

Nematodes in Horticulture: An Overview

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Citation: Lopes-Caitar VS, Pinheiro JB, Marcelino-Guimarães FC (2019) Nematodes in Horticulture: An Overview. J Horti Sci & Crop Res 1(1): 106

Abstract

Most important studies about plant-parasitic nematode have been performed especially for major crops, such as soybean, rice, corn, and wheat. However, the damage caused by these pathogens in general horticulture should have more attention. Nowadays, horticulture yield results have been relevant, allowing to show its worldwide power in economies and food. In addition, human hunger and diets changes have highlighted the current horticulture scenario and increased efforts towards solutions in diseases and losses caused by phytopathogens. Nematode infection has been the cause of important yield losses in horticulture and the genus *Meloidogyne* and *Pratylenchus* are reported to be the most important threats. In addition, as horticulture is associated with a wide number of products, the compilation of information regarding damages, symptoms, resistance, novel solutions and other concepts for phynematode management allows for the better comprehension of the whole situation. Herein, we integrated information about the damage and losses caused by these pathogens in horticulture. Resistant genotypes seem to be the best alternative and, due to wide horticulture aspect, the focus is especially for life sustaining horticultural, such as banana, cassava, potato, and sugar beet. In addition, it was also provided evidence regarding how studies have been conducted on new strategies for resistance and control, such as the elucidation of effector's functions. Nematode effectors studies, focus on the development of new resistant plant genotypes, is an auspicious strategy against this parasites.

Keywords: Fruit and Vegetables; Life-Sustaining; Management Strategies; Yield Losses

Horticulture Global Scenario

Plants are fundamental to the existence of life on Earth and have a wide spectrum of uses, but the most obvious is for human sustenance [1]. Plants supply all of our food demands, directly or indirectly, as animal food intermediaries. The intensive use of plants for people is the definition of horticulture. Its origins are inseparable from the beginnings of agriculture [2]. Horticultural practices, by occidental native people, began independently in several regions of the continent. Records indicate the occurrence of pumpkin and pepper crops in approximately 7,000 B.C. in America, even before the first corn crops, which occurred in approximately 2,500 B.C. [3]. Egypt's papyri list many wines, medicinal plants and their associated drugs in approximately 3,150 B.C. [2].

Horticulture is a widely used term that presents four main subdivisions: pomology or fruticulture (tree fruits and nut crops), olericulture (vegetable production), floriculture and the landscape and nursery industry [4]. The variety of species in horticulture enables its application under different agro-climatic conditions and soil features, allowing rising incomes and employment generation. At a global level, horticulture is a sector in full expansion and vaporization [5,6]. According to the Food and Agriculture Organization of the United Nations [7], fruit and vegetables production around the world increased from 69 million tons in 1995 to 137 million tons in 2016. Global olericulture production includes cauliflower, lettuce, celery, beans, peas, cassava and others. However, potato is the most widespread and abundant horticultural product around the world, followed by tomato, onion and cabbage [8]. China, India and Nigeria are the dominant vegetable producers. Melons are the most commonly produced fruit, followed by bananas, apples and grapes [6]. China, India and Brazil are the dominant fruit producers. These countries are responsible for approximately 50% of the world's fruit production and 65% of the world's vegetable production. Of the total global annual consumption of flowers, approximately 80% is concentrated in Western Europe, Germany, the USA, the UK, France, the Netherlands and Switzerland, and these locations are the dominant producers, starting with the Netherlands, the USA and Sweden.

Although it is unquestionable how important world horticultural advances are in terms of quality and production over recent years, we still stand at a crossroads. We all need to understand that horticulture has other benefits, as well. Currently, more than two billion people, the majority in developing countries, are suffering from hunger and micronutrient deficiencies. Additionally, the forecast for the world population in 2050 is approximately 9 billion people [9]. Another important factor boosting horticultural production is world dietary pattern changes. People are increasingly conscious about their diet, health, and quality of life [10, 11]. Vegetarian and vegan habits have been widely disseminated and are adhered to worldwide, whether for religious, cultural or ethical reasons. Therefore, it appears that the world needs a new 'green revolution' [12].

Therefore, all the efforts to increase world horticulture production will be essential for feeding the future. These efforts will help improve world human health, playing a vital role in solving the global malnutrition problem, increasing incomes and generating job opportunities. We still have so many challenges to overcome to achieve the full potential that this agricultural sector can show. The stress caused by biotic and abiotic factors has significantly limited greater results in horticultural production. Nematodes are one of the main problems among all plant pathogens, not only by suppressing plant growth but also by adversely affecting the overall yield [13].

An Overview of Nematode Parasitism in Horticulture

Among all phytopathogens, plant parasitic nematodes (PPN) are an important cause of yield losses and food security issues. PPN cause losses estimated at 14.6% of the total production of all tropical and subtropical crops. This means an estimated annual economic loss of more than US \$ 173 billion worldwide and consequently a significant impact on the world population's food [14]. Due to their nonspecific symptoms, horticultural losses caused by nematodes are often underestimated. The annual yield loss of the world's major horticultural crops due to nematode infections has been estimated to be 12% for fruit and nut crops, 11% for vegetables, and 10% for ornamental crops. These losses result in more than US \$ 30 billion in costs to life sustaining and other important horticultural crops [15]. Based on a survey of the literature, Table 1 shows estimated annual yield loss details due to nematode infection of horticulture crops.

