

Nematode problems in tuber crops and their sustainable management

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Introduction

In many subtropical and tropical countries, the most significant food commodities produced are those that are grown from tubers and roots (R&T). The R&T include yams (*Dioscorea* spp. L.), cassava (*Manihot esculenta* Crantz), and sweet potato (*Ipomoea batatas* (L.) Lam.) and edible aroids such as Taro (*Colocasia esculenta* Schott.) and Tannia (*Xanthosoma sagittifolium* Schott.). These crops represent the second-largest global source of carbohydrates, after cereals, in the tropical world, with a projected two billion people in Asia, Africa, and Latin America relying on them for food, feed, and income. Around 45% of R&T crop production is used for human consumption, with the remaining 55% going to either the production of animal feed or industrial processing that results in products such as starch, distilled spirits, and a variety of other minor products. The R&T produce starchy-storage organs known as rhizomes, corms, or tubers, which are modified stems or roots. Their production is hampered by a variety of biotic and abiotic factors. Plant parasitic nematodes (PPNs) are one of the important biotic factors that reduce the yield or quality of tubers. This chapter discusses the major PPNS affecting R&T in the subtropical and tropical regions, symptoms and damages caused, long-term management measures to combat the threat posed by nematodes, and future prospects.

Root-knot nematodes

The root-knot nematodes (RKNs) belong to the genus *Meloidogyne* Göldi, 1887 and today, it accounts for over 100 nominal species recorded within the taxon (Eisenback & Hunt, 2009; Karssen et al., 2013). The *Meloidogyne* species are considered the most destructive PPNs because of their worldwide distribution, extensive host ranges that include most cultivated plants and many native plants, adverse effects on crop yield and quality, and ability to survive (Khan, 2008; Karssen et al., 2013). The threat posed by this group of nematodes is further aggravated by their association with pathogenic fungi and bacteria in root disease complexes (Khan, 1993). The RKN species damage plants across crop production systems under all kinds of climatic conditions especially in the subtropical and tropical regions (Fabiya, 2021a, 2021b; Khan, 2007; Onkendi et al., 2014; Sasser, 1980).

Distributions

RKNs are widespread PPNs that can be found in all root- and tuber-grown regions (Coyne & Affokpon, 2018). *Meloidogyne* species are global in distribution parasitizing the root and tuber (R&T) crops throughout the world. *M. incognita* has been reported as the most prevalent RKN on R&T crops, followed by *M. javanica* (Coyne & Affokpon, 2018; Namo & Akinbola, 2016; Wendimu, 2021). There are ongoing reports of the most aggressive root-knot nematode, *M. enterolobii* (guava root-knot nematode) parasitizing several R&T crops such as yam, cassava, sweet potato, and potato (Oyetunde et al., 2021; Rutter et al., 2019).

Economic importance

Meloidogyne is one of the most economically significant PPNs in the world and a highly damaging pest in all root- and tuber-growing areas due to early growth-stage damage (Sasser, 1989). High inoculum levels in the field may result in severely stunted plants or simply a dieback of plants (Khan, 2008). The *Meloidogyne* species cause significant tuber losses during production and storage, reducing their marketability or rendering them unmarketable (Kolombia et al., 2020).

On yam

A correlation between galled tubers and tuber weight was found, with severely galled tubers losing more than twice as much weight as nongalled tubers during storage (Mudioppe et al., 2012). In Nigeria, it was reported that RKNs and *S. bradys* caused a significant number of yam farmers to give up their farms and abandon large areas of land (Adesiyun & Odihrin, 1978). Severe yield losses have been reported on yam due to an infection of RKNs, and the impact of RKNs on yam is seen to be varying from nematodes and yam species. Yam yield reduction of 24%–80% caused by *M. arenaria* was stated in China (Gao, 1992) while a complete destruction of *D. trifida* by *M. incognita* at a rate of 30,000 nematode population/100 g of soil was reported in Martinique (Kermarrec, 1974). However, studies have shown that the yield reduction of *D. rotundata* due to *M. incognita* and *M. javanica* infection may not be an important part of nematode damage (Acosta & Ayala, 1975; Atu & Ogbuji, 1986; Nwauzor & Fawole, 1981). There is no refutable argument for the damage caused by *Meloidogyne* species on yam tuber's quality and storability. Yam tubers harvested with *Meloidogyne* spp. are unattractive and have little to no market value (price reduction estimated between 39% and 52%



FIG. 1 Unsold galled yam tubers abandoned in a market. Source: Yao A. Kolombia, IITA Ibadan, Nigeria.

compared with healthy tubers) due to their warty appearance and as a result affect the income of farmers who rely on yam farming for their livelihoods (Nwauzor & Fawole, 1981). This is an important loss for smallholder farmers considering the proportion of galled tubers in their stores. As an indication of damage extent, reports indicated in Nigeria up to 70% for *D. rotundata* and 90% for *D. alata* galled tubers among yam tubers collected (Adesiyun & Odihirin, 1978). A survey carried out across the country indicated that over 59% of tubers in the markets and 27% in farmers' barns were galled (Kolombia et al., 2020) and this is often translated by tubers with no market value was abandoned (Fig. 1). Losses are also visible in terms of reduced edible portion as more infected tuber portions must be peeled away.

On cassava

Conflicting results on the damage extent caused by RKNs on cassava have been reported in different cassava-growing regions (Razak, 1978; Roman, 1978). The observations were further shown to be (1) *Meloidogyne* species-specific and race variability on cassava fields, (2) the cassava varietal reaction to different *Meloidogyne* species, and (3) an underestimation due to the rough texture of feeder roots, which could conceal the infection from detection (Coyle, 1994). With yield losses ranging from 42% to 98% (Akinsanya et al., 2020), RKNs have been reported to predispose the tubers to rot disease caused by fungal and bacterial pathogens (Akinles, 2014). The nematodes can decrease both the yield and the quality of cassava alone but probably more importantly as an element of a disease complex.

On aroids

It has been reported that *Meloidogyne* has caused severe losses in India, which has led to the abandonment of the cultivation of *Colocasia* as a result of the nematodes (Srivastava et al., 1969). *Colocasia* (Taro) and *Xanthosoma* (cocoyam) may be less susceptible to *M. incognita* than other crops, and high preplant densities are necessary for damage to take place (McSorley et al., 1983b). The deformity caused by galling reduces the commercial value of corms (Srivastava et al., 1971). In India, the Sree Pallavi, a susceptible cultivar's yield decreased by 21% after 1000 *M. incognita* is being inoculated in pots. Despite the absence of external galls, high nematode densities in Tanzania caused severe damage to cocoyams (Runkulatile & Teri, 1990).

