

Evaluating the Consequences of Parasitic Nematodes on Agricultural Productivity

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Abstract:

One of the world's biggest challenges today is providing enough food for a growing population, especially in areas like Africa where resources are few. The need for food is predicted to increase by 75% by 2050, while the global population is estimated to increase by 35%. Parasitic nematodes substantially threaten crop yields and quality, although they are often overlooked. Tiny, unsegmented roundworms known as parasitic nematodes cause significant harm to plants; they parasitize. The specialized features of certain nematodes, such as root-knot, cyst, lesion, and foliar nematodes, enable them to enter plant cells and take up nutrients, resulting in stunted development, lower yields, and, in extreme situations, plant death. Because the damage they do is typically hidden by other factors that hinder progress, their significance is frequently undervalued. A comprehensive strategy focusing on population control instead of eradication is necessary for effective nematode management. To lessen their effects on crop productivity and guarantee global food security, this chapter emphasizes the serious agricultural risks these nematodes represent and stresses the significance of integrated control strategies.

Introduction:

A significant global issue in the years ahead will be securing adequate food supplies for an increasing worldwide population. This concern is particularly urgent in resource-limited areas, such as Africa, where populations proliferate. By 2050, the global population is projected to rise by 35%, while the demand for food may jump by 75% due to economic development and shifting eating habits (World Bank (2008) World Development Report, 2008). To satisfy this demand, it

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is essential to significantly enhance resource use efficiency significantly. Improving crop yields to achieve maximum efficiency will necessitate effective management of pests and diseases, particularly as the production of specific products changes. Consequently, it is vital to thoroughly tackle all limitations in crop production, including the frequently overlooked problem of nematode restrictions.

Over 90 nations across the globe are currently utilizing indoor farming techniques to grow a diverse range of crops, such as fruits and flowers, with vegetables representing the most significant category (Hickman, 2019). The primary crops produced on indoor farms include tomatoes, cucumbers, peppers, eggplants, and strawberries, with yearly production amounts reaching 910 million kg, 400 million kg, 370 million kg, 53 million kg, and 41.5 million kg, respectively (FAO, 2017). Countries that extensively practice protected agriculture consist of China, Spain, South Korea, Turkey, Japan, Mexico, Brazil, Italy, Morocco, and Israel, holding 70% of the global area dedicated to protected agriculture, covering 5.63 million hectares. Noteworthy is the fact that the Netherlands accounts for 70% of flower exports worldwide through protected agriculture. Furthermore, China contributes to 90% of the global output of protected vegetables, while Israel effectively cultivates high-quality fruits, vegetables, and flowers in arid desert climates through indoor farming methods (Chang et al., 2013; Hickman, 2019).

Parasitic nematodes are tiny, elongated, unsegmented roundworms found in various habitats, including soil, water, and within plants and animals. They play a significant role as plant pathogens, consuming plant tissues and leading to significant harm to crops (Chitwood, 2003). These nematodes have developed unique structures like styles that enable them to penetrate plant cells and draw out nutrients. Their parasitic lifestyle causes several physiological and morphological alterations in host plants, which can lead to stunted growth, decreased yields, and, in some cases, the death of the plants (Mandal et al., 2021). Plant-parasitic nematodes are distinguished by their style and the sub-ventral and dorsal esophageal glands, essential for survival as parasites. Although they appear segmented due to multiple annulations on their cuticle, they are unsegmented, providing flexibility without causing kinks. Their bodies possess specialized organs for feeding, digestion, nerve functions and waste elimination, alongside advanced reproductive systems, but they do not have circulatory or respiratory systems (Mandal et al., 2021; Kundu, 2022). Many nematode species are also called "farmer's best friends" because they can eliminate insect pests (Shah and Mahamood, 2017). Crop damage caused by nematodes often goes unnoticed, as it can be obscured by other factors that impair plant growth (Schmitt and Sipes, 2004). To effectively manage nematodes, a comprehensive strategy is necessary. Since total eradication is unattainable, the goal is to regulate their population and maintain their numbers below damaging levels (Schmitt and Sipes, 2004). Approaches include planting resistant varieties of crops, practising crop rotation, adding soil amendments, and applying pesticides. In some cases, soil solarization may also be beneficial (Schmitt and Sipes, 1998).

Agricultural productivity is vital in ensuring food security worldwide but often faces threats from various biological and environmental factors. One of the significant, frequently overlooked challenges is posed by parasitic nematodes. These small, soil-dwelling worms can inflict serious harm on crops, resulting in reduced yields, poorer quality of produce, and increased production costs. Despite their tiny size, the damage they cause can be extensive, impacting not only individual plants but also entire agricultural systems.

