

IMPORTANT PARASITIC NEMATODES AND VECTORS OF DISEASES OF VEGETABLE CROPS (A REVIEW)

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ABSTRACT

Plant-parasitic nematodes are ubiquitous residents of agricultural soil and important biotic factors in global vegetable production. This review discusses some important nematode parasite-vectors of diseases of vegetable crops, their significance in disease development and the limitations in assessing losses associated with nematode activities. Meloidogyne, Heterodera, Globodera, Pratylenchus, Hoplolaimus and Ditylenchus genera were some of the important parasitic nematodes affecting vegetables discussed. Plant-parasitic nematodes and the vectors may independently cause plant diseases by breaking through the pre-existing structural defence mechanism in plants through mechanical and enzymatic actions. Their interactions with secondary disease-causing agents (fungi, bacteria, and viruses) were also highlighted. There are limitations to the assessment of losses associated with nematode-related diseases under field circumstances due to farming systems, pre- and post-harvest activities, nematode diversity, population dynamics and incomplete harvest of some vegetables which serve as hideouts for these nematodes. The role of nematodes in the soil field of vegetable crops may not be appreciated without consideration to factors such as host-parasite interaction, life cycle and distribution and nematode's role in crop diseases development. It is therefore worthy of scientific attention in this regard to further establish the certainty of disease development in vegetables in the absence of nematode activities. These factors remain a huge challenge to plant pathologists in understanding the minutiae surrounding production and economics of vegetable crops. Therefore, further research effort in this regard can be of advantage to global vegetable economy.

Keywords: Ecosystems, nematode, ubiquitous, vegetable, parasitic, diseases.

INTRODUCTION

Phylum Nematoda (Nematode) commonly known as roundworms are reportedly one of the most primal and diverse groups of animals on earth with an estimated existence of about one billion years. This group of soft-bodied animals with the known oldest fossil record of over 120 million has evolved appreciably in complexity as parasites of plants and animals

(Lambert and Bekal, 2002). Their adaptation to all conceivable habitats confers on them extreme abundance and diversity. An estimated 40% of nematode species described are free-living parasites of bacteria, fungi protozoa, and other nematodes while about 44% are parasites of various vertebrates and invertebrates with only about 15% as parasites of plants (Lambert and Bekal, 2002).

Nematodes as parasites of plants have been largely underestimated over the years until recently when their activities were reported in association with plant diseases caused by fungi (Atkinson, 1982), bacteria (Hunger, 1901), and viruses (Hewitt et al., 1958). Nematodes may feed on all parts of the plant such as roots, stems, leaves, flowers, and seeds in a variety of ways, and in most cases, their activities are often injurious to the host plant and provide biological asylum for other disease-causing agents. Therefore, the overall activity of these nematodes and the presence of other secondary agents of plant diseases present a huge challenge to plant protection and disease management, resulting in poor field performance, yield losses, and assessment.

While there are many reports on nematodes and their role in disease complexes involving bacteria, fungi, and viruses in various crops, this review tends to discuss the most important nematodes affecting vegetables, their symptoms, life cycle, and distribution, examine the significance of nematodes in crop disease development and identify the limitations in the assessment of losses associated with nematode related diseases in vegetables.

IMPORTANT NEMATODES OF VEGETABLE CROPS

Plant-parasitic nematodes are important factors in vegetable production globally as they remain one of the most ubiquitous residents of agricultural ecosystems, even in extreme environments. Thus, the task for survival is an enormous one for parasitic nematode communities in the soil. However, various agricultural practices from the pre-

harvest to post-harvest management stages of vegetable production have informed the tenacity with which they persist and spread in fields of vegetable crops.