Symptoms

RKN infection symptoms include galls on the storage roots (tubers) and feeder roots, which can occasionally appear flaky and/or with abnormal root proliferation on tubers known as “crazy roots” (Coyne & Affokpon, 2018; Kolombia et al., 2021; Plowright et al., 2000). On R&T crops, the RKN infection has been linked to chlorosis, nutrient deficiencies, and retarded growth, in addition to secondary infections caused by other pathogens (Coyne & Affokpon, 2018). The symptom expression may greatly vary with the host crop.

On yam

Roots and tubers of yams are commonly knotted or galled as a result of RKN infection. More visibly striking, however, are the abnormal warty or knobby and flaky tubers that result from the infection. Females can be seen embedded in the discolored tissue beneath the crenulated surface in cross section. The tissue surrounding individual females in older tubers can become darkened and necrotic. Internal rotting caused by *Meloidogyne* spp. can occur in some yam species. Galled tubers are occasionally associated with root proliferation known as crazy root symptoms. Typically, tuber weight loss is greater during storage than harvest, and *M. incognita* and *M. javanica* may not reduce tuber weights at harvest (Atu & Ogbuji, 1986; Nwauzor & Fawole, 1981). The nematodes *M. arenaria* and *M. incognita* can cause severe stunting or death on the seedling of medicinal yam (*D. composita*, *D. floribunda*, and *D. spiculiflora*) with foliar chlorosis and leaf dieback associated with *M. incognita* infection (Jenkins & Bird, 1962).

On cassava

Gall formation on feeder’s roots is the common and obvious symptom of RKN infection (McSorley et al., 1983a) with abnormal branching that may occur (Jansen van Vuuren & Woodward, 2001). Further, galls on the cassava tubers (storage roots) are also observed (Fig. 2). Where the nematodes have infected the tissue, the surface can appear flaky and show high levels of necrosis beneath the surface when thin sections are cut away (Abidemi, 2014; Oyetunde et al., 2021). Stem height and weight reduction (Gaspin, 1980), reduction of sprouting and establishment of cuttings (Bridge et al., 2005), and wilting of early cassava leaves (Chinnasri et al., 2014) and cassava dieback (Bridge et al., 1991) have been reported to be a result of heavy infestation (presence of high population density) of *Meloidogyne* spp.

On sweet potato

During the early stages of infection, small galls are visible on the roots whereas, at the most advanced stage of plant development, fibrous roots produce round- to spindle-shaped swellings (galls) along with egg masses on the surface. Also, RKNs have been shown to produce galls and longitudinal cracking, which can reduce yield and marketability. Plants affected by RKNs become stunted with the foliage turning yellow and flagging. The plants can also mimic plant expression of nutrient deficiencies with a reduction in their vigor and abnormal flower production (Namo & Akinbola, 2016; Overstreet, 2013).



FIG. 2 Galled Cassava tuber and feeder roots. Source: Adewuyi Omowumi, IITA Ibadan, Nigeria.

On aroids

RKN infection can cause galling of roots and corms. Galls are often small and irregular on young feeder roots. Older roots that are infected get thick and swollen. In some cases, symptoms are not always obvious on infected roots despite the presence of high nematode density (Runkulatile & Teri, 1990). Nematodes cause blister-like swellings on corms, which develop into large round or oblong galls 2–15 mm in diameter, deforming the corms and causing them to rot in storage (Coyne & Affokpon, 2018). Even when no external symptoms are present, yellow-colored areas of varying sizes within corms can be seen. Above-ground symptoms manifest themselves as patches of plants that are unhealthy and stunted, with yellowing leaves that may turn brown and die (Bridge et al., 2005).

Biology and life cycle

The *Meloidogyne* species (RKNs) are obligate plant parasites that have a wide range of hosts and a global distribution (Moens et al., 2009). Most RKN species that harm root and tuber crops reproduce through mitotic parthenogenesis (Chitwood & Perry, 2009). Their life cycle with an egg, completely or partially embedded in a root of a host plant, is deposited by a female. When the juveniles (J2) hatch, they invade the host plant's roots and/or tubers, inducing a trophic system of giant cells that serves as the feeding site in vascular tissues. The characteristic galls are formed by cortical cell proliferation. The remainder of the life cycle is similar to endoparasitic nematodes, with the exception that most species surrounding the gall tissue prevent females from typically bursting out of the root (Hunt et al., 2018).

In the yam tubers, the nematodes concentrate in depths ranging from 2 mm to 6 mm (few at 14 mm) with the life cycle estimated to be 35 days (Nwauzor & Fawole, 1981). It has been observed that juveniles developing inside tubers in species such as *D. composita*, *D. floribunda*, and *D. spiculiflora* are killed by the surrounding lignified cells, preventing hatched juveniles from migrating (Bruhn & Koch, 1962). However, in Nigeria, the nematode life cycle was completed in yam tubers with viable eggs after two to three months of storage (Nwauzor & Fawole, 1981). A similar observation was made on a white yam, *D. rotundata* cv. Mekakusa tubers under storage conditions where different life stages of RKN were observed inside the tuber (Fig. 3) implying that the nematode could have a continuous life cycle in the tubers during storage (Kolombia, 2017). Through propagation materials, *Meloidogyne* juveniles or eggs that have survived in stored tubers will be disseminated. However, damaging populations may readily survive on weed hosts or infest fields through the infected seeds/seedlings of yam or other crops (Rich et al., 2009).

Interaction with other pathogens

Fungal and bacterial rots are more likely to occur in tubers infected with *Meloidogyne* species than in nematode-free tubers (Khan, 1993; Nwauzor & Fawole, 1981). Furthermore,

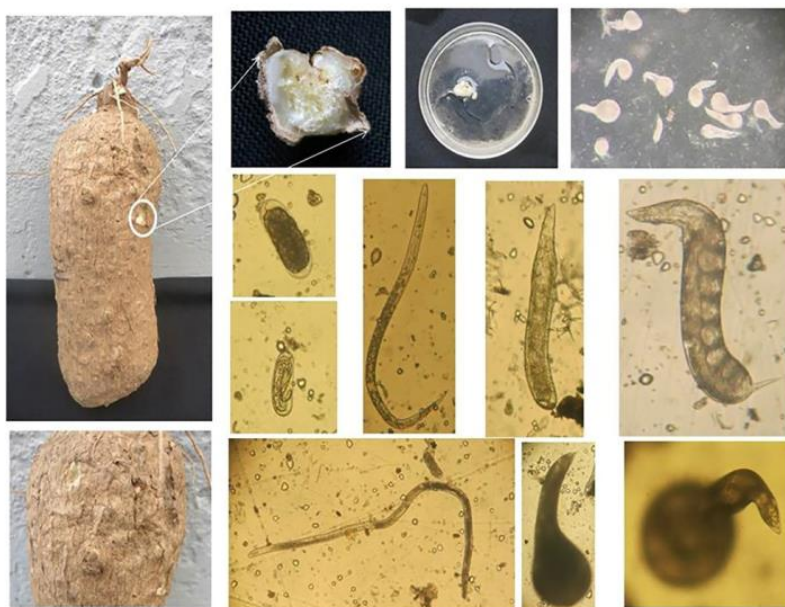


FIG. 3 Root-knot nematodes at different life stages three months after storage. Source: Yao A. Kolombia, IITA Ibadan, Nigeria.

