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Challenges in Tropical Plant Nematology

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Abstract

A major challenge facing agricultural scientists today is the need to secure food for an increasing world population. This growth occurs predominantly in developing, mostly tropical countries, where the majority of hungry people live. Reducing yield losses caused by pathogens of tropical agricultural crops is one measure that can contribute to increased food production. Although plant-parasitic nematodes are often not as important as some other biotic and nonbiotic constraints on crop production in the tropics, they can nevertheless cause extensive damage and substantial yield losses. The effects of agricultural, environmental, socioeconomic, and policy changes on the occurrence of plant-parasitic nematodes in the tropics and the losses these pathogens cause are largely undocumented. Recent developments pose new challenges to tropical nematology. The increased application of molecular diagnostics may widen the knowledge gap between nematologists working in developed countries and in the tropics. Uncertainties concerning the validity of nematode species will lead to practical problems related to quarantine measures and nematode management. The study of interactions between nematodes and other pathogens in disease complexes provide opportunities for multidisciplinary research with scientists from other disciplines but remain underexploited. Difficulties in recognizing emerging nematode threats prevent the timely implementation of management strategies, thus increasing yield losses. Research is needed to address these challenges. Examples are presented mainly but not exclusively from banana, peanut, and rice nematology.

INTRODUCTION

A major challenge facing agricultural scientists today is the need to secure food for a world population that between 1970 and 2006 increased by 3 billion to the current 6.5 billion people, and is predicted to continue growing. This population increase has occurred predominantly in developing, mostly tropical countries, where the majority (820 million) of hungry people live, a number currently growing at the rate of 4 million a year (71). Although the hunger problem is not confined to food shortage, raising food production in the developing, tropical countries, where 60% of the arable land is situated, remains an important objective to meet the UN Millennium Development Goal to reduce by 2015 the proportion of people who suffer from hunger by half (compared with the number in 1990).

Reducing yield losses caused by pathogens of tropical agricultural crops is one measure that can contribute to increased food production. Higher yields may also generate higher cash incomes and thus alleviate poverty. Damage and yield losses caused by pathogens are on average greater in tropical than in temperate regions because of greater pathogen diversity, more favourable environmental conditions for pathogen colonization, development, reproduction and dispersal, and lack of human, technical, and financial resources. Although plant-parasitic nematodes are often not as important as some other biotic and nonbiotic constraints on crop production in the tropics, they can nevertheless cause extensive damage and substantial yield losses (173). Prevention or alleviation of these yield losses would contribute to increased food production and cash income.

Funding for agricultural research in general and tropical agricultural research in particular has decreased substantially in both developed and developing countries. Problems caused by pathogens are addressed only if their importance has been established. Pathogens are increasingly studied as one of the many interacting components of agro- and pathoecosystems. These studies are often undertaken by multidisciplinary research networks in the framework of international collaboration. Changes associated with globalization, agricultural, environmental (climate), socioeconomic or political, have reached to almost every village worldwide. However, the effects of these changes on the occurrence of plant-parasitic nematodes and the damage and yield losses that they cause in the tropics are largely undocumented.

Agriculture in tropical regions is primarily carried out by resource-poor smallholder farmers, who are affected only marginally by the phasing out of pesticides such as methyl bromide. The development of sustainable management strategies that do not rely on pesticides has always been a major objective in tropical nematology, except in commercial plantations. Therefore, we do not deal here with nematode management strategies [for reviews on this topic see (10, 21)]. In addition, we have concentrated on such research areas as molecular diagnostics and the effects of change on agricultural practices, areas of important developments during the past decade.

Finally, the examples presented strongly reflect our own research with banana nematodes. Thus banana nematology is the common thread throughout the review.

IDENTIFYING POTENTIAL NEMATODE PROBLEMS

In general, donors will only consider providing funds to alleviate the effects of nematodes on an agricultural crop if the extent of the problem has already been established. For tropical agriculture this information is often lacking, thus creating a Catch 22 situation: no funds are provided unless the nematode problem has been established, but without funds the extent of the nematode problem cannot be established.

This situation is further aggravated by: (*a*) unawareness by the farmers of even the existence of nematodes, (*b*) the microscopic

nature of nematodes, (*c*) the atypical symptoms caused by nematodes, (*d*) the occurrence of multispecies nematode populations, (*e*) the association with other pathogens, (*f*) lack of trained taxonomists, (*g*) the complexity of planning and executing nematode surveys, and (*h*) the lack of logistic and financial resources.

Exceptions might occur when commercial interests are at stake or when large-scale yield decline is reported by the farmers themselves, by extension workers, or by researchers conducting preliminary surveys. Examples of such exceptions are the problems caused by *Ditylenchus africanus* on peanut in South Africa and by several plant-parasitic nematodes on banana in Eastern Africa. Peanut is an important cash crop for both commercial and small-scale farmers in South Africa. In 2003, 100,000 t of peanut in shell were produced on 96,000 ha. When *D. africanus* (first identified as *Ditylenchus destructor*) was discovered in the late 1980s attacking and damaging the pods of peanut in every production region in the country (50, 107), the South African government immediately mobilized extra resources to study its biology (11, 12, 14, 54, 55, 208), histopathology (108, 214), and reproductive and damage potential (13, 212), and to develop management strategies (51, 52, 121, 213). Bananas are an important staple food for the inhabitants of the East African Great Lakes region: the highlands of Uganda, Burundi, Rwanda, the Kivu region of the Democratic Republic of Congo, the Kagera region of Tanzania, and Western Kenya. In this region, bananas are cultivated at 1000–2000 m above sea level in areas with high population densities and are mainly grown in subsistence farming systems characterized by mixed cropping systems. In addition to being a traditional staple food crop for both rural and urban populations, banana is also a source of income for millions of households. With an annual production of 10 million t, representing almost 10% of the total world production, and a per capita consumption of around 185 kg/year, Uganda is the region's leading producer and consumer of bananas. Over the past two and a half decades, banana production has declined by more than 25%, from 8 t/ha in the 1970s to less than 6 t/ha in the 1990s (83). This decline has given rise to a number of nationally and internationally funded programs charged with identifying its causes and implementing remedies. Nematodes were identified as one of the most important causes leading to this decline. The burrowing nematode *Radopholus similis*, the root-lesion nematode *Pratylenchus goodeyi*, and the spiral nematode *Helicotylenchus multicinctus* were reported to be the most predominant nematode species on banana in Uganda (112, 186). *R. similis* was identified as the most destructive species as it caused greater root necrosis, more plant toppling, and lower bunch weight compared to *P. goodeyi* (202) and *H. multicinctus* (9, 186). Production losses of East African highland bananas ranging from 15% to 50% per crop cycle have been associated with *R. similis* and *H. multicinctus* attack (123, 188–190). Under poor crop management, *P. goodeyi* can also cause considerable damage to East African highland bananas (202). Projects were undertaken to study, inter alia, the use of nematode-free planting material following paring and hot water treatment (66), and to develop nematode-resistant banana varieties (63).

