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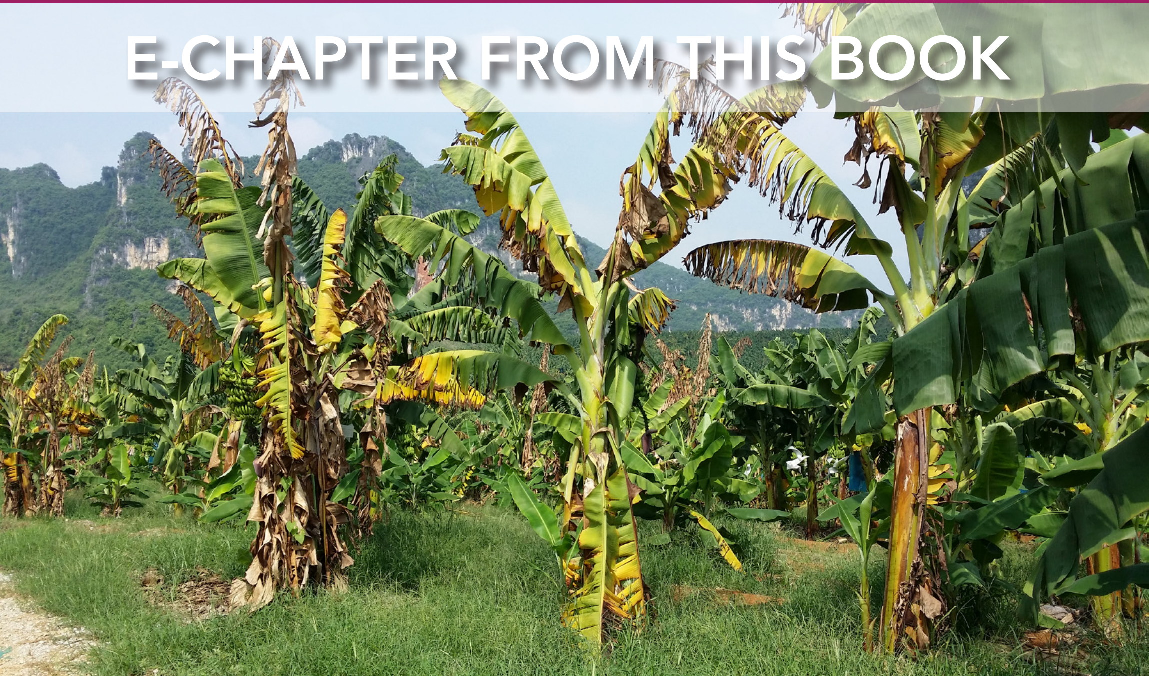

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Nematodes in banana

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1 Introduction

Banana and plantain (*Musa*) is the fourth most important global food crop and is produced in 130 tropical and subtropical countries (FAO, 2020). Banana production has increased in the last few decades from an estimated 69 million metric tonnes in 2000–2002 to 116 million metric tonnes in 2017–2019 with an approximate value of US$31 billion (FAO, 2020). However, just 15% of total global banana production is traded on the international market where it represents a considerable portion of export revenue for many Latin American and Caribbean countries. It is an essential source of income and employment for many households in these regions. Production for export accounts for about 22 million tonnes (FAO, 2021), while the remainder is consumed domestically, providing a substantial source of nutrition and food security for more than 400 million people, mostly in producing countries in Africa, Asia, and Latin America (FAO, 2020; Voora et al., 2020). Sub-Saharan African countries, which produce one-third of the world's bananas, depend on banana both as their staple food and as a source of income.

Various banana genotypes are available, but the main variety worldwide is Cavendish (AAA) as it is the only export variety and accounts for approximately 47% of global production (Kema et al., 2021). In sub-Saharan Africa, especially

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East and West Africa, other banana varieties such as plantains and eastern highland cooking bananas (EAHB) are used more frequently and make up about 70% of the crop grown in the continent (Dale et al., 2017; Kikulwe and Asindu, 2020). Elsewhere in Asia, banana is not consumed as a staple food and a much more diverse range – from starchy to sweet banana material – is consumed (Dale et al., 2017).

Yields in different parts of the world differ greatly (Table 1). Reasons for these differences are the use of different banana types and varieties, which are divided between Cavendish type bananas and 'plantains and others' (FAOSTAT, 2022). Another important factor is the use of two different production systems – commercial versus smallholder farming systems. While in commercial systems, fertilizer, irrigation, and pesticides are recommended to be applied regularly, this is very different in smallholder farming systems. In the latter, yields are drastically lower (Table 1) due to no or very limited fertilizer applications, drought, and poor soil conditions as well as bacterial and fungal diseases. In both farming systems, nematodes also play a considerable role in reducing yields.