Horticulture crops	Annual Loss (%)	Reference
Banana (<i>Musa</i> spp.)	19-30	(Brentu <i>et al.</i> 2004; Sasser and Freckman 1987)
Bean (<i>Phaseolus vulgaris</i>)	27-60	(Kimenju <i>et al.</i> 1999; Singh and Kumar 2015)
Beet (<i>Beta vulgaris</i>)	12-60	(Singh and Kumar 2015; Syngenta 2010)
Bitter melon (<i>Momordica charantia</i>)	4-48	(Ali 1997; Anwar and McKenry 2012; Kaur and Pathak 2001)
Cabbage (<i>Brassica oleracea</i> var. Capitata)	2-24	(Anwar and McKenry 2012; Olthof <i>et al.</i> 1974; Singh and Kumar 2015)
Carrot (<i>Daucus carota</i>)	25-50	(Anwar and McKenry 2012; Bossis <i>et al.</i> 1989; Singh and Kumar 2015)
Citrus (<i>Citrus</i> spp.)	4-70	(Brooks 2008; Sasser and Freckman 1987)
Chickpea (<i>Cicer arietinum</i>)	14-60	(Ali and Sharma 2003; Das 2015; Sasser and Freckman 1987)
Chilies (<i>Capsicum annuum</i>)	19-70	Ali, 1997; Anwar and McKenry, 2012; Singh and Kumar, 2015
Cowpea (<i>Vigna sinensis</i>)	15-71	(Ali 1997; Sasser and Freckman 1987; Singh and Kumar 2015)
Cucumber (<i>Cucumis sativus</i>)	25-88	(Anwar and McKenry 2012; Giné <i>et al.</i> 2014)
Eggplant (<i>Solanum melongena</i>)	17-43	(Anwar and McKenry 2012; Singh and Kumar 2015)
Garlic (<i>Allium sativum</i>)	60-80	(Sturhan and Brzeski 1991)
Ginger (<i>Zingiber officinale</i>)	51-74	(Ali 1997)
Grape (<i>Vitis</i> spp.)	12-80	(Brooks 2008; Sasser and Freckman 1987)
Peanut (<i>Arachis hypogaea</i>)	13-70	(Mc Donald <i>et al.</i> 2005; Patel <i>et al.</i> 1996)
Lettuce (<i>Lactuca sativa</i>)	10-64	(Olthof <i>et al.</i> 1974; Viaene and Abawi 1996)
Melon (<i>Cucumis melo</i>)	14-45	(Anwar and McKenry 2012; Kim and Ferris 2002; Sasser and Freckman 1987)

Horticulture crops	Annual Loss (%)	Reference
Mushroom (<i>Agaricus bisporus</i>)	13-70	(Aman <i>et al.</i> 2002; Kumar <i>et al.</i> 2010)
Okra (<i>Abelmoschus esculentus</i>)	20-90	(Ali 1997; Devi <i>et al.</i> 2011; Sasser and Freckman 1987)
Onion (<i>Allium cepa</i>)	60-80	(Sturhan and Brzeski 1991)
Ornamentals	11-84	(Ali 1997; Sasser and Freckman 1987)
Pea (<i>Pisum sativum</i>)	20-85	(Greco <i>et al.</i> 1991; Greco and VITO 1994; Singh and Kumar 2015)
Pigeon pea (<i>Cajanus cajan</i>)	13-67	(Saxen and Reddy 1987; Sharma <i>et al.</i> 1993)
Potato (<i>Solanum tuberosum</i>)	12-85	(Anwar and McKenry 2012; Greco <i>et al.</i> 1984)
Pumpkin (<i>Cucurbita spp.</i>)	27	(Anwar and McKenry 2012; Singh and Kumar 2015)
Spinach (<i>Spinacea oleracea</i>)	25-49	(Anwar and McKenry 2012; Olthof <i>et al.</i> 1974)
Sponge gourd (<i>Luffa cylindrica</i>)	15	(Anwar and McKenry 2012; Singh and Kumar 2015)
Strawberry (<i>Fragaria. ssp.</i>)	60-80	(Bohmer 1981; Mohotti <i>et al.</i> 1997)
Tobacco (<i>Nicotiana spp.</i>)	14-60	(LaMondia 2002; Sasser and Freckman 1987)
Tomato (<i>Solanum lycopersicum</i>)	20-85	(K. R <i>et al.</i> 1976; Singh and Kumar 2015)
Watermelon (<i>Citrullus lanatus</i>)	12-37	(López-Gómez <i>et al.</i> 2014)
Yam (<i>Dioscorea spp.</i>)	17-85	(Amusa <i>et al.</i> 2004; Singh and Kumar 2015)

Table 1: Percentage of Annual Yield Losses Associated with Nematode Infection in Horticulture Crops

As stated previously, PPN feed mainly on underground higher plant tissues, such as roots, rhizomes, tubers, bulbs and hypogeous fruits. Hence, they are considered to be ‘invisible enemies’, as the plant symptoms occur on the aerial parts and are often confused with those from abiotic stress, such as lack of nitrogen or water deficit. However, some other nematode species can feed on organs such as stems, leaves, flowers, fruits and seeds. In addition to the lack of specific symptoms, there are some situations where it is difficult to identify the presence of nematodes only by eye, especially when they are not sedentary [16].