Farmers' Unawareness of Nematode Problems

The few studies that have examined farmers' knowledge of nematode problems demonstrate a general lack of awareness of even the existence of plant-parasitic nematodes. This is attributable to the microscopic nature of nematodes, the atypical symptoms they cause, and the farmers' limited previous exposure to extension and community information.

In a study of farmers' perceptions of banana pest constraints in Uganda, banana weevils, ants, termites, and vertebrates were reported as the most destructive pests in banana fields (84). Root nematodes were normally overlooked; their damage (for example,

stunting, small bunches, toppling), if noted, was attributed to weevils or senescence.

In Cameroon, an evaluation of pest awareness in *Musa*-based cropping systems indicated that of the 216 farmers interviewed, 72% were aware of weevils and could correctly describe the pest and damage caused by them, 9% percent were able to describe damage caused by weevils but gave an incorrect cause (often ants), whereas only 19% had never heard of weevils or were unable to recognize damage caused by them (103). By contrast, when asked about nematodes, only 15% of all farmers correctly attributed the damage. Even in these cases, the actual concept of a nematode (a worm of microscopic size) was unknown, or an incorrect cause was given (often ants). Of the farmers interviewed, 85% had never heard of nematodes.

Nematode awareness by farmers is important not only to implement nematode management strategies, which require that farmers are able to recognize and understand the pathogen problem in their fields. When nematode management (paring and hot-water treatment of planting material) was applied, the farmers were able to recognize the effect of the treatment but did not attribute it to control of the nematodes because of their microscopic size (191).

Multispecies Nematode Populations

The commonest nematode species associated with the majority of tropical crops are generally known. For some crops, these species profiles differ little from region to region, even from continent to continent. However, for other crops, the species profiles may differ markedly from region to region.

One of the best characterized nematode species profiles in the tropics is that associated with banana and plantain (*Musa* spp.). Banana or plantain roots worldwide typically contain a combination of *R. similis*, *Pratylenchus coffeae*, *P. goodeyi*, *H. multicinctus*, and *Meloidogyne* spp. The species profile of *Musa* nematodes is relatively well known because, especially in East and West Africa, substantially the same methodology was followed in studying them, often within the framework of international collaboration. This regional approach provided nematologists with relatively good insight in determining agricultural and environmental factors affecting the frequency of occurrence and the abundance of the different nematode species. In *Musa*, infected planting material has contributed to the spread worldwide of certain nematode species (120), and altitude affects the geographical distribution of important *Musa* nematodes such as *R. similis* and *P. goodeyi* (112, 151, 152, 202). Species profile studies combined with observations on nematode damage can also lead to a regional evaluation of the pest status of nematodes [for example for *Musa* nematodes, see (187)]. This may, in turn, attract the attention of international donors who are interested in regional strategies for control [e.g., banana nematodes in East Africa (19)]. For Asia, where bananas are also a very important food crop, the absence of any such a regional approach led to a rather fragmentary image of the frequency of occurrence and abundance of the different *Musa* nematode species and their pest status (207).

In rice, the nematode species profile may differ significantly from region to region according to ecosystem and environmental conditions (156). *Aphelenchoides besseyi*, the causal agent of the white tip disease, can be present in all rice ecosystems. In deepwater rice ecosystems *Ditylenchus angustus*, the causal agent of the ufra disease, and *Meloidogyne graminicola* are the predominant plant-parasitic nematodes in addition to *A. besseyi* while in irrigated rice ecosystems *Hirschmanniella* spp. are omnipresent. In upland rice ecosystems *Meloidogyne* spp. and *Pratylenchus* spp. have the greatest potential to cause damage.

Nematode Surveys

Nematode surveys can provide information from taxa identified to either the species or the genus level, or on the idenitification of

the predominant damaging species. There are many examples for most tropical agricultural crops of the former surveys but fewer examples of the latter.

A list of nematode taxa associated with a crop is of limited utility because it does not indicate which plant-parasitic nematode species are predominant and potentially damaging, although it can confirm that a certain plant-parasitic nematode species is not present on a crop in a specific production area. For example, a nematological survey of bananas carried out in north, central, and south Vietnam failed to find *R. similis*, leading to the conclusion that this important banana nematode species is not present on banana in the country (37).

Additional observations on the frequency of occurrence and abundance of individual nematode species can be combined to give a prominence value. This information can be combined with preliminary observations on plant damage to identify potential nematode problems. Even a limited survey (>100 samples) systematically carried out in a production area can be informative. In Central Uganda, for example, a nematological survey of banana conducted at 17 sites identified *P. goodeyi*, *R. similis*, and *H. multicinctus* as the predominant nematode species based on the prominence value and observations on plant damage (186).

Plant-parastic nematodes are seldom the only pathogens attacking a crop. A survey should also collect information on the incidence and damage caused by other biotic constraints to establish the importance of plant-parasitic nematodes in relation to these other biotic constraints. For example, in a survey in southern Nigeria to identify the predominant nematode species of plantain, the effects of damage caused by the banana weevil *Cosmopolites sordidus* and the fungus *Mycosphaerella fijiensis*, the cause of black Sigatoka, a leaf disease, were also noted. Principal component analysis of these damage observations suggested that two plant-parasitic nematode species, *P. coffeae* followed by *R. similis*, are the major biotic constraints of plantain production in southern Nigeria.

More comprehensive, systematic nematological surveys can also identify relative risk of nematode damage caused by certain species in different production areas. In South Africa, Jordaan et al. (109) surveyed 175 wheat fields in the seven major wheat-producing areas. The predominant plant-parasitic nematode species were identified based on the prominence value. The seven wheat-producing areas were then ranked on the incidence of the plant-parasitic nematodes, pinpointing areas where yield losses due to nematodes warranted investigation. Application of the Kruskal-Wallis rank sum test with Yates' correction factor was used to rank the areas according to the frequency of occurrence and average population density of each of the predominant nematode species.