Table 1 Yield data (t/ha/year) on the average values for 2018–2020 for Cavendish and plantain and others per country (FAOSTAT, 2022)

Country	Banana	Plantain and others	Country	Banana	Plantain and others
Central and Latin America			**Australasia**		
Brazil	14.68	–	China	33.38	–
Costa Rica[a]	47.51	10.50	Taiwan	23.35	–
Dominican Republic[a]	42.06	21.11	India	35.30	–
Honduras[a]	51.64	12.16	Indonesia[a]	55.71	–
Colombia[a]	26.08	8.52	The Philippines	32.55	11.92
Ecuador[a]	37.89	5.88	Malaysia	14.41	–
Haiti	4.89	6.49	Australia[a]	29.55	–
Europe					
Spain[a]	44.22	–	Papua New Guinea	16.11	–
Africa					
Benin	4.87	–	Uganda	–	4.24
Cote d'Ivoire[a]	44.70	3.76	Kenya	22.50	12.06
Cameroon	13.03	14.22	Zambia	4.45	–
Ghana	11.28	11.15	Malawi	30.82	10.29
Nigeria	–	6.25	South Africa[a]	60.91	–

[a] Indicates mainly commercial farming systems especially for Cavendish bananas.

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2 Plant-parasitic nematodes

Nematodes are major economic pests that need to be managed to ensure sustainable fruit production. It is estimated that parasitism by nematodes results in yield losses of 30–60% of bananas globally (Sikora et al., 2018). According to Tripathi et al. (2015), plant-parasitic nematodes cause losses of up to 70% in plantains and cooking bananas in Africa. In South Africa, damage by plant-parasitic nematodes was estimated to result in yield losses of 19% (Willers, 1998), while yield losses of 30–50% were projected in Costa Rica and Panama (Davide, 1995).

Banana roots are attacked simultaneously by several plant-parasitic nematode species, with the most important being *Radopholus similis*, *Pratylenchus goodeyi*, *Pratylenchus coffeae*, and *Helicotylenchus multicinctus* but also including sedentary endo-parasites such as *Meloidogyne* and *Rotylenchulus reniformis*. There are many other species associated with banana roots, but they are currently not considered serious pests for banana (Gowen et al., 2005; Daneel and De Waele, 2017).

2.1 Burrowing nematode

The most damaging and widespread banana nematode is *R. similis*, commonly known as burrowing nematode.

2.1.1 Life cycle and symptoms

Burrowing nematodes are a migratory endo-parasite that spend their entire life cycle of about 20–25 days inside the root and rhizome tissue of the banana plant (Sikora et al., 2018) (Fig. 1a). Females and all juvenile stages are infective and cause damage to the root tissue, while males when present do not cause damage. Eggs are deposited in the root tissue and the females lay one to six eggs per day.

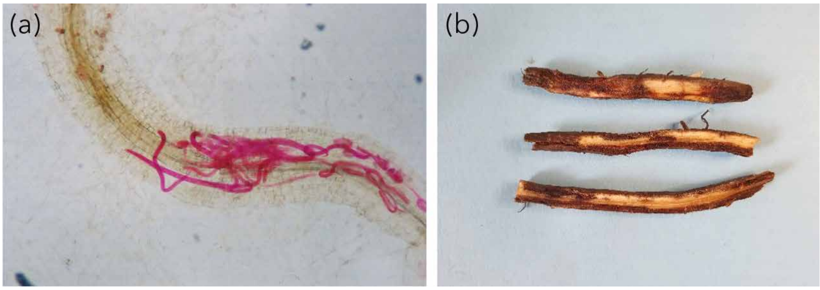

Figure 1 (a) *R. similis* coloured using the Byrd et al. (1983) method in the roots of bananas. (b) *R. similis* damage in the cortex of the roots.

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Figure 2 Plants fallen over due to *R. similis* in combination with wind damage.

Figure 3 Pseudostem with typical burrowing nematode damage showing leaves not releasing from around the pseudostem.

Burrowing nematodes enter the soft roots at the root tip or in the region where hair roots are produced, rather than through hardened, old, or decaying roots. It normally takes less than 24 h to enter the roots. They do not normally leave the root tissue, except when moving out of decaying roots or in case of overcrowding. They then move to healthy roots and infect adjacent plant material (Haegeman et al., 2010).

As the nematodes move inside the root tissue, lesions enlarge and coalesce and symptoms in the roots are expressed as necrosis and reddish lesions in

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the internal tissue, including root cortex and, rarely, stele of the roots (Fig. 1b). Burrowing nematode damage in the roots restricts nutrient and water uptake, resulting in yellowing of the leaves, stunted plant growth and lack of vigour, reduction in the number and size of leaves, leaves not releasing from around the pseudostem, smaller bunches, longer time between ratoons, and toppling of the plants due to poor anchorage in the soil (Gowen et al., 2005; Quénéhervé, 2008) (Figs. 2 and 3). The presence of nematodes also results in a shorter plantation life (Coyne et al., 2022).

