other disciplines included in plant protection, nematology is now in a mature stage in which the initial optimism deriving from the widespread use of chemicals and fumigants lent space to a more pragmatic, comprehensive and integrated vision of control and management, including traditional approaches like resistance-based management or innovative approaches like biocontrol or use of natural compounds.

A wide literature already covers chemical or biological control of nematodes, but there is still a need for a more holistic vision of management, accounting for different experiences and solutions, developed worldwide. In this series we attempted to fill this gap aiming at providing an informative coverage for a broad range of agricultural systems which coexist in the world today, focusing on solutions fitting the corresponding background economies. Chapters are mainly organized and centered on crops and/or regional problems, ranging from nematodes of tropical crops like banana, cocoa and coffee, to species affecting more widespread crops like citrus. Regional aspects are described in chapters dealing with tropical fruit or commodity productions (Venezuela, Mexico, Nigeria) or with export-oriented cropping systems (Chile). Chapters in Section 2 review nematodes and related management options for more temperate crops, i.e. *Prunus* spp., grapevine, pistachio and olive nematodes, with a chapter on the management options for virus-transmitting nematode species. Emphasis was also given to long-term technological solutions, updating the actual knowledge on the application of resistant germplasm in several of the cited crops.

In the first chapter, the integrated management of banana nematodes is reviewed, starting from the botanical and economical backgrounds of this crop. Dessert banana crops for export and the geographic distribution of associated nematode species are revised. Concepts definition and applications are then discussed, in the light of integrated nematode management. Damage and economic importance of main nematode species and control strategies are reviewed, with reference to nematicide use. The search for alternatives to chemical control are then illustrated, with basic studies on nematode biology for the different species. Nematode problems of banana crops in Africa, Asia, Oceania and America are reviewed, focusing on the occurrence, importance and potential damage caused by main species. Current management options, including the production and dissemination of clean planting material, the application of cultivated fallow and alternate cropping systems, as the use of mulching and fertilisers, are then reviewed. Future and common strategies and plant health measures applied are revised, with emphasis on the search for sources of resistance to the burrowing nematode *R. similis*, the lesion nematode *Pratylenchus* spp., root-knot *Meloidogyne* spp. and the spiral nematode *Helicotylenchus multicinctus*. The nematode tolerance, the production of new synthetic banana hybrids and their response to nematodes are also examined. Finally, resistance and plant defence mechanisms are reviewed, followed by transgenic resistance, biological control and antagonistic microorganisms, induction of suppressiveness and available improvements for cultural practices.

In the following chapters, problems and solution applied on a regional scale for management of nematodes of fruit and commodity crops follow, illustrating some case-studies ranging from South to Central America and West Africa. A compehensive review of the main nematode species of tropical fruit crops is given in Chapter 2, describing the case-study of Venezuela. In the following chapter, concepts in management in export-oriented, fruit production systems in Chile are reviewed, focusing on the conservation of soil fertility by means of irrigation and fertilization, placing nematodes management options in a more general view of root and plant protection, as well as soil fertility conservation. In Chapter 4, the broad diversity of coffee cropping systems of Mexico is analysed, with a review of the main properties and problems of natural or mountain systems, including traditional polyculture and specialized systems, commercial polyculture and sunlight system. The main phytosanitary aspects of these coffee cropping systems are reviewed, focusing on nematodes and related investigations.

Nematode problems of cocoa production systems in West Africa are revised in Chapter 5. After discussing the production, climatic requirements, cultivation techniques and practices, the main nematode species attacking cacao are reviewed, with data on their geographic distribution, damage and symptoms. Apart of root-knot nematodes, other nematode parasites and related disease complexes are examined. The options for management and control in cacao are then reviewed, focusing on the integrated approach to nematode control, the use of resistant planting material, the production of nematode-free seedlings in nurseries, the use of nematicides in the field, and of organic amendments and biological control.

In the following chapter the status of nematodes management in citrus orchards is reviewed. This chapter deals with the citrus nematode, *Tylenchulus semipenetrans* and the related slow decline symptoms. Other nematode species of citrus are also examined, including *Radopholus similis* and *R. citri*, *Pratylenchus* spp., *Belonolaimus longicaudatus*, *Meloidogyne* spp., *Hemicycliophora* spp. and dorilaimid species. Data are provided on their biology and ecology, on the interactions with other soil organisms, biotypes, rootstock resistance, economic importance and crop loss prediction. Management, sampling and extraction techniques are also reviewed, together with sanitation practices and exclusion, as well as cultural practices, use of fumigants and nematicides.

In Section 2, six further chapters deal with nematodes of temperate fruit crops, with a revision of forest nematodes management, mainly updating the situation for *B. xylophilus*, a major emerging problem in Europe. The integrated management of nematodes parasitic on *Prunus* spp. is reviewed in Chapter 7, dealing with root-knot, lesion, ring and dagger nematodes. The chapter focus is on management and control methods based on prevention and quarantine. Pre-planting measures are reviewed, including fallow, crop rotation, site preparation, soil solarization, biofumigation, steam application, soil fumigation, chemical control with non-fumigants nematicides, seedling treatments and resistance. Post-planting measures examined include chemical and biological control, cultural methods and integrated management.