MOLECULAR AND OTHER DIAGNOSTICS FOR NEMATODE SPECIES IDENTIFICATION

In nematology, species identification has been based primarily on light microscopy observations and measurements of morphological and morphometrical features mainly of females and males (46). Many nematode genera, especially plant-parasitic nematode genera, exhibit little morphological diversity. Intraspecific variation of the features important for distinguishing species, the possibility of observational and interpretative mistakes, among other factors, make the precise and reliable identification of nematode species a formidable task even for well-qualified taxonomists (45). Correct identification up to the species level is crucial to the prevention, locally and internationally, of the spread of pathogenic nematodes and the success of effective nematode management strategies.

During the past two decades, plant nematologists have increasingly used molecular techniques, both protein- and DNA-based, to confirm the validity of existing nematode species and to assist in the identification and description of new species. In this section, we examine the involvement of tropical

nematologists in the development and use of molecular techniques, and we consider to what extent species of tropical plant-parasitic nematodes were used in molecular studies.

Protein-Based Diagnostics

Protein electrophoresis was the first molecular technique to be applied in plant nematology. Esbenshade & Triantaphyllou (67) used polyacrylamide-gel electrophoresis to define the isozyme phenotypes of 16 *Meloidogyne* species from approximately 300 populations originating from 65 countries from various continents. They found esterase and malate dehydrogenase to be the most useful isozymes for the identification of the most economically important species. A few years later, simplification and miniaturization of the electrophoretic procedures led to the development of commercially available automated electrophoretic systems using precast slab gels. Identification of most common and some rare *Meloidogyne* species became routine based on isozymes from the soluble protein extract of a single young egg-laying female (38, 68, 111, 130, 131) or from galled root pieces harboring a female (97).

Extensive characterization of isozyme phenotypes has subsequently been carried out for other plant-parasitic nematode genera (5, 6, 69, 77, 98, 99, 129). For many genera, these studies revealed a wide variation in isozyme phenotypes between populations of the same species with the exception of *Meloidogyne*, in which limited intraspecific variation was detected.

In the relatively few studies where protein-based diagnostics have been used, nematologists have obtained a much better insight into the diversity of *Meloidogyne* species present and the frequency of occurrence and abundance of the individual species.

Protein-based diagnostics of *Heterodera* species were carried out in India on cyst nematodes associated with graminaceous and leguminous host plants, such as *H. avenae*, *H. cajani*, *H. filipjevi*, *H. graminis*, *H. sorghi*, and *H. zeae* (16, 78, 99, 124, 125, 175, 211). These studies were also mainly based on differences among esterase and malate dehydrogenase phenotypes. Differences in esterase banding patterns also allowed the separation of *H. elachista*, *H. oryzae*, *H. oryzicola*, and *H. sacchari* that attack rice (140).

Andres et al. (5) used differences in isozyme banding patterns obtained from isoelectric focusing to differentiate and establish the genetic relatedness among 40 nematode populations comprising *R. similis* and 9 *Pratylenchus* species from broad host and geographic origins, including some important tropical *Pratylenchus* species. Ibrahim et al. (98) studied the usefulness of alpha and beta esterase banding patterns in three populations of *A. besseyi* and one population each of *A. arachidis*, *A. bicaudatus*, *A. fragariae*, and *A. hamatus*, two undescribed species of *Aphelenchoides* from rice, and *D. angustus* and *D. myceliophagus* using native and SDS-PAGE electrophoresis. Certain enzyme bands were common between the species whereas other bands were specific.

DNA-Based Diagnostics

DNA-based diagnostics has several advantages over protein-based diagnostics, especially in being able to exclude the effects of environmental and developmental variation (149, 197).

Using the polymerase chain reaction (PCR), single target molecules of DNA can be amplified into millions of copies and the amplified products electrophoretically separated and visualized. Nematode target DNA generated by PCR amplification can be further characterized by various analyses including digestion with restriction enzymes, amplified fragment length polymorphism (RFLP, AFLP), dot blotting, or sequencing.

DNA fingerprinting has been applied to the identification of many plant-parasitic nematode genera (17, 149).

Almost all DNA-based studies have been carried out in the northern hemisphere

(United States and Europe). Often, however, tropical nematode populations were included in these studies, especially in studies of evolutionary and phylogenetic relationships among the species of a taxon (3, 48, 94, 101, 110, 196, 198). Most DNA fingerprinting studies (about 80%) have been done on nematode species that are economically important in the temperate regions and are often of regulatory concern.

Of particular interest for tropical plant nematology are the studies on *Meloidogyne* spp., *Pratylenchus* spp., *Radopholus* spp., and *Heterodera* spp. In *Meloidogyne*, DNA-based diagnostics have focused mainly on the four most economically important species, *M. incognita*, *M. javanica*, *M. hapla*, and *M. arenaria*, and on *M. chitwoodi* and *M. fallax*, which are two important quarantine pests in Europe. Primer sets for sequence characterized amplified regions (SCAR) were developed that enable the sensitive, fast, and reliable identification of these six species (222, 223). The length-variant SCAR-markers can be amplified from DNA from egg masses, second-stage juveniles, and females and have also been successfully applied to DNA extracts from infected plant material, a major advantage for the quarantine inspectorate. In the tropics, DNA-based diagnostics for *Meloidogyne* spp. were mainly developed in Brazil and China. In Brazil, the SCAR-PCR assay and random amplified polymorphic DNA (RAPD) polymorphism were successfully used to identify *Meloidogyne* spp. on coffee (35, 36, 160, 162), whereas satellite DNA probes were developed for the identification of *M. exigua*, also on coffee (161). In China, the SCAR-PCR assay and amplified mtDNA RFLPs and genomic DNA RAPDs were developed for the identification of the major *Meloidogyne* spp. occurring in the country (105, 126, 170, 200, 220, 221). DNA-based diagnostics were also used to identify *Meloidogyne* spp. associated with banana in the Carribean (Martinique, Guadeloupe), French Guiana, and Brazil (42, 43); tobacco in Australia (192); and several crops in Libya (1) and South Africa (76). Differences in mtDNA are being used to differentiate *M. mayaguensis* from related species (18, 27).

Many studies have been dedicated to DNA-based diagnostics of *Pratylenchus* and *Radopholus* spp., especially *R. similis*. DNA-based diagnostics have now been applied to many populations belonging to about 20 *Pratylenchus* species including the major root-lesion species occurring in the tropics. The most recent developed diagnostics use PCR-RFLP techniques after digestion of the PCR products with several restriction enzymes (142, 216) and PCR following the production of unique amplicons with species-specific primers (2). With this latter assay single females can be identified to species level.