2.1.2 Distribution and spread

R. similis occurs throughout the banana-producing areas worldwide and prefers temperature ranges between 24°C and 32°C, with an optimum temperature for reproduction of 30°C and altitudes less than 1400 m above sea level (Kashaija et al., 1994; Sarah et al., 1996; Coyne and Kidane, 2018). *R. similis* is also commonly found in subtropical regions such as South Africa (Daneel and De Waele, 2017) and Australia (Pattison et al., 2002). Several biotypes of *R. similis* exist and their pathogenicity differs depending on their rate of reproduction (Tarté et al., 1981; Kaplan et al., 2000; Cobon and Pattison, 2003).

Although *R. similis* has many alternative hosts (Sarah et al., 1996), *Musa* and *Ensete* are two of the most important, which have helped the distribution of this nematode throughout the world with plant material, for example, suckers and rhizomes (O'Bannon, 1977). The use of tissue culture planting material is limiting its distribution and it is probably also the reason why *R. similis* is not present in areas such as Israel, the Canary Islands, the Cape Verde Islands, Cyprus, Crete, Mauritius, Taiwan, the highlands of Eastern Africa, most of South Africa, Mozambique, and parts of southern Mexico (Wehunt and Edwards, 1968; Stover, 1972; Gowen and Quénéhervé, 1990). Another reason for its limited spread within certain countries such as South Africa is the presence of strict quarantine regulations prohibiting the movement of sucker material between regions and even farms (Daneel and De Waele, 2017).

2.1.3 Control strategies

In tropical regions, *R. similis* can produce up to four generations per year, while in subtropical regions this is significantly less due to a colder winter period in which both plant and nematode are much less active. The potential for crop losses is therefore much higher in tropical regions, requiring more extensive control activities underpinned by a larger amount of research on this topic (Araya and Lakhi, 2004; Jesus et al., 2015; Salguero et al., 2016).

Burrowing nematodes are controlled using different strategies, depending on commercial or smallholder farming systems. In commercial systems,

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chemical control is the main control strategy, although biological control and cultural practices are also used. The number of applications of nematicides or biologicals depends on whether plantations are situated in tropical or subtropical regions, the amount of nematodes present, and the additional control strategies implemented in management strategies. For organic farmers, other options have to be followed, including the addition of organic material such as banana waste material, manures, and mulches (Ngosong et al., 2019). In smallholder farming systems, often no control is practised, although the use of paired or hot water-treated rhizomes is recommended (Coyne et al., 2010).

2.2 Root lesion nematodes

Another migratory endo-parasitic nematode infecting banana roots and rhizomes is *Pratylenchus* or root lesion nematode. Two species commonly found are *P. coffeae* and *P. goodeyi*.

2.2.1 Life cycle and symptoms

Pratylenchus are migratory endo-parasitic nematodes that feed on the cortex of banana, plantain, and *Ensete* roots, resulting in brown to purplish necrotic lesions in the cortical and epidermal tissue where they feed and multiply. All stages of these nematodes can invade the roots while eggs are laid in the root tissues or in the soil. After entering the roots, lesion nematodes migrate between and within the cells in the cortex, parallel to the stele. Cavities that coalesce are caused by feeding on neighbouring cells (Pinochet, 1978). The damage described by Pinochet (1978) is similar to *R. similis* damage described by Blake (1961, 1966), except for the absence of cell enlargement or increase in size of cell nucleus or nucleolus. The average life cycle from egg to egg is about 27 days at a temperature range of 25–30°C.

Symptoms caused by lesion nematode damage are due to reduced nutrient and water uptake resulting in chlorosis, stunting, lengthening of the vegetative cycle, reduction in leaf size and number, smaller bunches, and toppling. Above- and below-ground symptoms of lesion nematode damage are similar to damage caused by burrowing nematodes.

2.2.2 Distribution and spread

Pratylenchus, similarly to *R. similis*, is generally spread through the distribution of infected planting material (Gowen et al., 2005).

P. coffeae has a wide host range and distribution in most tropical and subtropical countries, but its impact is more localized than *R. similis* (Sikora et al., 2018). In some areas such as the Pacific Islands, it is the most important

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pest species of banana, while in other areas it is more specific to certain varieties. In Thailand, it affects Pisang Awak (ABB), while in Honduras it is the most important nematode species affecting Cavendish cultivars (AAA). In Ghana, losses of up to 60% in plantain production have been reported (Bridge et al., 1997; Burke et al., 2015). In Gabon, *P. coffeae* is the most dominant species (Loubana et al., 2007). In East Africa, the species is becoming a more important pest (Seshu-Reddy et al., 2007; Luambano et al., 2019), while in West Africa, *P. coffeae* has already replaced *R. similis* (Coyne, 2009). In South Africa, *P. coffeae* is endemic and found in most banana-producing areas in contrast to *R. similis*, which is not present in all areas (Daneel and De Waele, 2017).