Biology and Ecology of plant parasitic nematodes:

Classification:

Plant-parasitic nematodes are classified based on their taxonomic ranks and the morphological characteristics that define different families and orders. According to the classification system provided by De Ley and Blaxter in 2002, it is used, which integrates molecular phylogenetic results with morphological analyses. The major nematode orders containing plant-parasitic species are Rhabditida, Dorylaimida, and Triplonchida. Below is the detailed classification (Mekete et al., 2012):

Order: Rhabditida

Infraorder: Tylenchomorpha

1. Superfamily: Aphelenchoidea
 - Family: Aphelenchidae
 - Family: Aphelenchoididae
 - Family: Paraphelenchidae
2. Superfamily: Criconematoidea
 - Family: Criconematidae
 - Family: Hemicycliophoridae
 - Family: Tylenchulidae
3. Superfamily: Myenchoidea
 - Family: Myenchidae
4. Superfamily: Sphaerularioidea
 - Family: Allantonematidae
 - Family: Anguinidae
 - Family: Iotonchiidae
 - Family: Neotylenchidae
 - Family: Parasytylenchidae
 - Family: Sphaerulariidae
 - Family: Sychnotylenchidae
5. Superfamily: Tylenchoidea
 - Family: Atylenchidae
 - Family: Belonolaimidae

- Family: Dolichodoridae
- Family: Ecphyadophoridae
- Family: Heteroderidae
- Family: Hoplolaimidae
- Family: Meloidogynidae
- Family: Pratylenchidae
- Family: Psilenchidae
- Family: Telotylenchidae
- Family: Tylenchidae
- Family: Tylodoridae

Order: Dorylaimida

1. Superfamily: Dorylaimoidea

- Family: Dorylaimidae
- Family: Longidoridae
- Family: Xiphinematidae
- Family: Trichodoridae

Order: Triplonchida

Suborder: Diphtherophorina

1. Superfamily: Diphtherophoroidea

- Family: Diphtherophoridae
- Family: Trichodoridae

Suborder: Tobrilina

1. Superfamily: Pristomatolaimoidea

- Family: Pristomatolaimidae
2. Superfamily: Tobriloidea
- Family: Pandolaimidae
 - Family: Rhabdodemaniidae
 - Family: Tobrilidae
 - Family: Triodontolaimidae

Suborder: Triplonchida

- Family: Bastianiidae
- Family: Odontolaimidae

Suborder: Tripylina

3. Superfamily: Tripyloidea

- Family: Onchulidae
- Family: Tripylidae

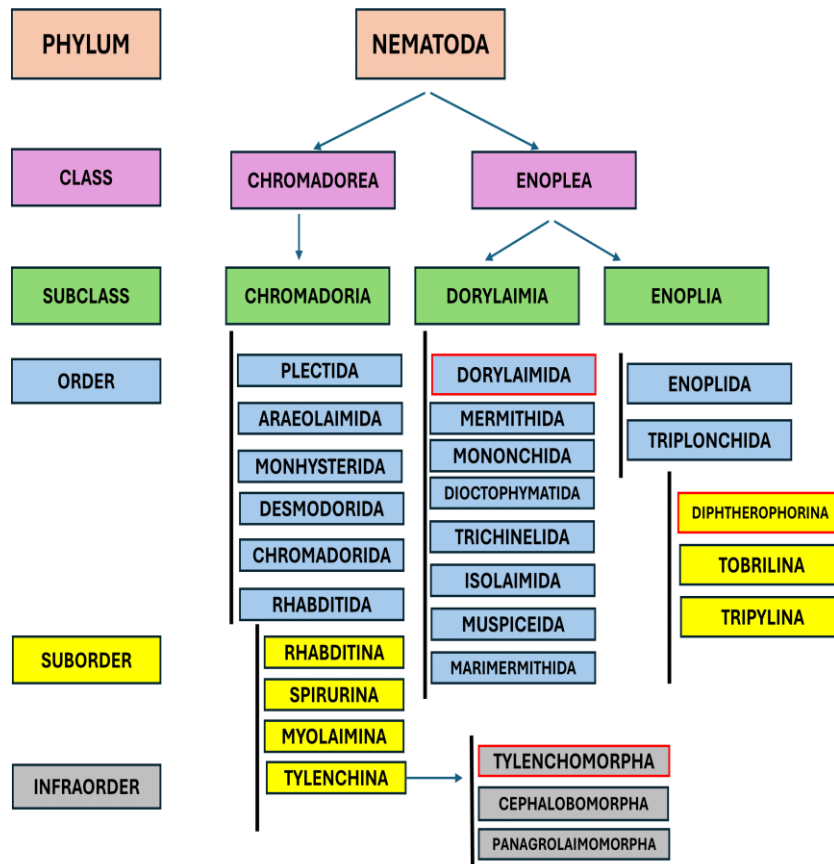


Figure 1. Taxonomic classification of Parasitic Nematode (De Ley and Blaxter, 2002)