PCR-RAPDs have been used to study the degree of genetic similarity within and between *R. similis* populations (89, 90). Two new species were identified from Indonesia, *R. bridgei* from turmeric (178) and *R. citri* from citrus (117), before morphological data of these species were available and the synonymization of *R. citrophilus* with *R. similis* confirmed (110). Differences in host range and in relative reproductive fitness and consequent aggressiveness of different *R. similis* populations are well documented (70, 91, 171), but studies failed to provide a genetic basis for these observations (69, 110, 119).

In contrast with root-knot nematodes and root-lesion nematodes, very few tropical *Heterodera* species were included in DNA-based diagnostics studies. Most molecular studies concentrated on *Heterodera* species that are important in the northern hemisphere in temperate regions, such as *H. avenae* and *H. schachtii*. The inclusion in the studies of tropical *Heterodera* species demonstrated the potential of this technique to identify cyst nematodes (40, 199, 201).

A Blessing or Not?

The application of protein- and especially DNA-based diagnostics has increased interest of the scientific community in nematode taxonomy and systematics and has revolutionized

nematode phylogenetic analysis. However, as outlined by Coomans (45), nematode taxonomy has also undergone a conceptual revolution. The concept of a nematode species has become uncertain. In a number of nematode genera, the relatively high degree of genetic divergence between morphologically similar species is leading to the description of morphologically similar but genetically different species and to the proliferation of species complexes.

As shown below, closer examination of *Meloidogyne* populations associated with coffee in Brazil combining morphological observations with molecular diagnostics has led to the description of several new *Meloidogyne* species and the suggestion that *Meloidogyne* spp. populations on coffee from Brazil and other Central and South American countries must frequently have been misidentified (36). The wide range of root-knot nematode species with diverse pathogenicity makes accurate identification to species essential for developing efficient and sustainable IPM programs, especially those based on host resistance (36).

Similarly, closer examination of the intraspecific variability in morphology (100, 128), biology, isozyme phenotypes (5), and of polymorphism as detected with rDNA-RFLP (216) of many diverse populations of *P. coffeae* and of closely related species (64) has led to the conclusion that nematode isolates decribed as *P. coffeae* must be a complex of several species, many of which are still undescribed.

The description of a new nematode species or taxon should be based on a consensus of all available data. The term polyphasic taxonomy has been coined for this type of integrated taxonomy, which is based not only on phenotypic and genotypic differences, and phylogenic relationships, but also on differences in the ability of populations to infect host plants. While few descriptions of nematode species and taxa based on polyphasic taxonomy are currently available, one example is that of *Meloidogyne floridensis* by Handoo et al. (93), which presents information on molecular and cytological characteristics and host-ranges in addition to morphological and morphometrical data. An example of the application of polyphasic taxonomy is the study on the genetic diversity of *Meloidogyne* spp. on coffee from Brazil, Central America, and Hawaii in which 18 populations of *Meloidogyne* species are identified to species based on a combination of their morphology and protein- and DNA-based diagnostics (36).

We anticipate that the increasing application of molecular diagnostics, especially DNA-based diagnostics, will have major consequences for tropical nematology and nematologists working in the tropics, widening the gap between knowledge generated in temperate and in tropical regions. Nematode identification can no longer be based solely on morphology combined with access to the descriptions of existing and new species, and diagnostic keys. Increasingly, use of molecular diagnostics will also be required, but these techniques demand skills, infrastructure, equipment, consumables, and financial resources that are often lacking in tropical areas. As can be seen from the existing literature, the contribution of tropical nematologists to the developments in this research area is, with a few exceptions, small. Moreover, biodiversity is greater in the tropics than in the temperate regions. After a century of taxonomic research, it is estimated that perhaps only 10% of the nematode biodiversity has been elucidated (44) and therefore characterization of many more new nematode species can be expected, especially tropical species.

Without increased research opportunities and international collaboration, tropical nematologists will have few prospects of participating in the application of molecular diagnostics to nematode surveys (15, 102, 143, 150) or the analysis of the origin and dispersal of nematode species based on molecular diagnostics [see for example (119, 141), to name only two applications]. In addition, uncertainties concerning the validity of nematode species, unless resolved, will present practical problems related to quarantine measures

and nematode management. The former is especially pertinent given that the expansion of international trade will increase awareness of nematodes of regulatory concern.

EMERGING NEMATODE THREATS

In tropical plant nematology, damage and yield loss studies deal mainly with previously noted diseases caused by nematodes. Studies on new nematode species associated with agricultural crops are usually limited to a description of the new species, rarely examining the extent of damage and yield loss inflicted. As a result, the pest status of most of these new nematode species is unknown, frequently because of the lack of human resources and financial support. Also, more than one nematode species can usually be found on a crop and the damaging effect of individual nematode species is difficult to establish.

The paucity of data makes it difficult to recognize emerging problems caused by plant-parasitic nematodes. In this section, we describe nematode species that may emerge as important threats to agricultural crops in the tropics or whose pathogenic significance is, in our opinion, underestimated. The number of nominal species mentioned is based on Siddiqi (179) supplemented with species newly described since 2000.

Meloidogyne spp.

By 2006, 92 nominal *Meloidogyne* species had been described, of which about half (47) were described during the past two decades. Of these new species 29 were described associated with plants in Central and South America, Africa, or Asia. Almost half of these new species (14) were described from China.

The application of protein- and DNA-based molecular diagnostics to identify the populations of *Meloidogyne* infecting banana in Brazil has resulted, since 1985, in the description of three new *Meloidogyne* species associated with coffee: *M. mayaguensis*, *M. paranaensis*, and *M. izalcoensis* (31, 33, 159). *M. mayaguensis* and *M. paranaensis* now appear to be geographically widespread and a threat to other crops as well as coffee. These species must have long been misidentified as one of the major *Meloidogyne* species that also can be found on coffee. In time *M. izalcoensis* may also be identified as being more widespread geographically.

Meloidogyne mayaguensis. *M. mayaguensis* was first described in 1988 (159) from eggplant (*Solanum melongena*) in Puerto Rico. This nematode is now considered to be one of the most important root-knot nematode species, posing a threat to agriculture in the subtropics and tropics because of its wide geographical distribution, broad host range, and ability to break resistance genes to the major root-knot nematode species (*M. incognita*, *M. javanica*, and *M. arenaria*) in tomato, sweet potato, soybean, and pepper (72, 153). *M. mayaguensis* has been reported from West Africa (Senegal, Ivory Coast, Burkina Faso), South Africa, Malawi, the Caribbean (Puerto Rico, Cuba, Dominican Republic, Guadeloupe, Martinique, Trinidad), Brazil, Florida, and in glasshouses in France (18, 27, 32, 34, 57, 74, 206, 219). It infects numerous crops including vegetables, ornamentals, potato, sweet potato, soybean, tobacco, and coffee and tropical fruit trees (guava).