as previously observed, galling and mechanical damage to roots or tubers will undoubtedly result in increased levels of root necrosis and reduced roots in infected plants compared to uninfected plants (Akinlesi, 2014).

Sustainable management with advanced and recent approaches

Managing *Meloidogyne* species on crops has been challenging and this has been exacerbated by the removal of the most toxic synthetic pesticides from the market for environmental regulatory reasons. The availability of resistant cultivars appears to be a long-term solution breeders should consider. In line with this vision, several resistance lines on root and tuber crops have been identified and used or are yet to be introduced to the market. However, the majority of the cultivars being currently used by farmers are susceptible to *Meloidogyne* species. In the absence of resistance lines, the use of rotation systems, intercropping (with avoidance of crops highly susceptible to RKNs) in conjunction with fallowing, mulching, and the use of biopesticides, antagonistic cover crops may be considered appropriate (Claudius-Cole et al., 2014). Combining these measures in an integrated management manner is highly recommended together with the best practice such as the use of nematode-free planting materials and/or seed treatment for RKN nematode control.

Root-lesion nematodes

Scutellonema spp. are mostly found in the tropical and subtropical regions with the majority of the species known as parasites of nonagricultural plants while few species have been recorded with high economic importance on agricultural crops in general and root and tuber crops in particular. These are mainly, *S. bradys* (the yam nematode) and a few other species such as *S. brachyurus* (the Carolina spiral nematode) and *S. cavenessi* (Coyne & Affokpon, 2018). *Scutellonema* species are found throughout tropical and subtropical areas, with Africa having the highest recorded number of species (Kolombia et al., 2017; Van den Berg et al., 2017).

Distributions

Scutellonema species are found throughout tropical and subtropical areas, with Africa having the highest recorded number of species (Kolombia et al., 2017; Sher, 1964; Van den Berg et al., 2017) where they are thought to have originated and radiated out from (Siddiqi, 2000). Records in the temperate regions have so far been the case only for the Carolina spiral nematode *S. brachyurus* (Haque & Khan, 2021).

Economic importance

The yam nematode is known to cause significant economic damage primarily to *Dioscorea* species across the globe (Coyne & Affokpon, 2018). Tuber weight loss while in storage, loss of edible portion, low tuber quality, and a decrease in planting material are all caused by the nematodes, present in tubers. The yam nematode is responsible for tuber weight loss during



FIG. 4 Vendor removing the dry rot from yam tubers infected with *Scutellonema bradys*. Source: Yao A. Kolombia, IITA Ibadan, Nigeria.

storage, edible portion loss, poor tuber quality, and planting material loss, leading up to 50% of yam tuber loss during storage (Coursey, 1967; Smit, 1967). In severe cases, a complete tuber loss may occur (Amusa et al., 2004; Kwoseh et al., 2007). As a result, infected tubers have little to no value from a commercial standpoint. In Nigeria, over 35% and 8% of the tubers evaluated were carrying dry rot from the markets and farmer barns, respectively (Kolombia et al., 2020). In the absence of a tangible solution, peeling of yam tubers to decapitate the infected areas is often used as a practical solution to circumcise the disease progression (Fig. 4).

Symptoms

Steiner and LeHew (1933) first observed the yam tuber disease commonly associated with *S. bradys* and the “dry rot” was first referred to by West (1934) as symptoms caused by the yam nematode *S. bradys*. It is now recognized as the primary symptom of *S. bradys* infestation on yam tubers (Coyne & Affokpon, 2018; Kolombia et al., 2020) and appears in the outer skin of tubers up to 2 cm deep. In the early stages, light-yellow and cream lesions appear beneath the tuber’s outer skin. As the nematodes continue feeding and migrating, the lesions that had appeared on the tuber spread. Dry rot gets its name from the fact that as the disease progresses, the lesion becomes light brown first followed by a dark brown color that eventually turns black while the tubers remain firm. In contrast, with the wet rot, tubers are soft with water dripping when squeezed. The skin of the tubers also shows external cracks, exhibiting patches of dry rot tissues, due to flaking off of the infected parts. The dry rot symptoms are most severe in mature tubers, particularly in storage, and lead to the decay of tubers. On mature tubers that have been in storage for a long time, severe damage is common. The nematode population multiplies nine to fourteen times in the six months following storage, resulting in total tuber degeneration (Coyne & Affokpon, 2018; Haque & Khan, 2021). On the above-ground, no symptoms have been observed on yams grown on *S. bradys*-infested soil (Jatala & Bridge, 1990).

Biology and life cycle

The *Scutellonema* species are migratory ectoparasites and/or endoparasites of feeder roots and storage roots (tubers) of various horticultural and agricultural crops (Haque & Khan, 2021; Van den Berg et al., 2017). They reproduce by parthenogenesis or by amphimixis depending to the species (Germani et al., 1985; Kolombia et al., 2017; Van den Berg et al., 2017). The yam nematode, *S. bradys*, inhabits the soil surrounding the host plant, but is primarily found as a migratory root and tuber endoparasite (Bridge, 1982). After hatching, the nematodes undergo all molting stages of the life stages and become adults under optimal conditions. Records indicated that the optimal temperature for development of *Scutellonema* spp. is around 24°C–28°C with the development is retarded when the temperature is below 15°C (Siddiqi, 2000). They are known to survive in the soil for several months. Demeure (1980) indicated that the female, male, and juveniles (3rd–4th stages) of *S. cavenessi* were able to survive in dry soil for up to 9 months (Demeure, 1980; Siddiqi, 2000). All stages of *Scutellonema* spp. are infective and they attack roots and tubers through the growing points of tissue, alongside emerging roots and shoots (Haque & Khan, 2021). The nematodes can also invade the plants through the roots, cracks, or injure areas in the tuber skin (Bridge, 1972). *S. bradys* is primarily restricted to the outer 1–2 cm of tubers' subdermal, peridermal, and underlying parenchymatous tissues, where it continues to feed during storage. The nematode's intracellular feeding in the tuber tissues causes cell wall rupture, loss of the contents of the cell, and formation of cavities (Bridge, 1982). The population can rise for 9- to 14-fold for a storage period of 5–6 months (Adesiyan, 1977; Baimey, 2006).