Root Knot Nematodes (RKN)

This group of nematodes is sedentary endoparasites consisting of members belonging to the family Meloidogyne (Eisenback and Hirschmann, 1991). In a recent survey in molecular plant pathology, root-knot nematodes were ranked at the top of the list based on scientific and economic importance (Jones et al., 2013). Members include *Meloidogyne incognita*, *M. hapla*, *M. javanica*, *M. arenaria*, *M. oteifae*, *M. decalineata*, *M. africana*, *M. chitwoodi*, and *M. fallax*, *M. enterolobii* and *M. coffeicola* (Coyne et al., 2018). They are considered the most pervasive group of nematodes affecting almost all known cultivated crops (Perry et al., 2009; Coyne et al., 2018). Common vegetables affected by the Root-knot nematodes include Solanaceous (tomato, chilli), Curcubitaceous (bitter melon, cucumber, pumpkin), Leguminous (cowpea, bean, pea), Cruciferous (cauliflower, cabbage, broccoli), Okra, and several roots and bulb crops (onion, garlic, lettuce, carrot, and radish) (Singh, 2011). The Above ground symptoms include poor growth, a decline in quality and yield of crops, reduced resistance to environmental stress (heat and drought). Also, below-ground symptoms have been observed as damaged roots, low utilization of water and nutrients, galling, stunting and chlorosis, root swellings. The lifecycle includes egg, juvenile, and adult stages and is completed in 25 days at 27°C. Male Root-knot

nematodes are worm-like and about 1.2 to 1.5mm long by 30 to 36µm in diameter while the females are pear-shaped, 0.40 to 1.30mm long by 0.27 to 0.75mm wide (Singh et al., 2011). Root-knot nematodes are widely spread and reputed as one of the greatest threats to vegetable production globally. In West Africa, Root-knot nematodes (*Meloidogyne* spp.) are among the most important group (Jones et al., 2013; Sikora et al., 2018) and can infect, thrive and reproduce on a wide range of crops. For example, *Meloidogyne enterolobii* was recently recovered from crop field for the first time in Nigeria (Kolombia et al., 2016). Vegetable crops, when grown under intensive farming systems, are steadily subjected to root knot nematode challenge and thus, considered the lone greatest biotic limitation to vegetable production in West Africa region (James et al., 2010). For example, there are new reports of *M. enterolobii* from sweet potato (Karuri et al., 2017) and cowpea (Kisitu, 2016) in Nigeria, Kenya, and Mozambique, respectively.

Cyst Nematode

Cyst nematodes or cyst forming nematodes ranked second to root-knot nematodes in agricultural and economic importance (Jones et al., 2013). This group of nematodes are sedentary endoparasite and members consist of Heterodera and Globodera species (Eisenback and Hirschmann, 1991). Members of this group have a wide host range of vegetable crops including Solanaceous crops (tomato, pepper, potato, eggplant), Leguminous (cowpea, bean, pea), Cruciferous (cabbage, broccoli), and root and tuber crops (carrot, potato), etc. The above-ground symptoms of cyst nematodes usually resemble

those associated with root damage which includes stunting of shoots, yellowing of leaves, and general reduction in shoot parts. The lifecycle is reportedly completed within 21 to 30 days. Dead female cyst nematodes usually appear like a tough brown capsule containing several hundred eggs. The male is wormlike and about 1.3mm long by 30 to 40µm in diameter while the mature females are lemon-shaped and 0.6 to 0.8mm in length and 0.3 to 0.5mm in diameter (Singh et al., 2011). Cyst nematodes are widely distributed in various parts of the world and reportedly have numerous hosts particularly the solanaceous plants.

Lesion Nematode

Ranked third among the most damaging nematodes in agriculture with about 70 species of root-lesion nematodes (*Pratylenchus* spp.) distributed worldwide with a host range of nearly 400 plant species (Davis and MacGuidwin, 2000). Members of this group are migratory endoparasites of the family Pratylenchidae. The most common member of this group belongs to the genus *Pratylenchus*, with a wide host range of over 350 hosts reported so far (Coyne et al., 2018). The above-ground symptoms include chlorosis, stunting, and general lack of vigour resulting in wilt of the affected crop. Infected plants may also form patches in the field while roots show necrosis and brown to black lesions. General reduction in the yield of crops has also been reported. Both male and female nematodes are wormlike and about 0.4 to 0.7mm long and 20 to 25µm in diameter (Singh, 2011). Their distribution is worldwide, and they attack numerous vegetables. *Scutellonema* spp and *Pratylenchus* spp have

both been reported in some states in Nigeria (Abubakar, 2020; Daramola et al., 2013).