Notable Genera and Species:

- Root-Knot Nematodes (*Meloidogyne* spp.)

These nematodes are considered some of the most harmful parasites affecting plants, as they create root galls that hinder the plant's capacity to take up water and nutrients. Species like *Meloidogyne incognita* and *Meloidogyne javanica* are prevalent and target a range of crops (Subedi et al., 2020).

- Cyst Nematodes (*Heterodera* spp. and *Globodera* spp.)

Cyst nematodes create cysts on plant roots, which can survive in the soil for many years, complicating management efforts. *Heterodera glycines* (the soybean cyst nematode) and *Globodera rostochiensis* (the potato cyst nematode) are notable threats to their respective crops (Ibrahim et al., 2017).

- Lesion Nematodes (*Pratylenchus* spp.)

Lesion nematodes infiltrate root tissues, resulting in necrotic lesions that diminish the plant's functionality. Common species such as *Pratylenchus penetrans* and *Pratylenchus neglectus* impact various crops (Jones and Fosu-Nyarko, 2014).

- Foliar Nematodes (*Aphelenchoides* spp.)

These nematodes attack the aerial parts of plants, such as leaves and buds, leading to deformation and tissue. *Aphelenchoides fragariae* is particularly known for its impact on strawberries and various ornamental species (Handoo et al., 2020).

1.3. Life Cycle and Reproduction:

Nematodes experience a life cycle consisting of six distinct stages: an egg stage, four juvenile stages, and an adult stage. The first four stages are deemed immature and categorized as juvenile stages (Wharton and Wharton, 1986). This life cycle is straightforward. Generally, female nematodes deposit their eggs in soil or within plant tissues, either individually or in clusters. These eggs are oval and have protective layers, including an outer coating, an inner lipid layer, and a valid shell. The first moult occurs within the egg, leading to the second-stage juvenile (J2) emergence as it breaks free from the eggshell. These larvae can either stay within the host throughout their life or migrate away from the feeding areas. In terms of appearance, the larvae closely resemble adult nematodes. Adult nematodes predominantly inhabit the soil, feeding on newly developed roots (Maggenti and Allen, 1959). A depiction of the nematode life cycle is presented in Figure 1.

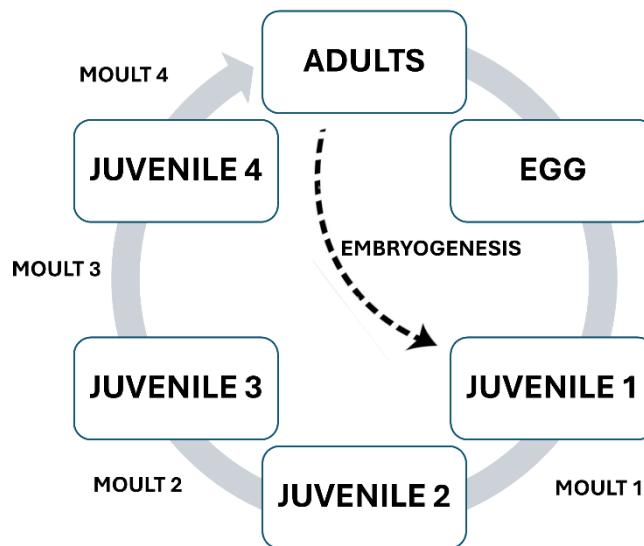


Figure 2. Life cycle of plant parasitic nematodes (Mandal et al., 2021).

Host range and Specificity:

Cyst Nematode (*Heterodera* spp.)

Distribution:

Cyst nematodes, such as *H. filipjevi* and *H. latipons*, have been identified in various locations, including North Africa, Algeria, several European nations, and the Mediterranean region (Smaha et al., 2019).

Host Range:

The genus *Heterodera* includes 70 identified species, among which 12 species from the *H. avenae* are especially detrimental economically. These nematodes mainly target crops such as potatoes, soybeans, oats, wheat, and barley (Bohlmann and Sobczak, 2014).