Interaction with other pathogens

In the absence of other organisms, *S. bradys* can produce the symptoms of dry rot (Adesiyan et al., 1975; Bridge, 1973). However, as a wounding agent, infection with *S. bradys* may make tubers more susceptible to secondary infections by fungus and bacteria, which can speed up tuber loss (Bridge, 1982; Ekundayo and Naqvi, 1972).

Sustainable management with advanced and recent approaches

Several management options have been deployed to manage and control damages caused by *S. bradys* on yam tubers. These methods include:

Chemical application

Despite chemotherapy's success, smallholder farmers do not use it due to its cost and/or unavailability as several pesticides are removed from markets (Castagnone-Sereno, 1988; Haydock et al., 2006; Nyczepir & Thomas, 2009). A novel "wrap-and-plant" method using a banana fiber matrix as a carrier for microdoses of abamectin (widely used insecticide and anthelmintic) drastically reduced *S. bradys* densities and increased tuber yields (Opperman et al., 2016). Residual effect analysis will clarify its use.

Cultural means

Given *S. bradys*' diverse host plants (Adesiyan, 1976), some cultural practices are not always economical or practical (Jatala & Bridge, 1990). Therefore, it is recommended not to

include crops supporting high nematode population densities (Coyne & Affokpon, 2018), and nonhost plants should be used to reduce tuber damage. Weed control and/or the exclusion of *S. bradys* weed hosts, such as *Eupatorium*, *Synedrella*, and *Chromolaena* around yam will contribute to reducing damage caused by nematodes (Adesiyan, 1976). Intercropping yam with maize, ginger, and cocoyam lowers nematode population densities in soil by 38%, 42%, and 54%, respectively (Oluwatayo et al., 2010).

Use of nematode-free/clean planting

Clean planting materials can limit the spread of the seed-borne pathogen, *S. bradys*. With new yam propagation techniques, nematode-free planting materials from tissue cultures, vine cuttings, and SAH are now a reality and should be encouraged (Olugboyega et al., 2019). In the absence of nematode-free planting materials and when using mildly infected tubers, hot water treatment is encouraged as long as sprouting inhibition is minimized (Coyne et al., 2010). Tuber treatment with the insecticide-fungicide (Mancozeb and Diazinon/Chlorpyrifos)-based treatment is also recommended to protect the crop (Mcnamara & Morse, 2014; Morse & McNamara, 2020).

Resistance and tolerance

There has been no conclusive finding of resistance to *S. bradys* in the main food yam found in any landraces or accessions that have been reported (Jatala & Bridge, 1990). However, few cultivars of *D. cayenensis* and *D. dumetorum* have been reported to support minor *S. bradys* reproduction (Kwoseh et al., 2007). With the development of new propagation techniques that offer nematode-free planting materials, the high throughput techniques are under development for the yam germplasm evaluation. The water yam, *D. alata* cv Florido, was observed with potential resistance to the yam nematode attack (Ayala & Acosta, 1971) and later identified with resistance to major yam pests and diseases (Doumbia et al., 2004).

Biological control

Controlling yam nematodes using biological control agents is gaining attention. Studies have shown a wide diversity of arbuscular mycorrhizal fungi (AMF) on yam (Tchabi et al., 2009) and high mycorrhization of the crop (Lu et al., 2015). Preinoculation of micropropagated yam plantlets with AMF species *Funneliformis mosseae* and *Glomus dussii* led to significant nematode suppression in tuber, root, and soil after 6 months (Tchabi et al., 2010). At Ibadan, the application of AMF and *Trichoderma* revealed enhanced yam yield with AMF and nematode control with *Trichoderma* (Kolombia et al, unpublished data).

Root-lesion nematodes

The genus *Pratylenchus* was ranked the second most important PPN in the world (Sasser, 1989). These nematodes parasitize a large number of crops including root and tuber crops (Onkendi et al., 2014). The common *Pratylenchus* species affecting R&T crops are *P. brachyurus*, *P. coffeae*, *P. goodeyi*, *P. sudanensis*, and *P. zae* (Coyne & Affokpon, 2018).

Distributions

The major two species of *Pratylenchus* commonly parasitizing R&T are *P. brachyurus* and *P. coffeae*. The *P. brachyurus* attacks cassava (Cameroon, Nigeria, and Uganda), potato (Brazil and South Africa), sweet potato (Uganda and Japan), and yam (Cameroon, Cote d'Ivoire, Ghana, Guatemala, Nigeria, and Uganda), whereas *P. coffeae* attacks yam (Brazil, China, French West Indies, Ghana, Jamaica, Pacific Island, and Puerto Rico) and sweet potato (Japan). Other species are found on cassava (*P. zae*: Philippines), potato (*P. zae*: Cuba), sweet potato yam (*P. goodeyi*: Uganda), and yam (*P. sudanensis*: Uganda, *P. Zae*: Ghana and Nigeria).

Economic importance

Pratylenchus is considered the second economically important nematode in view of the damage caused and the losses caused (Sasser, 1989). On R&T crops, they cause plant damage and eradication of seedlings and affect tuber quality and quantity, resulting in crop yield losses. *P. coffeae* is an important tuber parasite, reducing edible portions, market value, and, especially, storage qualities (Coyne & Affokpon, 2018). It has been reported that 30%–100% yield losses have been reported (Acosta & Ayala, 1976a, 1976b; Bridge & Page, 1984). The absence of seed sprouting has been recorded in the case of severe infection of *P. coffeae* (Coates-Beckford & Brathwaite, 1977). *P. pseudopratensis* decreased the weight of the fresh storage roots by 45% and the dry top weight by 21% (Reddy, 2015). In Togo, *P. brachyurus* was attributed to a gradual yield decline of cassava over several years, where population densities up to 400/g of root were observed (De Guiran, 1965).