Reniform Nematode

Members of this group are sedentary semi-endoparasites belonging to the family Tylenchulidae (Robinson et al., 1997). This nematode group has been reported to have a wide host range as members attack many vegetables. Reniform nematodes are considered a pest of great significance after root-knot nematodes (Coyne et al., 2018). Symptoms on infected plants may include stunting in growth, reduced and discoloured root system and there are reports on cases of reduction in germination and crop stand, observed in infected emerging seedlings (Singh, 2011). Duration for the life cycle of this group is about 4-5 weeks under optimum conditions and they are widely reported in the South-eastern USA, Hawaii, West Africa, India, and Cuba (Robinson et al., 1997).

Lance Nematode

This group of nematodes belongs to the family Haplolaimidae and genus *Hoplolaimus* with a wide host range of vegetables (Robinson et al., 1997). The symptoms on affected plants may include patches of yellowing and dying of plants. Also, there may be a thickening of the cell wall and the formation of tunnels in the cortical region (Singh, 2011). Members of this group are sedentary ecto-parasites and in many cases, juveniles may completely enter cortical tissue in infected plants. They have been reported in so many parts of the world with some documented cases on other crops such as Yam (Bae et al., 2008) and Pineapple (Daramola and Afolami, 2014) in Nigeria.

Stem and Bulb Nematode

Members of this group belong to the family Anguinidae and genus *Ditylenchus* species. They are widely distributed in temperate climates, affecting many root and tuber vegetables such as potato, pea, and carrot and bulbs such as onion and garlic (Brzeski, 1991). Members of this group produce above-ground symptoms such as twisted, deformed and enlarged seedlings. There may be stunting and eventual death of infected plants in extreme cases. Rarely found in the soil, stem, and bulb nematodes feed on stem, leaves, and bulbs. Duration for the life cycle is about 19 to 23 days at 15°C; they have four moulting stages and four juvenile stages with their first moulting occurring in the egg stage (Singh, 2011). For example, According to Sturhan and Brzeski (1991), *Ditylenchus destructor*, or potato rot nematode, attacks almost solely the subterranean parts of plants such as tubers, rhizomes and stem-like underground parts. It is a near-cosmopolitan species, common in temperate regions and responsible for huge losses in potato and hop production (EPPO, 2013a). *Solanum tuberosum* (potato) is the major host, tubers develop wet or dry rot which spread to other parts and tubers in storage (Sturhan and Brzeski, 1991).

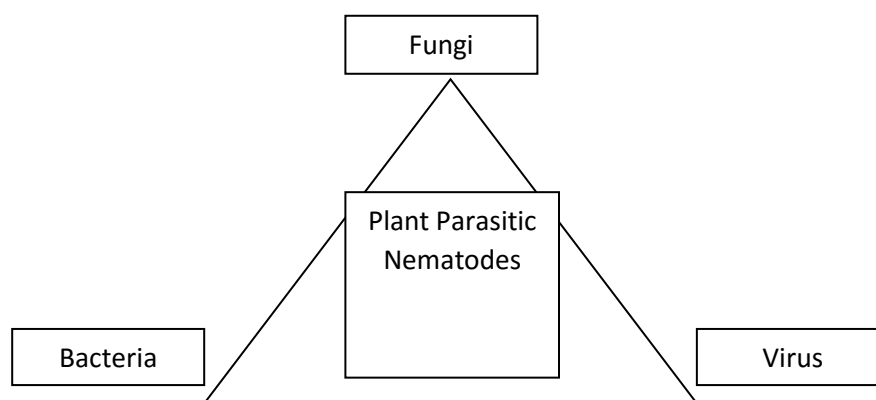
SIGNIFICANCE OF NEMATODES IN CROP PLANT DISEASE

DEVELOPMENT

The presence of stylets in nematode's mouth and various salivary secretions confers huge success on nematode's mechanisms (mechanical and enzymatic) of penetration into plant tissue. There are several external and internal defence structures or

passive/static structures existing in plants (Chaube and Pundhir 2005). Plant-parasitic nematodes may independently cause plant diseases by breaking through these structures thus compromising the immune system of the plants concerned. This may be achieved usually in two ways; firstly, by altering the pre-existing structural defence mechanisms and/or secondly by opening an “infection

window” for other soil-borne microorganisms (fungi, bacteria, viruses) leading to disease complexes. These possibilities stem from the fact that the plant’s pre-existing structural defence mechanisms serve as the first line of defence in plants (Chaube and Pundhir 2005), which when compromised, may lead to a weak condition that may prevent or reduce the effect of the invading nematodes.