M. mayaguenis often occurs together with *M. incognita*, *M. javanica*, and *M. arenaria*. The perineal patterns of females of *M. mayaguensis* are morphologically variable and are sometimes similar to those of *M. incognita*, whereas the morphometrics of male and second-stage juveniles may overlap with *M. javanica* and *M. arenaria* (27). Only after its description was confirmed by protein- and DNA-based diagnostics (73, 75) were nematologists able to differentiate *M. mayaguensis* from the other closely related species. Its widespread distribution and wide host range suggest that *M. mayaguensis* was probably often misidentified as *M incognita* or one of the other major root-knot nematode species and thus not noticed.

Meloidogyne paranaensis. *M. paranaensis* was first described in 1996 (33) from coffee in Brazil. In contrast to *M. mayaguensis*, the known geographical distribution of *M. paranaensis* is restricted and its known host range is small (30). Until recently, this nematode species was thought to occur only in Brazil, but Carneiro et al., using esterase phenotyping and RAPDs, demonstrated that it is also the most widely distributed *Meloidogyne* species on coffee in Guatemala (36, 95). Moreover, in Colombia, a root-knot nematode population was found to exhibit a perineal pattern similar to that of *M. incognita* but produced a response to the North Carolina differential host test similar to that reported for *M. paranaensis* (30). *M. paranaensis* was also recently detected in soybeans in Brazil (167). The geographical distribution and host range of *M. paranaensis* may therefore be much larger than currently assumed.

The frequency of occurrence of this nematode species in most coffee-growing plantations in Brazil is so high (30) that it must have been identified as *M. incognita*, with which it frequently occurs, and have been there unnoticed for a very long time. The fact that this nematode species does not produce typical root-knot nematode galls on coffee (nematode feeding causes the tissues around the giant cells to die, resulting in necrotic spots where females are located) (33) probably contributed to its hidden status.

Heterodera spp.

By 2006, 79 nominal *Heterodera* species had been described, of which about 25% (22) were described during the past two decades. Ten of these new species were described associated with plants in the Middle East, Asia, or Australia and New Zealand. Half of these new species (5) were described from South Asia (India and Pakistan).

Heterodera ciceri. *H. ciceri* was first described in 1985 (215) from chickpea and other leguminous crops in northern Syria. It has subsequently also been found on leguminous crops (lentil, pea, faba bean, etc.) in the Mediterranean Basin (Spain, Italy, Turkey, Lebanon, and Jordan). In some provinces in Syria, 30% of the surveyed fields were infested with *H. ciceri* (87). The damage caused by this nematode can be very high: The tolerance limit of chickpea to *H. ciceri* is only 1 egg/cm^3 of soil. Yield losses of 20% and 50% can be expected in fields infested with 8 or 16 eggs/cm^3 of soil, respectively, and complete crop failure can occur in fields infested with more than 60 eggs/cm^3 of soil (88). Although *H. ciceri* can be controlled effectively by crop rotation because of its narrow host range (174), there is a risk that this nematode species might spread eastwards to countries in South Asia where leguminous crops are produced on a large scale.

Pratylenchus spp.

By 2006, 76 nominal *Pratylenchus* species had been described. About 40% of these species (33) were described during the past two decades. Of these new species 26 or about 75% were described associated with plants in Central and South America, Africa, Asia, or Australia. More than half of these new species (8) were described from Asia.

For most of the 26 *Pratylenchus* species described since 1985 only the morphological description is available, sometimes supplemented with mostly DNA-based comparisons with related *Pratyenchus* species.

Radopholus spp.

By 2006, 30 nominal *Radopholus* species had been described, one third of these during the past two decades, all associated with plants in Africa, Asia, or New Zealand.

The genus *Radopholus* contains a small number of species whose geographical distribution is restricted at present but are potentially destructive pathogens because they can cause heavy crop losses.

R. citri was described in 1996 (117) from roots of citrus seedlings in Indonesia. In

pathogenicity experiments, populations of only 1000 nematodes per plant caused severe root degradation and significantly reduced plant growth. *R. duriophilus* was described in 2003 (139) from roots of durian in the Western Highlands of Vietnam, where there was tree decline and death of young trees.

Achlysiella williamsi

A. williamsi, another potentially damaging nematode species (115), was originally reported as *Radopholus similis*, which attacks sugarcane in Mauritius. In 1964, Siddiqi determined that the population from Mauritius represented a new species, which he described as *Radopholus williamsi*. In 1989, Hunt et al. (96) erected a new genus, *Achlysiella*, to accommodate *R. williamsi*, which has some remarkable morphological and biological features. Juveniles, males, and immature females are vermiform and resemble the vermiform stages of *Radopholus* species in all aspects. However, the mature females of *A. williamsi* become sausage-shaped on entering a sugarcane root and form a gelatinous egg sac. Unlike other nematode genera that have sausage-shaped females, such as *Rotylenchulus*, no permanent feeding sites or specialized trophic cells are formed, nor is there any swelling or galling of the root; rather, necrotic lesions, purplish in color and similar to those caused by other root-lesion nematodes, are evident on the root surface around the swollen females. *A. williamsi* has also been found in many localities in Papua New Guinea, a wide area of the Pacific region (Fiji, Samoa, Tonga, Tuvalu, Vanuatu), and Queensland, Australia. Stereomicroscopic analysis shows that *A. williamsi* females resemble *Rotylenchulus* females, which must have resulted in misidentifications. The nematodes can spread via infected rooted sugarcane cuttings.

Hirschmanniella spp.

By 2006, 30 nominal *Hirschmanniella* species had been described. Five of these species were described since 1985, all associated with plants in either the Carribean or Asia. Only the morphological description of these new *Hirschmanniella* species has been provided.

Hirschmanniella miticausa. *H. miticausa* was described in 1983 (23) from roots of taro in the Solomon Islands. This nematode causes a corm rot disease know as "miti-miti" (the name in pidgin English given to affected corms because of their similarity to uncooked fatty meat). The disease and nematode have been reported from four islands in the Solomon Islands group (133) and the highlands of Papua New Guinea (26). Miti-miti disease makes taro corms inedible and, when severe, can destroy almost all consumable corm tissue of the crop. The risk potential of *H. miticausa* is high because this nematode can cause heavy damage and can easily spread with infected planting material. In this respect it resembles corm rot of giant swamp taro, also reported from the Pacific (134), which is caused by *R. similis* and also has a high risk potential.