Some nematode species have greater importance for commodity crops, such as *Meloidogyne spp.*, *Heterodera spp.*, *Globodera spp.*, *Pratylenchus spp.*, *Radopholus similis*, *Ditylenchus dipsaci*, *Bursaphelenchus xylophilus*, *Rotylenchulus reniformis*, *Xiphinema index*, *Nacobbus aberrans*, and *Aphelenchoides besseyi* [17]. Some PPN are highly polyphagous, such as *Meloidogyne spp.* and *Pratylenchus spp.*, which can infect many species of plants [18]. However, in horticulture crops, this situation can be quite different, depending upon nematode population density, environmental factors, and especially the most dense horticulture crop in a specific location and its susceptibility or tolerance to infection. In the Philippines, for example, at least 13 genera of PPN were found to be associated with 15 semi-temperate vegetables [19]. The top nematode threats in horticulture crops are described above but also include *Tylenchulus spp.*, *Helicotylenchus spp.*, *Trichodorus spp.*, *Longidorus spp.* and many others.

Meloidogyne spp. (Root-Knot Nematode - RKN)

The *Meloidogyne* genus is represented by close to 100 recognized valid species, and *M. incognita*, *M. javanica*, *M. arenaria*, and *M. hapla* are the most important ones [14]. Root-knot nematodes are major pests of horticultural crops and are able to infect more than 50 different horticultural plant species. *Meloidogyne* is a cosmopolitan genus, but its distribution is more common in temperate, subtropical, and tropical areas [20]. Three major successful features of this genus can be described: an elaborate parasitism strategy (induction of the host root cells to differentiate into nurse cells, which allows its development and reproduction), female morphology (its pear shape and sedentary behaviour allows the presence of two ovaries and the development of a large amount of eggs (average 400 eggs)), and different reproductive approaches (sexual and asexual reproduction). Even in male-independent reproduction, egg development is an energy-saving strategy [14]. The *Meloidogyne* life cycle consists of six developmental stages: egg, four larval stages (juvenile) and adult, taking approximately 25 days for completion. Once the second larval stage (J2) is attained, all the following stages are actively infectious, meaning that they are able to penetrate and parasite the host cells [21,22].

Infection by root-knot nematodes relies on the development of specialized feeding cells in the vascular cylinder, endoderm and cortex areas, called giant or nurse cells. During this process, there is also a hyperplastic and hypertrophic cell response in the infected area that causes root thickening, and each crop can respond differently. However, in the end, this process always culminates in gall development, which can compress xylem vessel elements, resulting in vascular cylinder disorganization and therefore interference in absorption and internal solute transport [23].

Many vegetable crops are susceptible to *Meloidogyne spp.*, particularly potato (*Solanum tuberosum*), tomato (*Solanum lycopersicum*), carrot (*Daucus carota*), lettuce (*Lactuca sativa*), aubergine, okra, cucumber, and gourds. The first symptoms of root-knot infection in tubers may be internal, but external symptoms are visible ~2 months later, with the appearance of galls on the surface. Galls can give a rough appearance to the surface and may be accompanied by cracks to large, isolated lumps [24]. The tubers show a ‘popcorn-like’ or ‘pimple-like’ structure with an associated rotted aspect due to starch loss in the tissue (Figure 1) [25]. Although visual diagnoses after a high level of infection can be easily performed, the extraction method improves the early detection of root-knot infection [26]. The root-knot damage in potato can be recognized by plants withering even in moist soil, yellowed leaves and growth problems [27]. *Meloidogyne hapla* causes more root gall proliferation in potato, while *M. arenaria*, *M. incognita*, and *M. javanica* cause knobbly tubers in addition to root galls. Root-knot infection symptoms in ginger include gall formation, but it is especially characterized by rhizome damage showing unusual brown to black lesions with an associated layer of accumulated fluid [25,28]. In carrots, infection results in excessive root growth, forking formations and galls around the lateral roots, while beadlike galls occur in the outward appearance of lettuce, and obvious galls can be easily observed in okra and pumpkin roots (Figure 2) [25,29,30].