P. goodeyi is mostly limited to the Afromontane highlands of Africa and is usually associated with higher altitudes and lower temperature ranges of 16–21°C (Kashaija et al., 1994; Pinochet et al., 1995; Price and Bridge, 1995). In Uganda and Kenya, the species is found only at altitudes of 1600 m above sea level or higher. In a study conducted in Cameroon, *P. goodeyi* was found in altitudes ranging from 800 m or more above sea level (Loubana et al., 2007). *P. goodeyi* is a major pest of highland bananas (EAHB) in East Africa and *Ensete* in Ethiopia (Kashaija et al., 1994; Bridge et al., 1995). The species is the main nematode pest in the Canary Islands (Guiran de and Vilardebo, 1962). *P. goodeyi* has been detected in association with banana in Egypt, Madeira, Crete, and Australia (Oteifa, 1962; Vovlas et al., 1994; Bridge et al., 1997). It is, however, worth noting that *P. goodeyi* distribution is shifting as this species has been detected more recently in hot tropical areas in Kenya (Seshu-Reddy et al., 2007) and Tanzania (Luambano et al., 2019).

2.2.3 Control strategies

Control strategies for lesion nematodes are similar to burrowing nematodes as it is also a migratory endo-parasite of banana that spends most of its life cycle inside the roots of the banana plant.

2.3 Spiral nematodes

Spiral nematodes or Hoplolaimidae is a large family consisting of many genera, among which *Helicotylenchus* is probably the most widely distributed. *Helicotylenchus* has many species but, in banana, *H. multicinctus* is the most damaging.

2.3.1 Life cycle and symptoms

Most spiral nematodes are ectoparasites, but *H. multicinctus* is considered a migratory endoparasite since the juveniles, adults, and eggs can be found in

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Figure 4 Spiral nematode damage in roots, showing dark necrotic lesions in the outer cortex.

the cortex of the plant root (Strich-Harari and Zuckerman, 1964). They feed on the cytoplasm of cells close to the epidermis (Blake, 1966) and cause cellular damage that is seen as small and shallow necrotic lesions in the outer cortex of the roots (Quénéhervé and Cadet, 1985) (Fig. 4). Females lay eggs in roots that hatch within 5–6 days; they have three more moults into third, fourth juvenile, and then adult stage. The different life stages are very similar to the adult except for size. Their life cycle is approximately 32 days in optimal conditions (Southey, 1986).

Typical plant-parasitic nematode damage symptoms include stunted plants and reduction in plant and bunch size. Toppling can be seen in severe *H. multicinctus* damage, but this is rare since it is mostly found in combination with other plant-parasitic nematodes.

2.3.2 Spread and distribution

H. multicinctus is commonly found in banana-growing areas and is regarded as an important parasite of bananas, especially in subtropical regions where conditions are suboptimal for banana production (McSorley and Parrado, 1986; Quénéhervé, 2009). However, it is difficult to estimate crop losses caused by this species since *H. multicinctus* is very seldom found on its own. In Uganda, a study was conducted where *R. similis* and *H. multicinctus,* both as a single and mixed population, were evaluated for nematode damage and only *R. similis* had a significant correlation with root damage (Barekye et al., 2005). In South Africa, *H. multicinctus* and *Meloidogyne* are the most common nematodes found in banana; however, damage is limited (Daneel et al., 2015; Daneel and De Waele, 2017). Coyne et al. (2018) found that *H. multicinctus* is commonly associated with *Musa* and when in combination with *Meloidogyne*, it can cause severe damage to plantains, particularly in West and Central Africa.

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2.3.3 Control strategies

Control strategies are not specifically targeted at spiral nematodes but rather for the nematode complex found in the plantations. Strategies include those described above.

2.4 Root-knot nematodes

Meloidogyne or root-knot nematodes are also commonly reported in association with banana and plantain; however, the genus is not considered an important pest of these crops. Root-knot nematodes are mostly found together with other plant-parasitic nematodes such as *R. similis* or *Pratylenchus* spp., which result in more severe damage symptoms than *Meloidogyne* can cause alone (De Waele and Davide, 1998).

2.4.1 Life cycle and symptoms

Root-knot nematode infestations result in gall formation on the roots, as can be seen in Fig. 5. The life cycle of *Meloidogyne* ranges from 4 to 6 weeks, depending on climatic conditions and species present (De Waele and Davide, 1998). It consists of an egg, four juvenile stages, of which the J2 stage is the only mobile stage, while the other juvenile stages stay sedentary and swell while developing into the adult female. Some juveniles can develop into vermiform males. The J2 moves towards the roots where it penetrates the root tip, or it moves close to other penetration sites or where minor wounds are present. It enters the endodermis and when entering the stele, it induces multinucleate giant cells on which the J2 feed. Surrounding this tissue, it induces the multiplication of cortical cells, resulting in gall formation (De Waele and Davide, 1998).