Ditylenchus africanus

D. africanus, the peanut pod nematode, was first found in hulls and seeds of peanut in South Africa in 1987. Nematode-infected pods show a black discoloration resembling black hull or black pod rot disease caused by the fungus *Chalara elegans* (107). A comparative morphometrical and morphological study first identified the nematodes isolated from the peanut pods as *Ditylenchus destructor*, the potato rot nematode (50). *D. destructor* was previously known mainly as an important pathogen of potato tubers and bulbs of flowers in temperate regions. Experiments showed that potato cultivars tested were poor hosts of the South African populations and that no damage was caused to potato tubers (55), and that the optimum temperature for development of the population was 28°C (54). Therefore, the South African

population was considered a different race and ecotype. A few years later, based on differences of morphology and RFLPs of rDNA, the South African population of *D. destructor* (isolated from peanut) was considered to be a new species and described as *D. africanus* (218).

D. africanus can survive, albeit in low numbers, without causing damage, on a variety of crops (11), although its main host is peanut. It has been found in all major peanut-producing areas of South Africa: Of 877 seed samples examined, 73% were infected with *D. africanus* (50). *D. africanus* affects the yield of peanut seeds by increasing premature germination before harvest, reducing fresh seed weight, and decreasing seed quality by increasing the number of blemished and unsound seeds (212). Its widespread distribution in South Africa suggests that it may also be present in other southern African countries, especially those neighboring South Africa. Peanut pods showing symptoms typical of *D. africanus* have been reported from Mozambique, Malawi, and Congo (53). In 1995, peanut seeds infected with a *Ditylenchus* species, originating from the Pacific, were intercepted in India. The nematode remained unnoticed in South Africa for so long because the symptoms it causes are very similar to those caused by the fungus *C. elegans* and the nematodes themselves have a weak stylet and resemble harmless fungivorous nematodes. *D. africanus* is a highly damaging nematode because its very short life cycle from egg to egg of only 6–7 days (54) enables it to build up extremely high population densities during the growing season (20). Also, *D. africanus* can survive dehydration and enter a state of anhydrobiosis (14). In pods left in the field, it can survive in the absence of host plants for at least 32 weeks; in whole seeds stored at 10°C it can survive for 24 weeks. Even if relatively few nematodes survive, those remaining are usually sufficient to build up large populations and to cause extensive damage. In stored seeds in which low numbers of *D. africanus* survive, the seeds may be symptomless, which may add to it being undetected and allow spread via contaminated seeds.

The symptoms caused by *D. africanus* and its biology are very similar to those of *Aphelenchoides arachidis*, the groundnut testa nematode, which has been found in peanut seeds in Nigeria (22). The experience with *D. africanus* indicates that *A. arachidis*, thought to be very localized in Nigeria, might also be much more widespread there and even in the surrounding countries than is presently recognized.

INTERACTIONS WITH OTHER PATHOGENS

Most plant-parasitic nematodes are active in the rhizosphere and in roots. Relative to other microorganisms present in the rhizosphere, nematodes are giants, often present in high numbers. When tens, sometimes hundreds, of nematodes attack a root system, they cause massive holes in the cell walls, not only creating openings for invasion by other pathogens but also leading to the massive leakage of plant metabolites in the rhizosphere that, in turn, will affect the other microorganisms present (209). Furthermore, plants attacked by nematodes will react with the production of defense-related chemicals that may also be involved in the defense-related reactions to attacks by viruses, bacteria, and fungi.

Our knowledge of disease complexes in tropical agriculture is very limited. The role of plant-parasitic nematodes in disease complexes is even less well understood, which is surprising because many plant-parasitic nematodes occur concommitantly with pathogenic microorganisms in the rhizosphere and in plant roots. In most disease complexes examined, the presence of plant-parasitic nematodes resulted in an increase in the incidence and/or damage caused by the other microorganisms present, although in a few instances, the presence of other pathogens resulted in a decrease in the reproductive and damage potential of the plant-parasitic nematodes. For example, on coconut, reproduction and damage caused by *R. similis* were

reduced in the presence of *Cylindrocarpon* spp. (184).

Most studies investigated the interactions between plant-parasitic nematodes and bacteria and fungi, but some also looked at interactions with other pathogens. In tobacco, the incidence of tobacco mosaic virus (TMV) may be greater when the roots are also infected with root-knot nematodes (146). In some of the mid-elevation (200–1000 m) tea-growing areas in Sri Lanka, a disease complex involving an insect and plant-parasitic nematodes causing yield decline has recently been observed (82). When the shot-hole borer (*Euwallaceae fornicatus*), the most serious insect of tea in this region, and the root-lesion nematodes *R. similis* and *Pratylenchus loosi* occur simultaneously, more damage is caused then when either of these pathogens occurs alone.

Bacterial and Fusarial Vascular Wilts

Vascular wilts are widespread and very destructive plant diseases in the tropics. The symptoms are rapid wilting, browning, and dieback of leaves and succulent shoots of the plants, followed by death of the whole plant. Wilts occur as a result of the presence and activities of bacteria or fungi in the xylem vessels of the plant. Root-knot nematodes are also involved in many vascular wilts in the tropics, which is not surprising since the induction of giant cells by these nematodes often disrupts the vascular plant tissues. The role of *Meloidogyne* spp. in vascular wilts is the most widely studied disease complex in the tropics involving plant-parasitic nematodes.

In general, vascular wilt symptoms are more evident when the bacteria or fungi occur together with root-knot nematodes. This has been observed in groundnut (145), coffee (137), tobacco (106), cotton (193, 194), and black pepper (176).

Often, the use of plant varieties resistant or tolerant to the causal agent is the only practical measure for controlling vascular wilts in the field. Breakage of resistance or tolerance to bacterial and fungal wilt by root-knot nematodes has been observed in tomato (39, 56, 104, 180), cowpea (164, 204), and cotton (193).

Synergistic effects between *Fusarium* spp. causing vascular wilts and plant-parasitic nematodes other than root-knot nematodes were observed in pigeon pea where wilt caused by *Fusarium udum* increased significantly when *H. cajani* was present (181) and in black pepper where *R. similis* may play an important role in yellow disease in which *Fusarium solani* also appears to be involved (135, 136). On black pepper, *R. similis* may also play a role in a slow wilt disease in which *Phythophtora capsici* also appears to be involved (4, 157, 158).