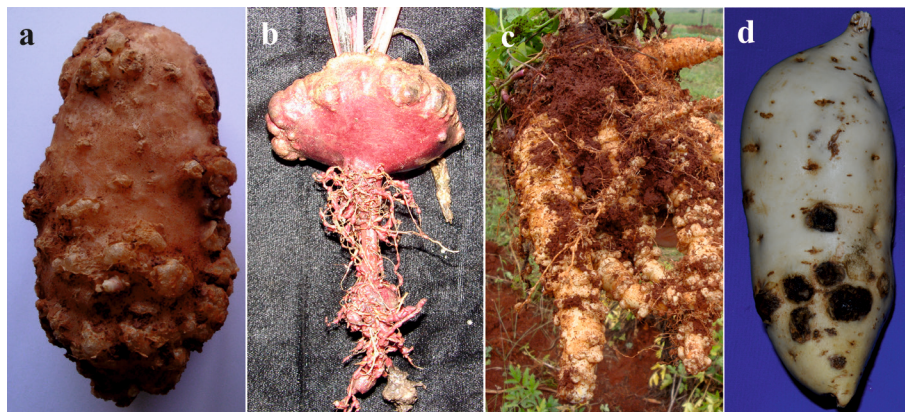


Figure 1: (a) Tuber symptoms caused by *Meloidogyne spp.* show a ‘popcorn-like’ structure in potato; (b) sugar beet; (c) Peruvian carrot, (d) and sweet potato

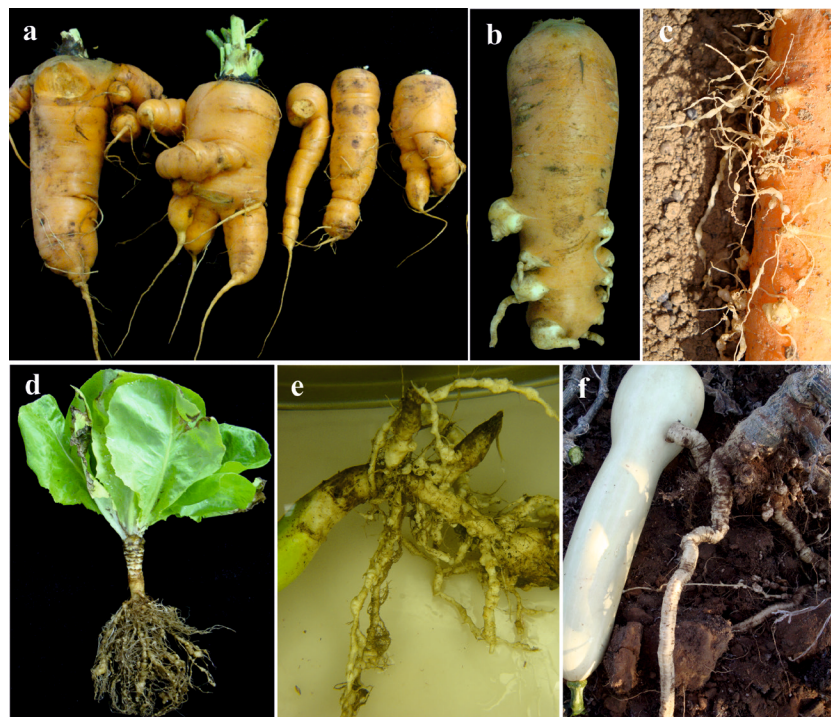


Figure 2: (a) Symptoms caused by *Meloidogyne spp.* infection in carrots show bifurcation and protuberances; (b) evident gall formation; (c) and galls in carrot secondary roots; (d) galls in lettuce roots; (e) galls in okra roots; (f) and big galls pumpkin roots.

Other important cultures affected by *Meloidogyne* infection are gilo, cabbage, pepper and melon, all presenting evident gall formation, affecting their development and production (Figure 3). Moreover, the damage caused to the roots and tubers (galls and injuries) are generally very compromising in terms of plant development [31]. Some cultures that are more uncommonly parasitized by other nematode species but are good hosts to *Meloidogyne* nematodes are bell pepper (*Capsicum annuum*), black pepper (*Piper nigrum*), garlic (*Allium sativum*), and onion (*Allium cepa*).



Figure 3: (a) Severe symptoms caused by *Meloidogyne* spp. infection in gilo roots; (b) cabbage roots; (c) pepper roots; (d) and melon roots

Among the fruits, important root-knot hosts include banana (*Musa spp.*), grapevine (*Vitis vinifera*), and papaya (*Carica papaya*), and infection may cause up to 33% and 50% losses in melon (*Cucumis melo*) and watermelon production, respectively [32]. A root-knot nematode species that has been recently highlighted in vegetable production is *Meloidogyne enterolobii* (syn. *M. mayaguensis*) (European 2014). The major problem in terms of *M. enterolobii* infection in horticulture has been their fast propagation and dissemination in the soil, with records all over the world. This root-knot species has a wide host range, being able to overcome the resistance of many horticultural products. In France and Switzerland, *M. enterolobii* was detected in 1983 as an important problem in tomato production areas [33]. In Northeast Brazil, *M. enterolobii* was described in 2001 in guava production areas and later as infecting green pepper rootstock and cucumber in other areas [34]. Its presence was also reported in jalapeño pepper and watermelon in Mexico [35]. Other economically important *M. enterolobii* hosts are aubergine, bean, sweet potato, and ornamental plants, such as *Brugmansia* and *Clerodendron*.