Symptoms

Damage is often caused by direct feeding and, usually, only cortical tissues are affected. Unuberized feeder roots with large nematode populations develop numerous lesions with their cortexes being destroyed (Jatala & Bridge, 1990). As migratory endoparasites, they destroy tissues of the root system, causing surface cracking and internal rotting of tubers and predisposing the parasitized tissues to secondary infections by fungi and bacteria (Castillo & Vovlas, 2007). The infection causes a decline in root development, as well as the production of lesions, necrotic regions, browning, and cell death, which is typically followed by root rotting caused by secondary assault by soil fungus or bacteria (Castillo & Vovlas, 2007; Reddy, 2015). Symptoms of *Pratylenchus* spp. damage on above-ground parts are not generally obvious, but the feeding activities promote stunting and yellowing by slowing plant development and increasing vulnerability to water stress (Mohandas et al., 1990).

On yam

Symptoms of dry rot caused by *P. coffeae* in yam tubers are identical to those caused by *S. bradys*. In Jamaica and Puerto Rico, *P. coffeae* is the main factor causing dry rot where the disease is locally known as “burn” (Bridge, 1972). The nematodes are found in the tuber skin and cause severe necrosis and deep cracks in the outer tissue layers (Lebot, 2009). Brown,

irregular dry rot extents (1–5 cm) may be observed depending on yam species (Acosta, 1974; Bridge & Page, 1984). Deep cracks and a corky appearance have also been reported as external symptoms of *P. coffeae* infection (Bridge & Page, 1984). Infection frequently begins prior to harvest and continues during storage, resulting in the loss of food and planting material for the following season's crop (Siddiqi, 1972). The severely infected tubers produce shorter, unhealthy, and less vigorous vines (Coates-Beckford et al., 1978). *Pratylenchus sudanensis* infection leads to cracked tubers, which correlates strongly with nematode densities (Mudiope et al., 2007).

On cassava

Common symptoms of *P. brachyurus* include root lesions and subsequent root rotting, stunted plants with yellowing leaves, and twig dieback with small or no tubers produced (Reddy, 2015). However, the nematode was reported to cause no obvious damage to the crop in Brazil on cassava (Zem, 1979). It has been reported that cassava cultivars respond differently to *P. brachyurus* (Corbett, 1976).

Sweet potato

Pratylenchus brachyurus attacks sweet potato. The fibrous roots develop necrosis resulting in vine stunting and a significant decrease in the quality of fleshy storage roots due to the nematode infection. Storage roots develop small, brown-to-black necrotic lesions, rendering them unmerchantable. Leaf growth reduction has been recorded as the effect of the nematode on the crop (Agu, 2004). *P. coffeae* is a harmful species of sweet potato in Japan. The skin of the tubers becomes coarse and develops scabs, which severely reduces their marketability (Inagaki, 1985).

On aroids

The root lesion nematode *P. coffeae* has been reported on taro in many parts of the Pacific (Bridge et al., 2005) and it is identified as the cause of diseases in Japan. Root rot, a diminished number of cormels, stunted growth, and ultimately death are some of the associated symptoms of taro (Coyne & Affokpon, 2018; Inagaki, 1985). Nematode infections have been linked to the development of necrosis, which appears as darkened areas of dead tissues, on the roots and corms of affected plants. These lesions predispose plants to bacterial and fungal infections (Bridge & Page, 1984).

Biology and life cycle

The *Pratylenchus* species are soil-dwelling, obligately biotrophic migratory endoparasites found in all agricultural regions of the world. Their life cycle is completed between 3 and 9 weeks, depending on environmental factors such as temperature and soil moisture (Jones & Fosu-Nyarko, 2014). Males are uncommon in mitotic parthenogenetic species like *P. brachyurus* or abundant in amphimictic species like *P. coffeae*. The nematode spends most of its life inside the host roots. However, *Pratylenchus* spp. can survive for a long term under adverse conditions at the egg stage or if they go through a process called anhydrobiosis when they can survive in the soil for several years (Castillo & Vovlas, 2007).

Interaction with other pathogens

In addition to the direct damage, *Pratylenchus* spp. may predispose plants to other pathogens (Khan & Khan, 1998). The interaction between *Pratylenchus* species and *Verticillium* wilt is the most well-known of such interactions (Rotenberg et al., 2004; Rowe & Powelson, 2007). It appears that modification of wilt disease incidence or severity may be related to the specific nematode-fungus combination and the interactions between soil-borne fungi and *Pratylenchus* spp. to be biological and physiological, rather than physical, in nature (Castillo et al., 1998).

Sustainable management with advanced and recent approaches

Cultural methods

The use of cover crops to protect host plants may be an option once an effective cover crop is identified. *Crotalaria* cover crop (*Crotalaria juncea*) was identified as an effective mean to suppress *P. coffeae* (Reddy, 2015). Crop rotation with an accurate selection of companion crops may significantly lower *Pratylenchus* population in the field. However, the effectiveness of the method will depend on the nematode species and the primary crop. For *Pratylenchus* species that have a large number of alternative host crops, crop rotation will be less effective (Jatala & Bridge, 1990). Crop rotation with peanut crops reduced the population of *P. coffeae* significantly (Reddy, 2015). Other practices such as increased fertilization with potassium or the addition of chicken manure as an organic amendment significantly affect nematode damage on the crop. Further, the use of any infected materials should be avoided at all costs to avert the spread of the pathogen across fields. The hot water treatment (See Use of nematode-free/clean seed in *Scutellonema* management) will also be effective in controlling *Pratylenchus* spp. on R&T.

Host resistance

The use of resistant materials is one of the best strategies to control *Pratylenchus* species' impact on crops. Several breeding programs have identified *Pratylenchus*-resistant materials in cassava and sweet potato (McSorley et al., 1983a; Uesugi et al., 2008). Several varieties of cassava have been found with some level of resistance to the lesion nematode (Reddy, 2015).

Chemical methods

Nematicides (e.g., dazomet, oxamyl, and fenamiphos) are frequently used as preplanting treatments to reduce nematode populations. Their use on taro is thought to be limited in Pacific Island countries (Coyne & Affokpon, 2018).

Cyst-forming nematodes

Primarily, *Globodera rostochiensis* is the principal pest of potatoes. Several other cyst nematodes which are of importance in agriculture include *G. pallida* (*Heterodera trifolii*

Goffart, 1932, *H. tabacum* (*G. tabacum*), *H. schachtii*, *H. glycines*, and *H. avenae*. A new species *Globodera ellingtonae* (Handoo et al., 2012) was added of late from America (Grenier & Benjamin, 2017).