Plant-parasitic nematodes are obligate parasites that feed exclusively on the cytoplasm of living plant cells although some may feed briefly on the surface root hairs or epidermal cells (Khan, 2015). Nematodes are obligate parasites that require a surety for their survival, and such by themselves rarely kills their host (Johnson and Santo, 2001). Pathologically, the role played by the nematodes in crop disease development often is described in the following sub-headings:

- (a) **Disease inciting agents:** mechanical wounding by nematodes promotes the involvement of fungi, bacteria and viruses in causing severe damage than either of the pathogen alone. Nematodes attack healthy tissues, thereby forming infection courts for these organisms. Some migratory endoparasitic nematodes like root lesion nematode (*Pratylenchus* spp.) cause necrotic lesions/wounds on the host

surface that serve as a food base for the establishment of facultative fungal pathogens (Moens and Perry, 2009).

- (b) **Aggravator:** nematodes that release metabolic by-products to kill host cell and predispose unaffected cells to invasion by pathogens and stimulate the growth of harmful organisms (Khan, 2015).
- (c) **Vector:** nematodes that expose healthy host tissues to pathogens by their feeding activities. Example; *Xiphenema* spp (Hewitt et al., 1958; Lambert and Bekal, 2002)
- (d) **Pre-disposer:** nematodes that can set conditions favourable for development of diseases in healthy host tissues by the activities of other organisms (Moens and Perry, 2009).

- (e) **Pathogen:** nematodes that can cause diseases by themselves. Example; Root knot, Cyst and Stubby root nematodes (Khan 2015).

Nematode vectors of fungus infecting vegetable crops

The first reported case of involvement of nematodes in disease complexes was by (Atkinson 1982) on cotton wilt (*Fusarium oxysporum* f.sp. *vasinfectum*); severe wilt was reported to have occurred in the presence of root-knot nematode. Some root-knot nematodes have been implicated in disease or “patho-complexes” with *Rhizoctonia solani* in Peanut and Tomato, and *Fusarium oxysporium* in Coffee (Walker et al., 2000; Bertrand et al., 2000; De et al., 2001). Some cyst nematodes have also been associated with disease complexes with *Phytophthora sogae* and *Fusarium oxysporium* in Soybean and *Rhizoctonia solani* in potato (Back et al., 2000; Kaitany et al., 2000). Others include members of the genus *Pratylenchus* spp in association with complexes with *Fusarium oxysporum* f.sp. *ciceri* and *Rhizoctonia solani* both in Chickpea, *P. neglectus* and *P. penetrans* both with *Verticillium dahlia* in Potato and Mint (Hafez et al., 1999).

Worthy of mention, is the fact that the soil environment can provide favourable conditions for the activities of pathogens particularly fungi and other plant-parasitic nematodes. Therefore, a variety of disease development in crops can depend on the complex interrelationship between host, pathogen(s), and prevailing environmental circumstances.

The mechanism of interactions of the plant-parasitic nematode with fungus is primarily

through enhancement of pathogenicity mechanism of fungus and this is made possible because affected plants are altered physiologically, increasing their susceptibility to pathogens (Khan, 2015). Most synergistic interactions between endoparasitic nematodes and fungi pathogens occur after 3–4 weeks of nematode infection. Root-knot nematodes are reportedly the cause of increased leakage of electrolyte from galled tissues which activate the resting spores of pathogenic fungi (Back et al., 2000). The galled roots exude more carbohydrates, protein, amino acids, etc., and these invite rapid fungal colonization on the root (Bertrand et al., 2000). Further, a mechanical injury made by nematodes is also responsible for the breakdown of resistance in some crop cultivars against the fungal pathogen (De et al., 2001).