***Pratylenchus* spp. (Root lesion nematode - RLN)**

Pratylenchus pratensis was first described in 1880 [30]. Currently, the genus *Pratylenchus* is found worldwide, with more than 75 species already described [36]. Also known as lesion nematodes, they compose an important group of root migratory ectoparasites in a great variety of hosts. The damage caused by lesion nematodes in roots and tubers is distinct, as they do not produce a feeding site like cyst or root knot nematodes. *Pratylenchus* attack creates galleries in host tissues due to their free movement through the root and feeding in the plant cortex, resulting in dark spots or lesions. This disparity among genera likely occurs because the ability of members of the nematode phylum to parasitize plants appears to have arisen through several independent evolution events [37,38].

Reproduction in members of the *Pratylenchus* genus may be sexual or asexual depending on the species. *Pratylenchus neglectus*, *P. thornei* and *P. brachyurus* reproduce by parthenogenesis, while male and female *P. penetrans* must mate before producing fertile eggs. *Pratylenchus* females lay an average of one egg per day, and, at appropriate temperatures, the cycles range from 45 to 65 days [39,40]. Once juveniles emerge from the eggs, approximately one week after egg deposition, all stages are capable of infecting and feeding from plant roots. Lesion nematode damage in plant roots is generally evidenced by necrosis and death, as exemplified in pepper (Figure 4).



Figure 4: (a) Necrosis Symptoms in Pepper Roots caused by *pratylenchus* spp. Lesion Nematode Infection in *capsicum annuum* (b) and *capsicum baccatum*

The most economically important species in potato and tubers worldwide are *P. penetrans* and *P. scribneri* [25]. These root lesion nematodes usually get inside tubers using lenticels and then invade the surrounding tissue, causing variable-sized circular lesions (Figure 5) [41]. Although these lesions are usually superficial, restricted to the outer 0.5 mm of the tuber, this damage always decreases the marketable quality of the product [30]. The symptoms of root lesion nematode infection in yam are more severe, and infection is characterized by a dehydrated aspect, cracked skin, and softness of the tuber when pressed.

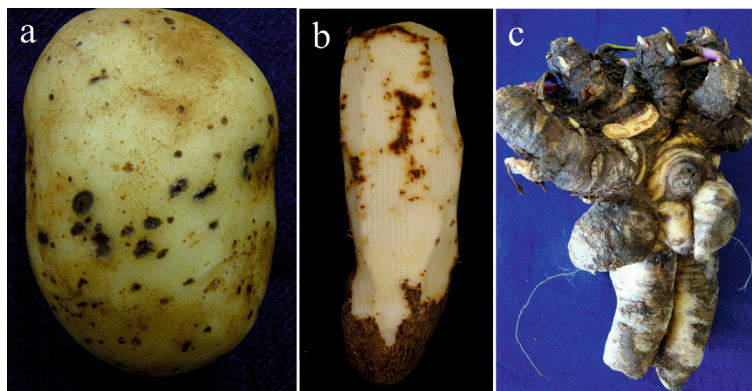


Figure 5: (a) Tuber Symptoms caused by *Pratylenchus* spp. Infection shows Necrotic Spots all over in Potato; (b) Peeled yam; (c) and Peruvian carrot

Pratylenchus attack in broadleaf plants, especially lettuce, results in a reduction in growth, yellowing, and small head formation, preventing their sale at market [29]. Peanut (*Arachis hypogaea* L.) is an important oilseed horticulture crop and showed a yield of 39.3 million tons in 2012 [42]. Indeed, root lesion nematodes have caused significant losses in peanut production worldwide, infecting roots and causing above-ground symptoms, such as a clustered arrangement of stunted plants, chlorosis and premature senescence [25]. However, peanut yield losses caused by nematodes are most often associated with damage to pods and pegs. Peanut pods infected by *Pratylenchus* can be identified by the presence of small brown tunnels (tan spots with dark centres) in the shells and shrivelled pegs. Root lesion nematodes have also been associated with losses in fruit, such as grape, banana, pineapple, and soursop. In soursop, *Pratylenchus* causes a symptom known as sudden death, characterized by dark lesions on the plant neck region, right below the soil [43].

***Radopholus* spp. (Burrowing nematode - BWN)**

The phytopathogenic *Radopholus* genus is known as burrowing nematode, and several species compose this migratory endoparasitic group. The *Radopholus* genus has a relatively wide host range of more than 300 plant species, and the most important species for horticulture are *R. citri* and *R. similis*, which can infect citrus and banana, respectively. Burrowing nematode causes damage worldwide and can be found especially in tropical and subtropical areas [44]. *Radopholus* presents similar behaviour and life cycles to those of *Pratylenchus* spp. Burrowing nematode females and juveniles are highly infective and complete their life cycles within the host root cortical cells, causing root cell death and necrosis. *Radopholus* reproduces sexually; 2 to 5 eggs are laid per day in the root tissues, and the entire life cycle can be completed in 3 weeks under favourable conditions [45]. The most characteristic symptoms of *Radopholus*-infected plants are lesions and burrows in the roots, a result of their movement inside the tissue, causing destructive damage and malnutrition [25].