Above-ground symptoms are similar to other banana nematodes. However, Rabie (1991) reported that, in combination with stress factors such as drought and/or cold temperatures, root-knot nematodes were involved in inflicting

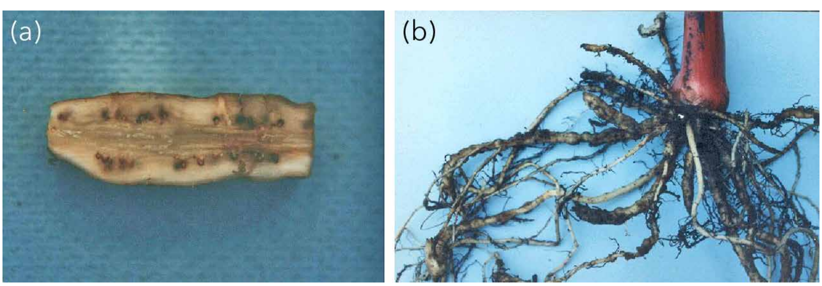

Figure 5 (a) Root-knot nematode damage on inside of roots. (b) Root-knot nematode damage on small tissue culture plants.

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symptoms described as 'false panama disease'. The symptoms, like panama disease, included progressive dying back of older leaves starting at the tip. Further investigation showed that galls occurred in the primary and secondary roots and distortion and bifurcations were visible due to severe infection with rhizomes showing brown-purple to reddish-brown discolouration.

2.4.2 Spread and distribution

Although *Meloidogyne* is found worldwide, root-knot nematodes are only predominant in banana when the climate is too cold for *R. similis*, or burrowing nematodes have not been introduced or *P. goodeyi* is not present, which includes subtropical areas such as South Africa, Mediterranean areas such as Crete and Lebanon, tropical regions situated at higher altitudes such as the Andes in Colombia, and in lowlands in Africa where *R. similis* has not been introduced (e.g. Ghana, Tanzania). In Southeast Asia, root-knot nematodes are often the most common and abundant nematode species of many native diploid and triploid varieties grown and they are also predominant in Cavendish bananas in the Philippines (De Waele and Davide, 1998). In South Africa, root-knot nematodes are the most common plant-parasitic nematodes recorded to parasitize roots and rhizomes of mostly younger banana plants, although damage is limited to these younger plants (Daneel et al., 2015; Daneel and De Waele, 2017).

As for other banana nematode parasites, root-knot nematodes can be distributed through infected planting material. However, due to their extremely wide range of host plants, they are present in most agricultural areas and can infect bananas directly.

2.4.3 Control strategies

As for other species, root-knot nematode damage is not treated on its own, but the entire nematode complex is managed.

2.5 Species complexes

The two lesion nematodes do not commonly occur together, although there have been instances where both *Pratylenchus* species were found to have infected banana (Araya et al., 2002). *Pratylenchus* does occur in mixed populations with *Meloidogyne* spp., *H. multicinctus*, and *R. similis*, and the most dominant species differ per country as can be seen, for example, in the study by Loubana et al. (2007) where the species complex differed between Cote d'Ivoire, Gabon, and Cameroon.

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Nematode damage in the roots restricts nutrient and water uptake, resulting in leaf yellowing, stunted plant growth and lack of vigour, reduction in the number and size of leaves, retarded growth, smaller bunches, longer time between ratoons, and toppling due to poor anchorage (Gowen et al., 2005; Quénéhervé, 2008).

3 Control of nematodes

To ensure sustainable banana and plantain production, plant-parasitic nematodes need to be managed in both commercial and smallholder farming systems. Besides chemical (Quénéhervé, 2009; Salguero et al., 2016; Coyne et al., 2018) and biological control (Shanti and Rajendran, 2006; Koffi et al., 2013; Olaniyi, 2014; El-Nagdi et al., 2015; Su et al., 2017), other alternative strategies to control or manage nematodes include the use of clean planting material, heat treatment of planting material, clean soil, cover crops, or alternate cropping, fallowing, flooding, resistant or tolerant plant material, transgenic resistance, and the addition of organic material (Quénéhervé, 2008; Coyne et al., 2010, 2018; Tabarant et al., 2011). These practices can be used on their own, but more often in combination to improve their effectiveness. More details on sustainable management strategies are presented elsewhere in this book.

3.1 Alternate cropping systems

Most smallholder farmers do not fallow or use cover cropping due to insufficient land and the potential loss due to lower or no production (Tripathi et al., 2015). Another challenge is that most nematode species associated with banana have a wide host range; therefore, a plant might be resistant to one species but not another. Examples of cover crops that have been successful in suppressing plant-parasitic nematodes include *Crotolaria juncea* and *Tagetes* spp. (Wang and Hooks, 2009). Furthermore, a wide range of plant species with resistance to *Meloidogyne* exist, but in banana production systems this might not be helpful, since *Meloidogyne* is only of limited importance in terms of causing nematode damage in banana. The literature suggests that long-term rotation with sugarcane reduced *R. similis* populations (Robinson and Galán Saúco, 2010), while other plants can also be planted between two consecutive banana crops such as Guinea grass + Siratro (Colbran, 1964), Pangola grass (Smith and Thames, 1969), Sudan grass (Milne and Keetch, 1976; Ternisien and Melin, 1989), horse bean (Zem and Lordello et al., 1983), and Jarra digit grass (Hall et al., 1993).