Distributions

Potato cyst nematode originated from the Andean mountains in South America. The intensification of breeding programs for late blight resistance brought in cyst nematodes to Europe in the 1850s. Julius Kuhn in 1881 pioneered the report of potato infection in Germany by the cyst nematode. The introduction of potato varieties from Europe to various parts of the world assisted the worldwide spread of cyst nematodes (Franco et al., 1998). This made Europe the secondary point for cyst nematode spread (Evans & Stone, 1977). Cyst nematodes are present all over the world. *Globodera rostochiensis* was first noticed in America in 1941, while it was discovered in India and Mexico in the 1960s and 1970s, respectively. Recently, 83 countries have identified *G. rostochiensis* (CABI/EPPO, 2020a). *Globodera pallida* is not as common as *G. rostochiensis*; it has only been identified in 64 countries and spread across six continents (CABI/EPPO, 2020b). Countries in the southern and northern regions of Africa have recorded infestation of the cyst nematodes as well (Kleynhans, 1998).

Economic importance

Yield loss of about 30% has been documented worldwide for potato cyst nematode infestation (Oerke et al., 1994). An estimated loss of about 12% was reported by Urwin et al., 2001. Tuber loss depends on the number of eggs per gram of soil. The economic threshold is a maximum of 20 eggs per gram of soil (Evans & Stone, 1977). However, the preplanting cyst population is directly related to the expected yield loss. In tropical conditions, yield loss between 10% and 80% has been recorded (Prasad, 1996).

Symptoms

The impairment materializes nutrient deficiency symptoms, thus making it arduous to identify. Infestation of cyst nematodes is demanding because of their long-term continuance in default of host. Potato tubers are habitually blanketed by white females and cysts (Vovlas, 1996). Gradually, retarded growth of plants on the field becomes noticeable, either slightly in localized small patches or heavy infection sufficient enough to cover a whole area of the field. The foliage appears dull and unhealthy with chlorosis and stunted growth. Finally, crops fail suddenly in the whole field. Crop failure is a result of the poorly developed root system. Conditions of crop growth and cyst population influence symptoms (Bairwa et al., 2021; Krishna Prasad, 2006).

Biology and life cycle

Cyst nematodes are economically salient pests due to their ceaseless endoparasitic mode of nutrition, which precipitates vascular tissue damage. The females produce a large number of eggs through their esoteric mechanism of parasitism in the host plant. The hatching factor is

the process by which chemical substances and root diffusates from potato aid the hatching of cysts. Root diffusates are available at the plant root tips 3 weeks after crop emergence; these diffusates may be influenced by cyst conditions or prevailing weather. Once the J₂ emerges from the cyst, it becomes very active and punctures the plant roots with a stylet. The head points to the steel as it settles to feed after entering through the epidermal cell walls. A feeding tube is formed while the J₂ feeds on cells in the endodermis, cortex, or pericycle. The root cells become enlarged, and a big transfer cell which contains granular cytoplasm is formed to supply nourishment for the developing nematode. Molting takes place, and the nematode remains in the transfer cell (syncytium) to complete its life cycle (Evans & Stone, 1977). During the developmental stage, sex is determined at the J₃ stage. The root cell ruptures for the posterior part of the female nematode to protrude while it remains attached to the plant root in a swollen and sedentary manner. The males move out of their roots to mate with the females. At the immature stage, *G. rostochiensis* females present a golden yellow color, while cream or white color is for the *G. pallida* females (Evans & Trudgill, 1978). The cyst tolerates hostile weather situations. It is the remains of the female after death and is usually brown in color. Several eggs numbering up to 500 are enclosed in the cyst and could survive up to 30 years (Turner & Evans, 1998). A generation is concluded in a single crop season; the life cycle is finalized within 35–40 days. The dormancy of *G. rostochiensis* is short between 40 and 65 days while *G. pallida* has a longer dormancy of 60–75 days (Evans & Trudgill, 1978). The cysts go into an intense dormancy state called diapause during which no hatch impulses could affect them. After this stage, 60%–80% of hatching could occur with root diffusates. Environmental factors could equally influence unprompted hatching without a host (Oostenbrink, 1950).

Interaction with other pathogens

Cyst nematodes, *Globodera* spp. have been reported to interact with some soil borne fungi (Khan, 1993). The Verticillium rot and subsequent wilt incidence and/or severity became higher on potato plants in the presence of *Globodera rostochiensis* (Corbett & Hide, 1971; Evans, 1987; Harrison, 1971) and *G. pallida* (Farley et al., 1971).

Sustainable management with advanced and recent approaches

Encysted eggs are difficult to eradicate owing to the resistant wall of the cysts. This has made them an endemic pest. In this regard, a single method of control is not reliable. A consortium of methods is thus sufficient to keep the cyst population under check to a profitable state of production.

Crop rotation

Potato farmers around the world have adopted rotation of crops as one of the options in cyst control to bring the population below the threshold level (Urwin et al. (2001). In Cochabamba, Peru, and Ecuador, lima beans and maize are planted before potatoes for optimum yield (Canto, 1995; Proinpa, 1996; Ravelo, 1984), while in Europe, the field is fallowed for a maximum of seven years after the harvest of a susceptible potato crop (Jones, 1970). In view of the limited host range of cyst nematodes, rotation with nonsolanaceous crops is ideal

(Bairwa et al., 2021). A four-year rotation program of potatoes with French beans and peas resulted in 98.7%–99.9% control of the cyst population after the program with over 90% yield of potatoes (Menon & Thangaraju, 1973).

Trap cropping

Trap cropping is known to reduce 80% of *G. pallida* population in France. Potato plants could also be grown as hatching stimuli; the plants are then brought down after nematode incursion. Tolerant potato varieties have equally been used to reduce cyst populations (Whitehead et al., 1994). Planting of *Solanum sisymbriifolium* as a trap crop is reported to have reduced the cyst population by 50%–80% (Scholte & Vos, 2000).

Resistance varieties

Several cultivars have been developed to mitigate against the cyst population (Joseph et al., 2019). Some potato accessions are known to be resistant to *G. rostochiensis* and *G. pallida* (Dalamu et al., 2012; Wolters et al., 1996). Varieties that are resistant to *G. rostochiensis* are available in Europe, while resistant cultivars are not available for *G. pallida* (Hockland et al., 2012). Tolerance among resistant cultivars varies (Mulder, 1994). In some cases, resistance genes have been found to become virulent after expansion (Phillips et al., 1998). Kishore et al. (1969) screened a large variety of germplasm to arrive at suitable varieties resistant enough for commercial purposes. The long-time reliability of resistant varieties is doubtful because of virulence development in nematode species.

Soil solarization

Solarization is one of the most effective methods in cyst population management. In hot summers, some layers of soil could get heated with significant effect (Whitehead & Turner, 1998). A 62-day solarization regimen was reported to reduce the cyst population by 95% (Mani et al., 1993). Reports by LaMondia and Brodie (1984) stated that 97% of inhibition of *G. rostochiensis* was achieved with solarization of the first 10 cm layer of the soil.