The disease caused by *Radopholus similis* in banana is known as ‘blackhead’ due to feeding on the root cortex, which can cause internal tissue necrosis. Other burrowing nematode infection symptoms in banana are impaired or stunted growth, incomplete or yellowing leaves, small bunches and uprooting [43]. *Radopholus similis* has already been recorded as the cause of 100% losses in Cavendish banana [24]. *Radopholus similis* is also a problem for ginger, and the symptoms are similar to those seen in *Meloidogyne* infection. *Radopholus citri* and *R. similis* can be serious problems for citrus. *R. citri* damage is considered to be an important issue, causing stunted growth in citrus and reducing fruit production in terms of quantity and quality.

***Ditylenchus* spp. (Stem and Bulb Nematode - SBN)**

Stem and bulb nematodes, as *Ditylenchus* spp. nematodes are called, are a group of migratory endoparasitic nematodes that can infect plant stems and leaves [46]. They are devastating phytonematodes that can be found worldwide, especially in temperate areas [47]. Outside of eggs, all stem and bulb nematode life stages are infective. Under adverse conditions, *Ditylenchus* species are able to produce a dormant structure known as ‘nematode wool’, which is a bundle of juveniles, to survive [48,49]. The plant symptoms

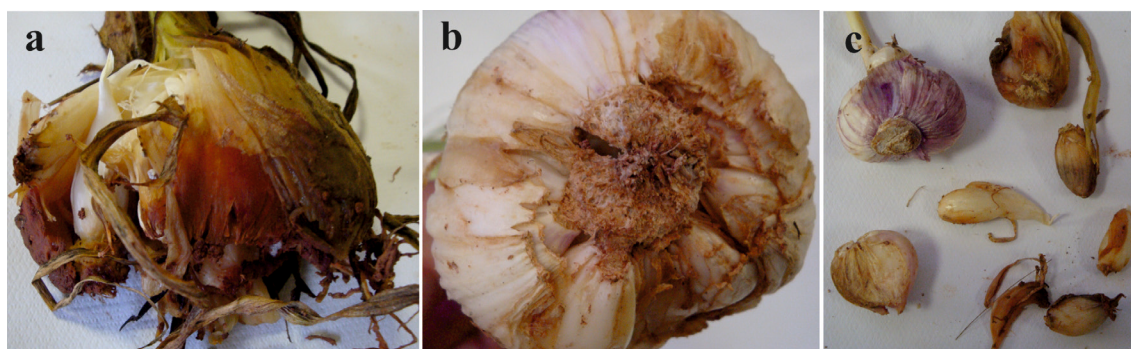


Figure 6: (a) Symptoms caused by *Ditylenchus* spp. Infection in Garlic. Twisted garlic bulb; (b) Rough-Looking bulb; (c) and Garlic Clove

of *Ditylenchus* infection are usually swollen, distorted stems, with reddish-brown to black lesions [50]. This genus can be a serious problem in potato crops, with *D. dipsaci* and *D. destructor* causing dry rot, whereas the latter species causes more severe damage [49]. However, horticultural losses caused by *Ditylenchus* have been most associated with *Allium* production (Figure 6) [51].

In onion, seedlings infected by *D. dipsaci* became gnarled and misshapen, often resulting in plant death. Throughout the crop cycle, onion leaves fall, bulbs become empty and roots yellow. In garlic, the symptoms are dwarfism, swelling, and extensive longitudinal splitting of the cotyledons and leaves, which are short and thick and often have brown or yellowish spots due to discoloration of the tissues, and swelling above the bulb in the pseudo-stem, causing the cigar formation [52]. Recently, *D. arachis* was associated with peanut pod rot, causing brown discoloured pods, pegs, hull endocarps, and smaller and shrunken seeds [50].

Other important nematode genera

There are many other important nematode genera that affect horticultural crops, such as *Heterodera*, *Globodera*, *Rotylenchus*, *Tylenchulus*, *Helicotylenchus* and *Xiphinema*. *Heterodera* species, also known as cyst nematodes (CYN), are sedentary endoparasitic nematodes that can infect cabbage, carrot, broccoli, and other crops. Cyst nematodes also cause very important damage in sugar beet. In guava production, *H. dihystra* has been reported as an important pest. Golden cyst nematodes (GCN), species of the *Globodera* genus, have a similar behaviour to that of *Heterodera* as sedentary endoparasites, but their cysts are globose in shape. The most important species of this genus are *G. rostochiensis* and *G. pallida*. *Globodera* is known as especially important in potato crops.

The *Rotylenchulus* genus, also known as reniform nematodes (RNN) due to their kidney-like shape, is most represented by the *Rotylenchulus reniformis* species. It is a sedentary semi-endoparasite that is commonly associated with the rhizosphere of several horticultural crops, especially in tropical and subtropical soils. *Rotylenchulus reniformis* has been a threat to pineapple production areas, suppressing yields and causing slight to severe stunting and reddening of the leaves. Citrus nematodes (CTN), species of the *Tylenchulus* genus, have a similar behaviour to that of *Rotylenchulus* as a sedentary semi-endoparasite, and they have a range of more restricted hosts. *Tylenchulus semipenetrans* is the most important species in this genus, and it is responsible for the slow decline of citrus. These symptoms are characterized by a gradual decline in growth, leaf health and size, fruit size and quality over the years.