Sarah (1989) recommended an extended natural fallow followed by growing groundnut for a 3–4-month period. Alternatively, the weed, *Chromolaena*

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odorata, could be used as a cover crop to reduce *R. similis* populations from the soil before the replanting of dessert bananas (Sarah, 1989). However, in Cameroon, in a maize and groundnut alternating cropping system, heavy *R. similis* infestations were observed in the subsequent plantain crop (Price, 1994). Quénéhervé (2009) found that when alternating crops such as maize and okra, groundnut and soybean, and sweet potato and amaranth were planted, only the latter combination was able to suppress *R. similis* for almost 18 months. Conversely, significant yield differences were observed for all the alternate cropping systems compared to a permanent plantain crop.

There is currently no easy solution available to reduce the population densities of plant-parasitic nematodes in banana and plantain roots and rhizomes. Effective control of plant-parasitic nematodes also depends on many factors, including climate, nematode community complex, and *Musa* material, to name just a few.

3.2 Agro-ecosystems biodiversity

Changes in the distribution of nematode species may be used as an alternative approach to reduce the potential impact of the nematode complex in bananas. For example, *P. goodeyi* is less damaging to banana than *R. similis* (Talwana et al., 2003; Coyne et al., 2018), so by replacing *R. similis* with *P. goodeyi,* root damage might be reduced.

Similarly, *H. multicinctus* is less damaging than *R. similis* (Barekye et al., 2005; Coyne et al., 2013), while both species are found in the same niche (Tixier et al., 2006, 2008; Quénéhervé, 2008; Duyck et al., 2009). If the contribution of each species to this nematode complex can be changed, banana root damage might be reduced (Duyck et al., 2009, 2011). By using the cultivar FB920, Tixier et al. (2008) were able to show that *H. multicinctus* could outcompete *R. similis*, while the total nematode numbers of the two species combined were lower as well. This could result in lower damage and less need for pesticides.

Changing agro-ecosystems can increase biodiversity, but it is important to understand the interactions between the different nematode species in such niches as well as gaining knowledge about plant–nematode interactions. By modifying the abundance of host plants, the balance of nematode species can be changed (Duyck et al., 2009). Other factors that play a critical role in species composition and niche partitioning are type of soil, climatic factors, and cultivars (Duyck et al., 2009, 2011; Quénéhervé et al., 2011). Research points to information on using multiple banana varieties as another option to enhance biodiversity and reduce nematode damage (Quénéhervé et al., 2011), while Poeydebat et al. (2017) looked at plant richness and the effect on nematode damage. However, the number of nematodes is not always reduced, as was

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shown by Poeydebat et al. (2017), where higher plant biodiversity increased the number of plant-parasitic nematodes. Quénéhervé et al. (2011), on the other hand, found that by planting varietal mixtures of banana material, *R. similis* damage could be reduced because it was replaced by *H. multicinctus*. It is, however, suggested that re-creating favourable conditions for plant biodiversity will increase global sustainability and resilience of banana agro-ecosystems (Tixier et al., 2008).

3.3 Chemical control

In commercial banana systems, which are mostly, but not exclusively, used for exported bananas, chemical control has been used successfully for decades. However, older nematicides are class I chemicals, indicating severe toxicity to humans, other organisms, and the environment (Chitwood, 2003; Desaeger et al., 2020). Problems with groundwater contamination, male sterility, and other effects (Taylor, 2003) have been observed over many years and pressure from consumers eventually led to the withdrawal of these products (Desaeger et al., 2020). New nematicides have been developed with a lower environmental impact, but they are very costly and not feasible for use in smallholder farming systems. Although chemical control provides immediate results and is highly effective, it is only a temporary solution and follow-up applications are necessary in tropical regions. Therefore, chemical control products will at least partly need to be substituted by a range of cultural practices, including clean planting material (*in vitro* plants), rotation crops, biological control, fallow, and organic amendments. New application technologies (e.g. nanomaterials) are being investigated that might provide additional control but must comply with new regulatory requirements in terms of quality and safety of the international banana trade, while new pesticides with improved safety profiles will add to the spectrum of available products.