Other Field Diseases

Root-knot nematodes have also been observed to increase the incidence and severity of *Phytophthora parasitica* var. *nicotiana*, the causal agent of black shank on tobacco (106); *Aspergillus flavus* on groundnut (127); *Cylindrocladium parasiticum* on peanut (47, 59–61); *Macrophomina phaseolina* on cowpea (58); *Rhizoctonia solani* on cotton (28), coffee (185), and cowpea (113); and *Sclerotium rolfsi*, the causal agent of southern blight on peanut (165, 166). By contrast, no interaction was detected between *S. rolfsii* and *Meloidogyne arenaria* in microplots (195) or between root-knot nematodes and *Thielaviopsis basicola*, the causal agent of black root rot on cotton (217).

Infection of plant roots by root-knot nematodes may also affect the incidence of other pathogens on above-ground plant parts. In tobacco, for instance, infection by *M. incognita* predisposed plants to brown spot caused by *Alternaria alternata* (177), while synergistic effects between plant-parasitic nematodes and other pathogens were also observed above ground. Rice plants infected with *D. angustus* and *A. besseyi* were more susceptible to rice blast caused by *Pyricularia oryzae* and stem rot caused by *Sclerotium oryzae* (122, 132).

Storage Diseases

The synergistic effects between plant-parasitic nematodes and other pathogens have been studied mainly on stored root tubers. In cassava, infection of stored roots by *M. incognita* substantially increased the incidence and severity of damage caused by *Botrodiplodia theobromae*, one of the main causal agents of root rot in cassava (24, 62). In yam, there are indications that dry rot is caused by a bacterium (*Corynebacterium* sp.) in association with the nematode *Scutellonema bradys*, which acts as a wounding agent (65), whereas roots infected with *Meloidogyne* spp. and *P. coffeae* are more prone to bacterial and/or fungal rot during storage than are tubers free of the nematodes (8, 26, 41).

EXAMPLES OF THE EFFECTS OF CHANGES IN AGRICULTURAL PRACTICES ON ENVIRONMENTAL AND SOCIOECONOMIC CONDITIONS AND POLICY ON NEMATODE PEST STATUS

Worldwide, land use and agricultural practices are rapidly changing as a result of the continuing growth of the human population, intensification of agricultural production, new agricultural developments, the unprecedented movement of plant-derived commodities around the globe, and climatic change. The repercussions of these changes on the occurrence of plant-parasitic nematodes and consequent damage and yield loss to tropical crops are largely undocumented. However, knowledge of and insight into these effects are needed to undertake timely actions to predict and prevent future damage and yield loss that plant-parasitic nematodes may cause.

Change can be studied either by long-term field observations or by comparing gradients along a transect. Such studies are rare in the tropics and when undertaken the monitoring of the population dynamics of plant-parasitic nematodes is seldom included. However, when plant-parasitic nematodes are also monitored, the results of these studies can be highly informative as seen in the following two examples from the semiarid tropics.

In Mexico, a long-term field experiment with zero tillage under rainfed conditions was initiated in 1991 by agronomists of the International Maize and Wheat Improvement Center (CIMMYT) at its semiarid highland experiment station to evaluate the effects of tillage, residue management, and rotation on maize and wheat production. From 1998–2003, the long-term effects on nematode populations densities and their effects on yield were monitored (86). Crop residue retention reduced the numbers of the nematode *Pratylenchus thornei* and increased yields in both maize and wheat, as did zero tillage compared with conventional tillage. Conventional tillage with continuous residue removal, the common farmer practice in the densily populated and intensively cropped subtropical highlands of Mexico, dramatically increased population densities of *P. thornei* and reduced yields.

In Senegal, ecologists of the French Institut de Recherche pour le Développement (IRD) examined the soil nematode communities, including plant-parasitic nematodes, along a rainfall and human density gradient transect, 900 and 750 km in length, respectively (29). This study led to the conclusion that soil type was the most important factor affecting the species composition of the nematode community and that, as a result, nematode communities followed a distribution in areas corresponding to the successive soil types but did not change in relation to the climatic or human density gradient. No effects were observed of short-term fallows on the occurrence and abundance of ectoparasitic plant-parasitic nematodes compared with the natural nematode community of fields located in the immediate vicinity, whereas the influence of human disturbance on the occurrence and abundance of nematode seemed to be compensated for by greater crop diversity, mainly near towns.

Meloidogyne graminicola

A prime example of how a combination of agricultural, environmental, socioeconomic, and policy changes can affect the pest status of a plant-parasitic nematode in the tropics is illustrated by *M. graminicola* on rice in Southeast Asia. A combination of socioeconomic and environmental (climate) changes is responsible for increasing water shortages, not only increasing the cost of rice production but also severely limiting yields of rice, thus threatening food security. Rice production, especially in the lowlands, has raised international concern since the traditional paddy production system consumes large amounts of water, and in many areas of Southeast Asia the water requirement is too high to sustain this type of rice production. Furthermore, competing demand for urban populations and industry impose legal restrictions in the use of water for agricultural purposes; thus, the amount of arable land available for the cultivation of lowland rice with its inherently high water demand is being reduced. In Asia, out of a total area of 79 million ha of irrigated paddy rice, 17 million ha may experience physical water scarcity and 22 million ha economic water scarcity by 2025. Thus water-saving rice production systems, such as direct wet seeding, intermittent irrigation, cultivation on raised beds, and the cultivation of aerobic rice varieties, are being developed and increasingly implemented. However, observations increasingly indicate that the large-scale introduction of these techniques is favoring the development of high populations of *M. graminicola*, drastically increasing its economic significance.

M. graminicola was first described in 1965 from grasses and oats in Louisiana (85). It has since been found on rice mainly in South and Southeast Asia but also in South Africa, United States, Colombia, and Brazil.

M. graminicola is equally prevalent on upland (rainfed) or lowland (irrigated) as on deepwater rice. It causes swellings and galls throughout the root system. Infected root tips become swollen and hooked, a symptom characteristic of this nematode species. In upland conditions and shallow intermittently flooded land, *M. graminicola* is considered to be by far the most damaging *Meloidogyne* species on rice. In *M. graminicola*-infested upland rice fields, nematicide application resulted in a yield increase of 12%–33% in Thailand (7) and 28%–87% in Indonesia (138), whereas under simulated upland conditions, yield losses from *M. graminicola* ranged from 20% to 80% (147, 155, 203). In *M. graminicola*-infested lowland rainfed rice, nematicide application resulted in a yield increase of 16%–20% in Bangladesh (144), and in simulations of intermittently flooded rice, yield losses from *M. graminicola* ranged from 11% to 73% (183).