Helicotylenchus is a genus that contains nematodes called spiral nematodes (SRN) due their bodies being wrapped into a spiral format. It is a migratory ecto-/endoparasite commonly associated with turfgrasses and other grass hosts. In addition, spiral nematodes can cause crop damage in banana and other fruit trees. The *Xiphinema* nematode genus can cause important yield losses in horticultural crops when found in high population numbers. These migratory ectoparasites are also known as dagger nematodes (DGN) and can seriously affect cashew tree and vine crops. The damage caused by these nematodes also occurs due to their involvement in virus transmission.

Members of the *Aphelenchoides* genus, also known as leaf and bud nematodes, show migratory behaviour, living in and feeding upon the aerial portions of a plant but are rarely associated with the soil. They cause serious damage to alfalfa and strawberries and are an emerging problem for gardeners because of this broad host range and their ability to spread quickly in hostas and many ornamentals [53,54]. The nematode feeds on mesophyll cells by infecting buds and the stomata of young leaves. The infected leaf areas become chlorotic and subsequently necrotic, usually surrounded by large vein structures. *A. ritzemabosi* is commonly called the chrysanthemum foliar nematode, and *A. fragariae* is called strawberry crimp. On strawberry and *Anthurium* seedlings, *A. fragariae* can easily lead to plant death.

Auspicious Strategies in Horticulture

Therefore, now the most important concern is how many horticultural crops are and will be grown in the near future, even facing this strong opponent? [44]. Nematicides have been used in many countries, but they are strongly limited by their high prices and low efficiency. However, this is not the most important concern. Some of the most effective nematicides have disadvantages not for being expensive but because they are extremely toxic to human and animals. As long as people are aware of environmental protection, intensive research efforts for the development eco-friendly alternative strategies in nematode management have become imperative [15]. Indeed, the future of nematicides in horticulture will depend on new compounds that are effective and environmentally safe. Crop rotation is another alternative that can be used to decrease phytonematode populations in the soil. This technique uses some resistant plants species as a 'trap' to attract the nematodes, especially *Crotalaria spectabilis* [55]. However, many of the resistant species that can be applied as a 'trap' in crop rotation are not economically profitable. Meanwhile, most of the researchers involved in creating a solution for plant nematode infection and consequent losses endorse that the genetic approach for plant tolerance or resistance seems to be the best alternative [56].

Several dominant, recessive and co-dominant resistance (R) genes, which affect nematode virulence, and quantitative trait loci (QTLs), which confer strong resistance, have been discovered in different horticulture plants, especially those for sedentary nematodes, such as the *Mi* gene in tomato and the *N* gene in pepper against *Meloidogyne* spp. [57]. The *Mi* gene, well described in the literature for incompatible plant-nematode interactions, confers resistance to *M. incognita*, *M. javanica*, *M. arenaria* and *M.*

enterolobii in tomato (*Solanum lycopersicum* L.) [58]. However, the effect of this gene depends on the root-knot nematode species or race [59,60]. So far, the *Mi* gene has been the main target for breeding programmes in attempts to develop complete resistance against *Meloidogyne* spp. in tomato cultivars.

Paal and co-workers [61] described the gene *Gro1-4* in tomato as being able to confer resistance to *G. rostochiensis* (pathotype Ro1). The *psorPM1* gene in *Prunus sogdiana* shows similar structure and high homology with the *Mi-1.2* gene, and it seems to play an important defence function against the root-knot nematode, mainly in the phloem or pericycle [62]. Stone fruit crops, *Prunus* spp., are severely damaged by root-knot nematodes (RKN), and some resistance genes have been identified, such as *Ma* and *Rjap* (*Prunus cerasifera* - plums), *RMia* (*Prunus persica* - peach) and *RMja* (*Prunus dulcis* - almonds). The *RMia* gene confers resistance to *Meloidogyne incognita* and *Meloidogyne arenaria* in peach genotypes [63]. However, no gene seems to confer a resistance spectrum as complete as the *Ma* gene in plums. *Ma* has been tested against more than 30 mitotic and meiotic reproduction strategies in *Meloidogyne* species, and it triggers a hypersensitive-like reaction (HLR) that results in high-level resistance, even at high temperatures [64].

Mao *et al.*, reported [65] that *CaRKNR* was induced by *M. incognita* in pepper plants (*Capsicum annuum* L.) and by virus-induced gene silencing (VIGS), and its function was correlated with resistance against root-knot nematodes. A myo-inositol-1-phosphate synthase gene, *MIPSI*, has been shown to improve tolerance to abiotic stresses in several plant species, such as salt and drought stress. This gene has also been shown to be involved in stem nematode resistance (*Ditylenchus destructor* Thorne) in sweet potato (*Ipomoea batatas*) [66] *tuberosum*, which confers resistance to *Globodera pallida*, and *rkn1* from *Gossypium hirsutum*, which confers resistance to *M. incognita*.