Biopesticides and biological control

Microorganisms like *Pseudomonas fluorescens*, *Purpureocillium lilacinum*, and *Trichoderma viride* have conferred protection on potatoes against cyst nematode multiplication (Khan, 2016; Umamaheswari et al., 2012).

***Ditylenchus* spp.**

The genus *Ditylenchus* contains the three most important nematode species attacking R&T crops; these are *D. dipsaci* (stem and bulb nematode), *D. destructor* (potato rot nematode), and *D. angustus* (ufra nematode). These species are commonly targeted worldwide in various regulatory programs (O'Bannon & Esser, 1987). In Taiwan, *D. destructor* is a quarantine pest (Tsay, 1995). The infection is transmitted via potato seeds; thus, it is put through an appropriate phytosanitary check. This has reduced the rate of movement of infected tubers (Darling et al., 1983).

Distributions

Ditylenchus destructor has been identified as pests of potatoes in several parts of Europe, Asia, Mediterranean, and parts of North America (EPPO, 2014). Potato seeds are commonly infected in the Ural regions of central Asia (Artem'ev, 1976). *D. destructor* causes a huge loss in chernozem (Chukantseva, 1983). Around 87% of nematodes on potato in Uzbekistan is *D. destructor*. (Adylova & Vasilevskii, 1983). About three regions namely Samarkand, Tashkent, and Fergana are highly infested by *D. destructor* (Usmanova, 1972). Similarly, potatoes in Kazakhstan and Azerbaijan are also heavily infected (German, 1972; Ismailov, 1976). Stoeen (1977) identified *D. destructor* from potatoes in Norway, while Jatala et al. (1977) in their findings also described nematodes from potatoes in Peru. Correspondingly, reports from Moldova, Lithuania, Ukraine, Bulgaria, Belarus, Russia, Iran, Korea, New Zealand, Japan, and China affirmed that *D. destructor* is a common pest of sweet potato.

Economic importance

In some parts of the world, *D. destructor* is regarded an economically important pest (Goodey, 1952; Jeger et al., 2016). At temperatures between 15°C and 20°C and humidity above 90%, *D. destructor* gets to the level of an economic pest, and the percentage of damage could be between 20% and 50% (Xie et al., 2004). A damage level of about 10% has been reported in the United States (Basson et al., 1991). In Sweden, an infested field planted with clean seeds had 0.3%–94% of damage. External symptoms of damage were depicted when infected seed tubers were planted (Andersson, 1971). In Estonia, infection ranges from 2% to 9% on the farm; however, infection materializes during storage with 90% of tubers infected (Kikas, 1969). In pervasive areas of the world, 100% yield loss is expected (Xu et al., 2015; Zhang et al., 2006). Sweet potato takes the fourth position among the crops cultivated in China. It is a huge impediment to sweet potato production (Yang, 1990).

Symptoms

The nematode, *D. destructor*, is a migratory endoparasite and penetrates tubers through lenticels. In infected tubers, above-ground symptoms hardly appear. However, pinhole lesions may be noticed on tuber surfaces. Disintegration of tuber cells comes up from protease and pectinase enzymes produced by the nematode. Dry rot conditions and sunken lesions appear. The infection brings about water loss and tuber cell shrinkage; this is accompanied by tuber size and starch content reduction (Sun et al., 1998; Wang et al., 1995). Infected tuber flesh becomes black, dark brown to grayish in color with a dry mealy outlook. The flesh has a dry and mealy appearance, varying in color from grayish to dark brown or black. External symptoms on the iris and tulip include gray-to-black lesions; heavily infested bulbs often have blackened roots and poorly developed yellow-tipped leaves. Black or dark roots may appear in heavily invested situations.

Biology and life cycle

Although some *Ditylenchus* species can go through an ectoparasitic period, the majority of them are migratory endoparasites that attack host plant bulbs, inflorescences, pods, seeds, and tubers. Cross-fertilization is the method of reproduction, and males are abundant. Eggs

are deposited singly in infected tissues. After hatching, the juveniles undergo all successive molting to attain adult stages. All life stages (juveniles and adults) are vermiform and infectious, the J₄ stage is the most common primary inoculum because it has the greatest potential for survival under adverse conditions through quiescence (Bridge & Starr, 2007; European and Mediterranean Plant Protection Organization (EPPO), 2004).

Interaction with other pathogens

Fusarium solani and *Rhizoctonia solani* are very well known to form a disease complex with *D. destructor*. Janowicz and Mazurkiewicz (1982) reported that the higher the population of *D. destructor*, the more the infection by *R. solani*. At 136 nematodes per 100 gram of soil, the infection on potatoes was very harmful because of the complexity involved. Likewise, tubers in storage at temperature between 6°C and 15°C were severely damaged with the addition of *F. solani* var. *coeruleum*, *F. culmorum*, and *F. oxysporum*. The damage observed was 49% against 27% when only rot fungi were present (Janowicz, 1984).

Sustainable management with advanced and recent approaches

D. destructor is a polyphagous species, so crop rotation is not a good management option. It is very important to clean tubers at the onset of the season. Resistance variety may be a good option; this has been proven to be effective (Wang et al., 1995). A high level of control could be achieved with the application of synthetic nematicides; the exorbitant cost of this option does not make it pocket-friendly. Although a significant reduction in nematode population has been documented with the use of granulated nematicides against *D. destructor*, even in situations where the potato field was planted with infested tubers, a 3.8% reduction in nematode population was achieved with the use of carbofurangranules (Vorona, 1984). A positive outcome was achieved with the tuber soaking in fostil (Melnik & Knaub, 1977). A similar result was noted with carbathion, though the substance is not safe (Chukantseva, 1976). Tuber dipping in thionazin had a significant control effect; the tubers were nematode free all through the planting season.

A safer alternative to synthetic nematicide is the use of hot water treatment for potato seed tubers. In some cases, infested field may be flooded as a form of control; this has been found to effectively control *D. destructor* (Young & Seung, 1995). Skin extracts of citrus medica brought about 93.3% of *D. destructor* adult under 2h of exposure. The toxin from *Erwinia nimmipressuralis* induced 68.8% mortality to *D. destructor* in 48 h of treatment. Some potato cultivars exhibit a high level of resistance; this is a good option of managing *D. destructor*. The polyphagous nature of the nematode makes crop rotation very difficult. Sugar beet is a nonhost; this may be used in rotation (Winslow, 1978).