M. graminicola is well adapted to flooded conditions enabling it to continue multiplying in the host tissues even when the roots are deep in water. Second-stage juveniles (J2s) invade rice roots in upland conditions just behind the root tip (163). They cannot invade rice in flooded conditions but quickly invade when infested soils are drained (118). Females develop within the roots and eggs are laid mainly in the cortex (168) as in most other *Meloidogyne* species. However, the J2s of *M. incognita* can remain in the maternal gall or migrate intercellularly through the aerenchymatous tissues of the cortex to new feeding sites within the same root (25). This behavior appears to be an adaptation to flooded conditions.

Although numbers of *M. graminicola* decline rapidly after 4 months, some egg masses and J2s can remain viable for at least 5–14 months in waterlogged soils (25, 169). This nematode species has a very short life cycle, less than 3 weeks at 22–29°C for a population from Bangladesh (25), and thus even a low number of surviving *M. graminicola* can build up high population densities during a single crop cycle. *M. graminicola* also has a wide host range that includes many of the common weeds of rice fields (116) and can

also be damaging to agricultural crops that are grown in rotation with rice, such as onion (80, 81).

The options to control *M. graminicola* are still limited. Only continuous flooding appears to be effective (114), although yield losses may be minimized when the rice crop is flooded early and kept flooded until a late stage of development (79, 183). Resistant cultivars hold out the most promise for effective and economic control. Genotypes resistant to *M. graminicola* have been found in *Oryza glaberrima* and *Oryza longistaminata* (148, 182). Rice breeders at the International Rice Reseach Institute (IRRI) in the Philippines are in the process of producing introgressed lines of resistant accessions of *O. glaberrima* in *O. sativa*. (R. Reversat & D.S. Brar, personal communication).

CONCLUSIONS

During the 22nd International Symposium of the European Society of Nematologists in Ghent, Belgium, in 1994, a colloquium on tropical nematology was held. Weaknesses and needs of tropical nematology were summarized as (*i*) limited basic knowledge, (*ii*) lack of tropical nematologists active in research, (*iii*) limited collaboration, (*iv*) lack of communication between temperate and tropical nematologists, and (*v*) lack of awareness among farmers, agricultural scientists, extension officers, and decision makers (154).

These weaknesses and needs are still valid. Nevertheless, progress has been made in some areas. For example, since 1992 190 young scientists from 41 developing countries have been trained in nematology in the Postgraduate International Nematology Course organized at the University in Gent, supported by funds provided by the Belgian Government to the Flemish Interuniversity Council. Another example is the project (2005–2010) to build capacity in plant nematology in East and Southern Africa funded by the Gatsby Charitable Trust. National agricultural research centers from Kenya, Uganda, Tanzania, Malawi, and Zimbabwe are to participate in collaboration with Rothamstead International, the University of Reading, and CABI Bioscience in the United Kingdom.

Dr. Joe Sasser, an excellent nematologist and visionary, conceptualized, organized, and implemented the widely acclaimed International *Meloidodogyne* Project [1975–1983] (172). This project, funded by USAID, aimed to coordinate and promote research on root-knot nematodes in many regions of the world. About 200 nematologists from 70 countries, organized into eight project regions, participated. This project not only increased our knowledge on the taxonomy, biology, diversity, and ecology of root-knot nematodes but also it stimulated collaboration among the participants. Although there have been a number of international nematology projects since then, such as the *Musa* Nematologists' Consortium (1994–1998) funded by CFC/World Bank/FAO (49) and the European Union-funded study on the occurrence and importance of root-knot nematodes and their parasite *Pasteuria penetrans* (206), more of these projects are needed, in conjunction with multidisciplinary collaborations between tropical plant nematologists and agronomists, soil scientists, plant pathologists, breeders, molecular biologists.

Finally, relatively recent technological developments such as the Internet have enabled fast and easy long-distance communication, and the interaction between tropical and temperate nematologists has certainly improved recently. Nevertheless, nematologists working in tropical areas still have problems in accessing papers published in expensive journals in the north, and papers published in local or regional journals in the tropics are often difficult to obtain by nematologists from the north, as we have experienced during the writing of this review. Access to all the information published is a prerequisite for progress in any research area. Therefore, a good initiative should be to make pdf files of past issues of journals from the tropical regions, such as the *Indian Journal of Nematology*, *Afro-Asian*

Journal of Nematology, and the *International Journal of Nematology*, available via the Internet, as has been done, for example, for past issues of *Nematropica*.

SUMMARY POINTS

1. Farmers' unawareness of nematodes, the occurrence of multispecies nematode populations, and the complexity of planning and carrying out nematode surveys make it difficult to determine the extent of nematode problems.
2. The absence of sufficient data on the impact of nematode species on agricultural crops prevents the timely identification of emerging nematode problems.
3. Because of misidentification, important and damaging nematode species may remain unnoticed for a long time.
4. The application of molecular diagnostics has made uncertain the concept of what constitutes a nematode species. Unresolved uncertainties concerning the validity of nematode species result in practical problems related to quarantine measures and nematode management.
5. The role of nematodes in tropical disease complexes is largely unknown.
6. In most disease complexes studied, the presence of nematodes increased the pathogenic effects caused by the other micoroorganisms present.
7. The effects of change on the occurrence and damage potential of tropical nematodes are seldom monitored.
8. International collaboration between nematologists from tropical and temperate regions is not intensive enough. Multidisciplinary collaboration falls short between tropical plant nematologist and agronomists, soil scientists, plant pathologists, breeders, and molecular biologists.

FUTURE ISSUES

1. Farmers' awareness for nematodes should be increased by training agricultural extension workers in the basics of plant nematology.
2. Yield loss studies carried out under the most common production conditions and over several crop cycles are necessary to demonstrate the damage and yield loss potential of the predominant nematode species.
3. The description of new plant-parasitic nematode species should be based on a consensus of all available data and information, including the ability of populations to infect host plants (polyphasic taxonomy).
4. The taxonomy of nematode species complexes involving tropical plant-parasitic nematodes should be studied in the framework of international collaboration between nematologists from the tropics and temperate regions.
5. The role of plant-parasitic nematode species in tropical disease complexes awaits quantification.

6. Long-term studies of the effects of change on the occurrence, damage and yield loss potential of the predominant nematode species are required.
7. Greater international collaboration and projects between nematologists from the tropics and nematologists from temperate regions are needed, as are more multi-disciplinary studies between tropical nematologists and agronomists, soil scientists, plant pathologists, breeders, and molecular biologists.
8. Nematological publications published in the tropics should be more easily accessible.

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