As proven in most cases, nematodes not only cause wounds to the roots of crops but also open the window for infection by other agents. For example, great yield loss especially in the presence of the fungus *Verticillium dahliae* in the soil was reported in Potato cyst nematode cases (Storey and Evans 1987).

Nematode vectors of bacteria infecting vegetable crops

A few cases of nematode–bacterial disease complexes in vegetables are known. However, plant-parasitic nematodes may also predispose vegetable crops to bacterial disease through mechanical injury caused on the susceptible host. In their work, (Furusawa et al., 2019) demonstrated that tomato plants are readily attacked by *Pseudomonas solanacearum* in nematode-infested soil. It was reported that Concomitant infection of *R. solanacearum* and root-knot nematode *Meloidogyne*

incognita increases the severity of bacterial wilt in tomato but the role of this nematode in disease complexes involving bacterial pathogens is not well known. It is important to note that although root wounding by nematode attacks seems to play an important role in the infection of plants by soil-borne pathogens, it may not entirely explain the degree of susceptibility of plants to these pathogens. The role of the nematode for most of the cases is to provide the bacteria with an infection court and/or easy access of bacteria into the host through wounding. Bacteria are also capable of parasitizing nematodes, and this has been exploited for managing crop problems and challenges associated with nematodes.

Nematode vectors of virus infecting vegetable crops

There are limited reports on the role of nematodes as vectors of vegetable crops. However, the roles of plant-parasitic nematodes as plant virus vectors have been established for more than five decades now. In a report, (Hewitt et al., 1958) proved the role of the *Xiphinema index* for the successful transmission of grapevine fan-leaf virus in the vineyards in California USA. This was the first report of reliable proof of transmission of plant viruses by plant-parasitic nematodes. So far, two families of polyphagous ectoparasitic nematodes, Longidoridae (Dorylaimida) and Trichodoridae (Triplonchida) include species capable of transmitting plant viruses (Gupta and Swarup, 1968). Bileva et al. (2008) reported that twenty-four nematode species within Longidoridae transmit twelve viruses of the genus *Nepovirus* and one of *Sadwavirus* whereas all three members of the genus *Tobravirus* are vectored by thirteen nematode

species belonging to the genera *Paratrichodorus* and *Trichodorus* (Trichodoridae). Important nematode vectors transmitting economically important viruses in vegetables include *Xiphinema rivesi*, a vector of Tomato ringspot nepovirus (TRSV), and *X. americanum sensu stricto*, a vector of TRSV (Martelli 2002).

Virus-vector nematodes can retain virus particles for a long term for up to three years in soil as also has been observed experimentally during their associations. Nematodes of the genera *Paratrichodorus* and *Trichodorus* are vectors of the two viruses of the genus *Tobravirus*: Pea early browning tobravirus (PEBV) and Pepper ringspot tobravirus (PRSV) (Bileva et al., 2008).

Some authors have suggested that for the successful transmission of plant viruses by the nematode species, the steps include acquisition, retention, dissociation, and inoculation (Khan, 2015). According to Hewitt et al. (1958) virus particles append on the cuticular lining of the feeding apparatus and the anterior part of the alimentary tract (oesophagus) of vector nematodes. During the feeding process, ingested virus particles are released through the stylet and oesophageal lumen (internally lined by cuticle) into the alimentary canal leaving a small portion retained (adsorbed) on the wall (Bileva et al., 2008). However, both the retention and dissociation of virus particles depend on the compatibility of the virus (coat protein) and the vector (the nematode position of oesophageal gland opening, gland secretion and its flow, pH, chemical nature of lumen, and feeding apparatus, etc. (MacFarlane, 2003). Usually, nematodes may be infective from 2 to 4 months and even longer and can

transmit the viruses after feeding on infected plants from 1 hour to 4 days. Also, both juveniles and adults can acquire and transmit viruses (Martelli 2002). All the plant-parasitic nematodes ingest virus particles during feeding on plants, but successful virus transmission has so far been reported in nematode species belonging to the Order Dorylaimida (Xiphinema, Longidorus, and Paralongidorus spp.) and Triplonchida (Trichodorus and Paratrachodorus spp.). The plant viruses transmitted by the nematodes are broadly grouped as below:

NEPO Viruses: These nematode vectored viruses have particles about 25–30 nm in size, polyhedral in shape, and are mostly transmitted by Xiphinema and Longidorus spp. The viruses belonging to this group are grapevine fan-leaf virus (Xiphinema index), tomato ringspot virus (Xiphinema americanum), and raspberry ring spot Scottish strain (Longidorus elongatus) (Bileva et al., 2008).

TOBRA or NETU Viruses: These are viruses transmitted by nematodes and they have particles of 180–210 nm and 45–115 nm in size depending on virus isolates. These rod-shaped (tubular) viruses are mostly transmitted by Trichodorus and Paratrachodorus spp. The viruses transmitted are tobacco rattle (Trichodorus similis), Pea early browning virus (Paratrachodorus anemones) and pepper ring spot virus (Paralongidorus maximus), (Bileva et al., 2008).

LIMITATIONS TO ASSESSMENT OF LOSSES ASSOCIATED WITH NEMATODE DISEASES IN VEGETABLES

Over the years, the production and consumption of vegetable crops have expanded rapidly in most areas of the world, with production significantly outpacing population growth since the 1960s. Surprisingly, the total production of most vegetables has decreased slightly over the last three to four decades and this is suggested to be due to several constraints that impede production, with plant-parasitic nematodes implicated in many instances as their activities are estimated to yield loss of 12.3 % (\$157 billion dollars) worldwide (Singh et al., 2015). The role nematodes play in limiting vegetable production depends to a large extent on the farming system, on-farm activities during pre- and post-harvest periods, the physicochemical disposition of the surrounding soil environment and climate. However, the often-overlooked role of nematodes in plant disease development is a major limitation and the cause of inadequacy in estimating and assessing losses in vegetable crops exclusive to nematode activities. This ambiguity has been avoided in some cases where loss assessment in vegetable crops has focused on the activities of bacteria, fungi, viruses, insects and rodents and other group pests. In addition, assessing the exact losses due to nematodes activities may not be feasible under field conditions due to dynamics in nematode population in the soil. Therefore, there is need for research focus and effort towards understanding the effect of nematode

population dynamics on field performance of vegetables.

Furthermore, the practice of incomplete harvest of some vegetables, by leaving rootstocks in fields after harvest is also a serious threat to effective management and control of nematodes. This is because such crop remains is a potential source of inoculums which confer biological asylum on nematodes prior to another fresh planting. They are also sources of inoculums for healthy transplants during pre- and post-emergence of seedlings and can lead to reduction in germination and early crop stand.

CONCLUSION

Plant-parasitic nematodes are one of the most numerous soil animals with very large-scale diversity. However, because of their small size and often unnoticed activities in the soil, they are generally unchecked. This is because the most taxonomic and pathological effort has targeted the notorious plant parasites and pests, such as bacteria, fungi, viruses, and insects. Therefore, it is no surprise that farmers have limited knowledge of nematodes and their impact on crop performance and yield. Importantly, the role of plant-parasitic nematodes in field of crops may not be fully grasped without consideration to host-parasite interaction, life cycle and distribution, nematode role in crop diseases development, and exact losses associated with nematodes in the field conditions.

Until recently, the secondary disease agents in vegetables have enjoyed much attention from plant pathologists especially with lesser regard to the role of nematodes in disease development and losses in vegetable crops. The role of nematodes as vectors of bacteria,

fungi, and viruses are well documented and it is worthy of scientific attention in this regard to further establish the certainty of disease development in vegetables in the absence of parasitic nematodes.

In all, losses in vegetable crops concerning nematode activities has presented with it enormous ambiguity especially with nematode symptoms having semblance with disease symptoms of other plant pathogens. These factors as presented above remain a huge challenge to plant pathologists in understanding the minutiae surrounding production and economics of vegetable crops. Therefore, further commitment and research effort in this regard can be of great advantage to global vegetable economy.

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