In the following chapter, the selection and application of resistant germplasm for management of nematodes attacking grapevine is reviewed. The chapter focus is on root-knot nematodes and the GFLV vector *Xiphinema index*. For root-knot nematodes, data on their biology, ecology, symptoms and control are provided. The selection and breeding of resistant rootstocks is then reviewed, with data on resistant *Vitis* and *Muscadinia* material. The advances in breeding for resistance, as well as the genetics of resistance mechanisms and its durability are also discussed. The chapter then reviews the biology, vection and classical control methods of *X. index* and other virus vector nematodes of grapevine, focusing on the selection and breeding for *Vitis* and *Vitis* × *Muscadinia* resistant rootstocks. The resistance features of *Muscadinia rotundifolia* are then discussed, together with the properties of the *V. vinifera* × *M. rotundifolia* F_1 hybrids obtained in California and France. Data on resistance to other nematodes and rootstock control of multiple nematode pests are also provided.

Given the importance of virus-vector nematodes, the following chapter reviews the management of virus-transmitting species with special emphasis on South-East Europe. The geographic distribution and spread of main species is reviewed, focusing on vectors and virus diagnostic techniques, including vectors identification, transmission assays, molecular detection and integrated management. Concepts in prevention and quarantine are then discussed, together with the main practices available for management, like agronomic and chemical control, exploitation of nematode resistance sources available in plants, and organic management. Data on assays with organic and natural products are then discussed, together with biofumigation, use of nematicidal plants and potentials of biological control agents.

In Chapter 10 a further regional and specific agricultural issue concerning pistchio production is reviewed, in reference to nematodes management in the Middle East. Pistachio crops are important sources of nutrients and income for local producers. The distribution of pistachio nematodes and the management options available are listed, including agronomic management, use of resistant rootstocks, biological control, as well as soil solarization.

In the following chapter the situation for the pine wood nematode, *B. xylophilus*, is reviewed. Pine wilt disease (PWD), caused by *B. xylophilus*, is one of the most severe disease affecting *Pinus* spp. in the Far East, North America and now the European Union (Portugal). In some countries, such as Japan, PWD was catastrophic, destroying native pine species at such an extent that some areas had to be totally replaced by other tree species. *Bursaphelenchus xylophilus*, endemic to North America where it causes minor damage, was introduced in Japan in the early XXth century and then spread to mainland Asia. Since its first arrival in the EU this nematode has been monitored and efforts are continuously provided to halt its spreading in the european continent. Experience from Japanese control actions include aerial spraying of insecticides to control the insect vector (the Cerambycid beetle *Monochamus alternatus*), direct injection of nematicides to the trunk of infected trees (mainly for added-value trees), slashing and burning of areas out of control, beetle traps, biological control and tree breeding programs. In Portugal, the damage, although lower than in Asia, is still significant and PWD has caused severe losses to the forestry industry. In this chapter, a brief history of PWD is provided, mapping its spread in Japan and to other East Asian nations, as well as updating the situation for Portugal. The economic impact of PWD is reviewed, in relation to the world importance of forestry and conifer production and trade. Inspection and quarantine issues are then discussed. The PWN biology and life cycle are reviewed, together with its relationship with the insect vector. Data on the taxonomy and progress using molecular biology techniques are also provided. The pine resistance and susceptibility to the nematode are also reviewed, including pathogenicity and the potentials of breeding programs. The authors also provide a comprehensive review about the control of PWN and its insect vector, with methods like insecticide spraying, nematicide injection, biological control and breeding for resistance. A discussion on the results achieved by means of management actions worldwide is also provided.

Finally, in the last chapter, the pathogenicity, geographic distribution and damage of nematodes associated with olive are revised, for species within the genera *Gracilacus*, *Helicotylenchus*, *Heterodera, Meloidogyne*, *Ogma*, *Pratylenchus*, *Rotylenchulus*, *Tylenchulus*, and *Xiphinema*. Research data on olive nematodes are reviewed, focusing on the effects of parasitism by root-knot nematodes, plant growth, cultivars and rootstocks susceptibility, nematodes interactions with the soil-borne pathogen *Verticillium dahliae*, replant problems and control strategies. These include chemical and biological control, solarization, use of soil amendments and organic management, biofumigation and application of nematicidal plants.

In conclusion, we acknowledge the authors for providing a broad range of data on nematode management solutions available worldwide in different agricultural systems. Thanks to the efforts and will of many nematologists studying and applying advanced solutions in their long term research efforts and field practices, we hope we were able to provide a tool useful in the deployment of environment friendly and sustainable menagement practices for the main crops and parasites listed. Our hope is that this volume will result useful and helpful for interested readers and students, inspiring and supporting research efforts invested in their field and laboratory work.

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Section 1

Tropical Fruit Crops and Commodities

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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.

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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.