There has been remarkable progress in quantitative nematode resistance analyses in horticulture. In analyses of three diverse sources of carrot (*Daucus carota*) resistance against *Meloidogyne incognita*, Parsons *et al.*, [67] were able to map its genetic resistance. The analysis revealed five non-overlapping QTLs on chromosomes 1, 2, 4, 8, and 9, conditioning resistance in the segregating population from three different crossings. However, the consensus map showed one QTL present in the same region of chromosome 8 in all three populations. The resistance of horticultural crops against migratory nematodes seems to occur in the first identification steps. The dagger nematode, *Xiphinema index*, attacks the deep perennial system of grape roots. The infection causes the depression of plant growth through root damage. Chin-Feng Hwang *et al.* [68] demonstrated that resistance to *X. index* was highly controlled by a major quantitative trait locus, XiR1, in hybrid lines from *Vitis arizonica/girdiana*.

Last but not least, effector elucidation is also an auspicious approach towards nematode control in horticulture. Although plant-parasitic nematode behaviour shows a variety of groups and life styles, morphological features have been successfully applied as an evaluative approach to establish the phylogeny of phylum Nematoda [38]. All nematode species present a stylet that is not just for feeding but also used for injecting secreted proteins, called effectors or parasitism proteins, which are produced in nematode oesophageal gland cells and affect the host apoplast and cytoplasm. These molecules can affect several plant processes, such as cell cycle activation, plant signalling, and cell morphogenesis, allowing infection success. The understanding of the factors that allow nematode harmfulness, plant susceptibility or immunity and host range can be crucial for developing new strategies for controlling nematodes and other important phytopathogens [69].

Currently, there are 15 phytonematode species compound sequence databases of ESTs and genes, including six for *Meloidogyne* and five for members of the migratory group, such as *Pratylenchus penetrans* [70]. It is clear that this information is accelerating the identification of new nematode parasitism proteins. Since 2010, more than 11 effectors in several nematode species have been identified, such as GrVAP1, a venom allergen protein, in *G. rostochiensis* [71], Hs10A06, related to defence suppression, in *H. schachtii* [72] and MiCRT, a calreticulin also related to defence suppression, in *M. incognita* [73]. *Rs-cr*, a calreticulin from *Radopholus similis*, is related to pathogen reproduction and pathogenicity in tomato. After the treatment of juveniles with *Rs-cr* dsRNA for 36 h, researchers showed that transgenic tomato plant resistance to *R. similis* was significantly improved, affecting pathogen reproduction and pathogenicity [74]. 14-3-3 protein and RBP-1 protein are new effector candidates from the beet cyst nematode, *H. schachtii* [75].

Some effectors can be identified particularly during their interaction with horticultural crops. The gene silencing of *Cg-1* from *M. javanica* leads to the acquisition of virulence in tomato [76]. As demonstrated before, *Mi-1* confers resistance against several species of root-knot nematode in tomato; however, a unique *M. javanica* strain is able to infect *Mi-1* plants. After silencing a candidate nematode effector gene, *Cg-1*, in nematode juveniles of the *Mi-1*-avirulent strain, the virulent progeny are able to infect tomato plants carrying the *Mi-1* gene, suggesting that *Cg-1* is responsible for virulence and is required in the nematode for *Mi-1*-mediated resistance. Li *et al.*, [74] performed studies with tomato and described a nematode calreticulin, *Rs-crt*, in *Radopholus similis*. After the treatment of juveniles with *Rs-crt* dsRNA for 36 h, they showed that the resistance of transgenic tomato plants to *R. similis* was significantly improved, affecting pathogen reproduction and pathogenicity.

Thorpe *et al.*, [77] performed genomic characterization for *Globodera pallida* effector identification. Also known as the potato cyst nematode, 128 orthologues of effectors were identified from other nematodes, as well as 117 novel effector candidates. Eves-van den Akker *et al.*, [78] provides the identification and characterization of a novel group of hypervariable extracellular effectors, termed HYP, in the potato cyst nematode, *G. pallida*. HYP expression was identified in secretory cells by *in situ* hybridization and detected the protein in apoplastic host cells by immunohistochemistry. In addition, effector silencing by RNAi in planta resulted in a reduction in nematode infection.

Fosu-Nyarko *et al.*, [75] performed an analysis of the transcriptome of the beet cyst nematode, *H. schachtii*, looking for effector candidates. After sequence comparison analyses with other already described plant parasitic nematode species effectors, 30 similar *H. schachtii* transcripts were found. Among these identified transcripts were new effector sequences for this species, such as a calreticulin, 14-3-3 protein and RBP-1 protein. This protein family includes highly conserved eukaryote-specific proteins involved in several cellular and biochemical processes through interaction with phosphorylated target proteins. As described in other phytonematodes, 14-3-3 proteins can play several roles in host-parasite communication.

Finally, it is clear how phytonematodes are an important threat to the world's horticulture. However, even with many studies focusing on the horticultural losses caused by this enemy, there is still a lot to be overcome. Although their detection and symptoms are already possible and well known, new methods for faster diagnosis and control should be developed. We see how horticulture is complex, diverse, interactive, and powerful, but also for these reasons, further studies need to be directed in order to identify resistant genes and nematode effectors to rise up new management approaches.

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgements

We wish to thank our laboratory co-workers from EMBRAPA Vegetables and Soybean for good support and the National Council for the Improvement of Higher Education (CAPES) for the granting of a scholarship to support this study. Our studies are funded by EMBRAPA - Brazilian federal government.

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