3.4 Resistance breeding

One of the main pillars of an IPM strategy is resistance breeding. Challenges faced by conventional banana breeding programmes, besides sterility and the lack of seed in the triploid plant material, include the fact that a wide variety of plant-parasitic nematode species attack an extensive variety of *Musa* hybrids planted worldwide, in addition to a combination of several pests and diseases attacking the banana plant concurrently. Transgenic crop improvement strategies may provide an alternative to classical breeding, as has been shown by Tripathi et al. (2015) in plantain field trials against *Helicotylenchus* and *R. similis* infections. While new research is attempting to incorporate banana genes

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(cisgenes) into Cavendish (Dale et al., 2017), the ultimate aim is to modify the Cavendish genome using gene editing to generate the necessary traits such as nematode resistance. Genetic modification, as indicated elsewhere in this book series (Dale et al., 2020), is probably the most cost-effective way to achieve effective disease resistance for smallholder farmers (Ahmad et al., 2012).

A big challenge in banana nematode control is the concurrent infection by several nematode species in the root system and as yet no hybrid has shown complete resistance to nematode complexes as required to provide good control (Pinochet, 1988; De Waele and Elsen, 2002; Lorenzen et al., 2010). Although resistance to *R. similis* has been identified (Quénéhervé et al., 2009), these materials are still moderate hosts to other species such as *Pratylenchus*, which is becoming a significant pest affecting the banana across sub-Saharan Africa (Coyne, 2009). It is also worth mentioning that species complexes differ considerably within and among locations, thus limiting resistance as a control strategy (Coyne et al., 2013).

Well-known sources of resistance against *R. similis* include 'Pisang Jari Buaya' (AA) (PYB) and 'Yangambi km5' (AAA) (Pinochet and Rowe, 1978; Wehunt et al., 1978; Sarah et al., 1992; Price, 1994), while 'PYB' has been introgressed to 'FHIA-01' (AAAB), which is also resistant to *R. similis* (Pinochet and Rowe, 1979; Viaene et al., 2003). 'Yangambi km5' is reported to be resistant to both *R. similis* and *P. goodeyi* (Fogain and Gowen, 1998). Other sources of resistance have been found in several genome groups in *M. acuminata* and *M. balbisiana*, in both wild and cultivated diploids (Moens et al., 2005; Dochez et al., 2006; Gaidashova et al., 2008; Quénéhervé et al., 2009). In Uganda, a conventionally bred hybrid, 'Kiwangaazi', was released, showing tolerance to *R. similis* (Nowakunda et al., 2015).

3.5 Genetic modification

An alternative way to control nematodes could be by use of genetically modified (GM) plant material, which could confer resistance to nematodes. However, broad-spectrum resistance is required to manage multiple nematode species that pose a threat to banana and plantain crops. Transgenic approaches have considerable potential for sustainable improvement of banana production (Dale et al., 2020). Across banana-producing areas, the banana plants used for production are sterile, with no or limited wild material being available, and material is propagated using tissue culture material or sucker material, reducing gene flow as an issue.

RNA interference (RNAi) based defences have been developed and have shown promise against *Meloidogyne* spp. (Huang et al., 2006; Yadav et al., 2006; Ibrahim et al., 2011; Papolu et al., 2013), *R. similis* (Haegeman et al., 2009; Li et al., 2015a, b), and *Pratylenchus* spp. (Joseph et al., 2012; Tan et al., 2013).

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Tripathi et al. (2015) reported that both a peptide and a cystatin provided a high level of resistance in plantain to *R. similis* and *H. multicinctus* with noticeable effects over an extended time period as both nematode species were unable to maintain their population densities in the roots until the crop reached harvest. Nevertheless, the issue of safety is a constraint when promoting transgenic plant material and needs to be considered. Hu et al. (2020) suggested that possibilities such as ‘gene-deletor’ techniques are or might become available in due course.

While in transgenic GMO approaches, external genes are incorporated from outside the *Musa* genome, new research aims to incorporate banana genes (cisgenes) into Cavendish (Dale et al., 2017, 2021). These approaches have resulted in banana varieties with enhanced levels of pro-vitamin A and increased resistance to *Fusarium* wilt. Such approaches can also be used to modify the Cavendish genome to generate traits such as nematode resistance. Genetic modification may in the short-term be the only way to achieve nematode resistance to enable smallholder farmers to grow banana with no additional chemical inputs (Ahmad et al., 2012).

4 Future trends in research

With predicted temperature increases, it is suggested that climate change will have a significant impact on agriculture and food production (IPCC, 2007; Knueppel et al., 2009). There is great concern regarding how this will affect crop production, including pests and diseases. Coyne et al. (2018) state that ‘given our limited knowledge in general on species distribution, temperature thresholds, and survival under different climates, it will be much guess work and many assumptions’.

Climate change has shown that it has the ability to alter the distribution of nematode species. For example, *R. similis* was previously not found in altitudes of 1400 m above sea level, but has recently been detected in higher altitudes in Uganda (Talwana et al., 2016; Erima et al., 2017).