Rotylenchulus reniformis

The reniform nematode, *Rotylenchulus reniformis*, is a semiendoparasitic species in which females penetrate the root cortex, establish a permanent feeding site in the root, and become sedentary (Khan, 2008). The nematode is predominantly distributed in subtropical, tropical, and warm temperate zones (Coyne & Affokpon, 2018; Wang, 2001).

Distributions

The reniform nematode has been reported in South America, North America, Africa, Caribbean, Asia, Australia, and the Pacific (Jatala & Bridge, 1990; Robinson et al., 1997).

Economic importance

It causes serious economic damages on R&T such as cassava (Coyne et al., 2003), sweet potato (Coyne et al., 2003), *Xanthosoma* “cocoyam” (Díaz-Silveira & Herrera, 1998; Quénéhervé et al., 2006), taro (Robinson et al., 1997), and yam (Abdulsalam et al., 2021a, 2021b). In sweet potatoes, losses ranging from 44% to 60% were estimated depending on the initial population (Gapasin & Valdez, 1979).

Symptoms

The infestation by *R. reniformis* induces root necrosis resulting in severe root pruning and subsequent dwarfing of plants. Tubers are deformed, cracked, and smaller which reduce their marketability (Clark & Wright, 1983; Gapasin & Valdez, 1979). The induced cracks are deep, and the exposed surfaces are regenerated with calius and periderm. No nematodes (adults and juveniles) are found inside the cracked sweet potatoes (Jatala & Bridge, 1990).

Biology and life cycle

The infective stage is adult, which is reached one to two weeks after hatch (Wang, 2007). Females reach maturity after root penetration. The males inseminate the female gonads. However, some reniform nematode populations reproduce parthenogenetically. The fertilized eggs are laid into a gelatinous matrix with up to 200 eggs (Wang, 2001). The nematode completes the life cycle in less than three weeks, depending on the soil temperature. It can, however, survive in dry soil for at least two years without a host due to anhydrobiosis, a survival mechanism that does not require water (Radewald & Takeshita, 1964).

Interaction with other pathogens

In crops other than cotton, the disease complex with *R. reniformis* is not much known (Khan, 1993). However, *Fusarium* species and *Rhizoctonia solani* are very well known to form disease complex with *R. reniformis* (Bridge & Starr, 2007; Khan & Sharma, 2020). In an interaction with *Macrophomina phaseolina* a maximum reduction in plant growth characters was observed when nematode inoculated one week before the fungus (Singh et al., 2012).

Sustainable management with advanced and recent approaches

It is recommended to rotate crops with plant species that are resistant or immune to *R. reniformis*. The use of cover, trap, and antagonistic crops has been found effective against the nematode (Robinson et al., 1997; Wang et al., 2002). It has been reported that *P. lilacinum* was effective against the reniform nematode (Reddy, 2015).

Other significant nematodes

There are numerous plant-parasitic nematodes found in R&T crops, but they only affect a small number of hosts or have no economic significance. Among other nematodes, there are:

Hirschmanniella miticausa

Especially in regions where taro is grown year after year, *H. miticausa* has the potential to cause significant damage to, or even a total destruction of the crop (Bridge et al., 1965; Bridge & Starr, 2007). *H. miticausa*-infested taro corms and cormels had thin, red-brown necrotic lesions near the base, surrounded by extensive soft rots. These plants produced fewer cormels, weighed less, and had significantly more root growth on main corms (Bridge et al., 1965). *H. miticausa* has been reported on taro in New Guinea, Solomon Islands (Bridge, 1988).

Radopholus similis

The burrowing nematode, *R. similis*, has been reported on yam in New Caledonia and Papua New Guinea (Bridge & Page, 1984; Coyne & Affokpon, 2018) where it causes dry rot of yam similar to the symptoms caused by *P. coffeae* and *S. bradys* on yam. Lighter brown color has been observed on the infected. *R. similis* infections to yam have been reported in Fiji, Solomon Islands, and India (Bridge, 1988) and sweet potato in Colombia, Costa Rica, Ecuador, Honduras, and Panama (Tarte et al., 1981) and South Africa (Milne & Keetch, 1976). Even at a low inoculum level of 100 nematodes/plant, sweet potato root weight, tuber weight, and tuber length decreased significantly in a pot experiment conducted in India (Koshy & Jasy, 1991).

Paratrichodorus porosus

Paratrichodorus porosus has been found associated with a black scurf-like syndrome of unknown etiology on the seedling of *D. opposita* in Japan (Nishizawa, 1973). The nematode significantly hinders tuber elongation and decreases their weight (Bridge et al., 2005).

Other nematodes of possible importance on R&T crops are *Belonolaimus longicaudatus*, *Cacoporus* spp., *Criconebella* spp., *Filenchus* spp., *Helicotylenchus* spp., *Hemicriconemoides* spp., *Hemicycliophora* spp., *Hoplolaimus* spp., *Paratrichodorus* spp., *Trichodorus* spp., *Tylenchorhynchus* spp., and *Xiphinema* spp.

Future prospects

Plant nematodes cause severe damage and yield decline in roots and tubers due to nematode activities. But due to the lack of awareness, the farmers are not able to recognize the nematode damage. Given that root and tuber crops are primarily propagated vegetatively and that some nematodes are carried along the planting material, farmers' awareness and understanding of nematodes and their life cycle will immensely contribute to controlling the nematode infestation, especially through the application of cultural methods (use of nematode-free planting materials and crop rotation). Farmers' awareness, combined with increased NARES capacity building, will allow for a proper risk evaluation of potential

problems, resulting in more effective nematode management. The capacity building should enable (1) adequate assessment of field nematode population density, (2) a reinforced capacity to conduct advisory programs (through agricultural extension programs or private crop consultants), and (3) accurate sample diagnostics with high-precision diagnostic tool kits for quarantine measures.

For farmers that have been aware of the damages caused by nematodes to crops, pesticide application has been the solution whenever farmers could afford the cost and this has never been always the case with smallholder farmers. The situation is exacerbated by the removal of the most toxic synthetic pesticides from the market for environmental regulatory reasons (degradation, nontarget organisms and groundwater, residues in foodstuffs, ozone depletion, legislation, human safety, and exposure during application). In the present situation, it is imperative to find alternative nematicides with low toxicity and more importantly, to intensify research toward the development and use of resistant materials is the ideal nematode management method. Intensification of the identification of new nematode natural enemies as biocontrol agents should be increased to formulate effective solutions for long-term nematode management and face project increase of pests and pathogens, the introduction of invasive pests due to climate change.

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III. Vegetable crops

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