A study in Martinique confirmed that temperature, rainfall, and soil type influenced the abundance of the six nematode species found in bananas, which further confirms that changing temperatures and variations in rainfall patterns as a result of climate change can have a considerable impact on nematode communities (Duyck et al., 2009). For example, the abundance of *H. multicinctus* decreased with increasing rainfall (Duyck et al., 2009). Similar behaviour in relation to *H. multicinctus* populations was also observed on plantains in the Caribbean (Hutton, 1978). By contrast, *P. coffeae* numbers increased with increased rainfall (Duyck et al., 2009). In Uganda, increased populations of *R. similis*, *H. multicinctus*, and *Meloidogyne* spp. were observed with increases in temperature (Erima et al., 2017). In Cameroon, *R. similis* and

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Hoploilaimus sp. infestations in banana were more prevalent during low-rainfall and high-temperature periods (Neba et al., 2014).

Changes in nematode species distribution and impact due to climate change will have a significant effect on farmers producing banana and plantain and more specifically smallholder famers, which dominate in sub-Saharan Africa (Coyne et al., 2018). Although climate change is a challenge for nematode management, it can also be used to our advantage. For instance, if nematode complexes change due to higher or lower temperatures and some of these newly introduced species are less pathogenic or damaging to the banana root system, it might be favourable to embrace this change while cultivar selection could be adapted to the advantage of the less damaging species. As mentioned earlier, *P. goodeyi* is less damaging than *R. similis*, and is found in higher altitudes than *R. similis*. However, the distribution of both species has changed as studies conducted with *P. goodeyi* in Kenya and Tanzania (Seshu-Reddy et al., 2007; Luambano et al., 2019) and with *R. similis* in Kenya (Nyang'au et al., 2021) have shown. To ensure that damage does not accelerate, it would be beneficial to manipulate the rhizosphere so that *P. goodeyi* is allowed to dominate species in higher altitudes, for example, by using specific *Musa* material preferred by *P. goodeyi* (Price, 1994).

On the other hand, studies have shown that *P. coffeae* is found in most places in mixed populations with *R. similis*. Again, it might be beneficial to enhance the occurrence of *P. coffeae* and suppress that of *R. similis* by using other banana varieties. However, some studies have shown that *P. coffeae* is as damaging as *R. similis* or has simply replaced *R. similis* (Coyne, 2009). In such cases, other strategies will have to be followed.

5 Conclusion

It is important to realize that effective and sustainable techniques for reducing nematode problems must be developed in addition to the above-mentioned cultural practices. Methods include changing the nematode community structure into a less damaging nematode complex, which can be achieved by changing banana varieties or planting alternate crops. By altering the root rhizosphere, conditions may be favourable for the survival and reproduction of some nematode species at the cost of others. This manipulation may allow less damaging species to dominate, resulting in reduced nematode damage. Therefore, more research is necessary to allow realistic predictions in this regard and for a wide variety of climatic and soil conditions. However, convincing farmers to apply such an approach will be challenging because it represents a different way of thinking.

Increasing biodiversity can also potentially reduce nematode problems since higher biodiversity generally limits pest and disease infections (Quénéhervé et al., 2011; Poeydebat et al., 2017). It is important to recognize

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that choice of plant species in crop rotation and intercropping approaches is likely an important factor.

Climate change is resulting in shifting distribution patterns of the major nematode species infecting banana, as has been proven by several publications (Seshu-Reddy et al., 2007; Luambano et al., 2019; Coyne et al., 2018). Perhaps this disastrous reality can be used to our advantage while manipulating the nematode community into a less damaging one.

Future research should focus on genetic modification as a priority in genetic improvement of the banana. Including or manipulating certain selected traits in the banana and plantain genomes could reduce the need for additional inputs of harsh chemicals. Adopting the CRISPR technique, for example, might help protect these crops against devastating pests and diseases since researchers can use the gene-editing tool to boost the banana's defences while retaining the desired productivity and consumer traits.

Improving biodiversity to reduce pest and disease problems should also receive sufficient attention. Biodiversity can be enriched by planting a combination of cover crops, intercropping, mixed crops, and planting a variety of selections of *Musa*. This diversity above-ground will definitely influence biodiversity in the rhizosphere, which can be improved even more by the addition of mulches, manures, and organic amendments, of which an abundance of material is available that still needs to be investigated for its efficacy on nematode control. A good example is mulch of *Tithonia diversifolia*, which reduced nematode numbers and improved yield (Coyne et al., 2005).

Increased biodiversity could be complemented with the manipulation of damaging nematode communities by providing feeding material to promote the less damaging nematode species. Furthermore, tools available in other industries such as infrared photography can be incorporated into management programmes to predict, anticipate, and manage nematode problems, specifically in commercial plantations. Improved monitoring approaches are key to reducing pest and disease problems and may lead producers to change their attitude towards farming practices. It is envisaged that a range of commercial biological control agents and softer chemical control agents will also become available in the near future for inclusion in IPM programmes. With climate change putting more pressure on natural resources such as water and increasing temperatures, cultivars/hybrids that will be suitable for these conditions are urgently required.

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