Symptoms:

Intense populations of cyst nematodes can lead to poor growth, wilting, and yellowing of the leaves, resulting in notable reductions in crop yield. After several weeks of parasitism, adult females can be observed attached to the roots of the host plants (Mitiku, 2018; Lilley et al., 2005).

Life Cycle Duration:

The life cycle of cyst nematodes spans up to 55 days, and they reproduce through an amphimictic method (Turner and Subbotin, 2006).

Feeding Habit:

Juvenile cyst nematodes are migratory endoparasites that penetrate plants' vascular tissue and consume their sap (Mitiku, 2018).

Root Rot Nematode (*Hirschmanniella* spp.)

Distribution:

Hirschmanniella miticausa has been found in Papua New Guinea and the Islands (CABI, 2019). These stationary nematodes are referred to as such due to the knot-like galls they create on the roots of affected plants (Subedi et al., 2020).

Host Range:

The genus *Hirschmanniella* consists of 24 species, with 12 of them parasitizing rice. They also infest other crops, including cotton, sugarcane, and maize (Regmi and Desaeger, 2020).

Symptoms:

Symptoms above the ground are not prominently visible, although infected plants might show signs of chlorosis and hindered growth. *H. oryzae* penetrates through lateral roots and moves into the aerenchyma, leading to tissue death. Additionally, subsequent infections by other microorganisms can cause browning of the rice roots (Bauters et al., 2014).

Life Cycle Duration:

Under optimal conditions, the life cycle of these nematodes can last up to 30 days and involves sexual reproduction. They display migratory endoparasitic behaviour (Regmi and Desaeger, 2020).

Sting Nematode (*Belonolaimus* spp.)

Distribution:

From Texas to Virginia, *Belonolaimus longicaudatus* was initially documented in the southeastern United States, typically along the Gulf of Mexico and the Atlantic coasts. This species has also been observed in Australia, Venezuela, and Brazil (Gozel et al., 2006).

Host Range:

The host plants of *B. longicaudatus* include corn, turfgrasses, peanuts, citrus fruits, strawberries, and various root vegetables (Abu-Gharbieh and Perry, 1970).

Symptoms:

High populations of *B. longicaudatus* can damage root areas, hindering the uptake of water and nutrients. This results in stunted plant growth, wilting, leaf yellowing (chlorosis), and, in extreme cases, the death of the plant (Mandal et al., 2021).

Life Cycle Duration:

This ectoparasitic nematode can have a life cycle lasting up to 28 days, with reproduction taking place through an amphimictic process (Mandal et al., 2021).

Citrus Nematode (*Tylenchulus* spp.)

Distribution:

Tylenchulus semipenetrans is found globally and frequently in citrus plants. This nematode mainly targets species from the Rutaceae family, particularly *Poncirus trifoliata* and its hybrids. Other hosts include grapes, olives, and persimmons (Inserra et al., 1994).

Symptoms:

T. semipenetrans can lead to economic losses in yield ranging from 10 to 30%. Visible signs above the ground include stunted plant growth, yellowing leaves, and decreased fruit production. The roots of infected plants become thicker than those of healthy plants, resulting in a gradual decline in the health of citrus crops (Verdejo-Lucas and McKenry, 2004).

Duration of Life Cycle:

Citrus nematodes exhibit a semi-endoparasitic feeding behavior. Their life cycle spans 4 to 8 weeks, with reproduction occurring via amphimictic, meiotic, and parthenogenetic methods (Shokoohi and Duncan, 2018).

Seed Gall Nematode/Ear Cockle Nematode (*Anguina* spp.)

Distribution:

Seed gall nematodes are located in various areas including West Africa, North Africa, Australia, Brazil, China, India, Turkey, France, Italy, Iraq, and the USA (Tulek et al., 2015). The *Anguina* genus consists of 11 different species (Powers et al., 2001).

Host Range:

The primary hosts for these nematodes are wheat, rye, and barley. Wheat can experience 52% to 100%, while rye losses are typically between 50% and 65% (Mukhtar et al., 2018).

Symptoms:

Second-stage juveniles infiltrate wheat seedlings in wet soil and feed on them externally. They subsequently invade the floral primordia internally. Symptoms of infestation include leaf rolling and curling, the formation of small blisters on leaves, and distortion of stems (Ozberk et al., 2011; Mukhtar et al., 2018; Ami and Taher, 2013).

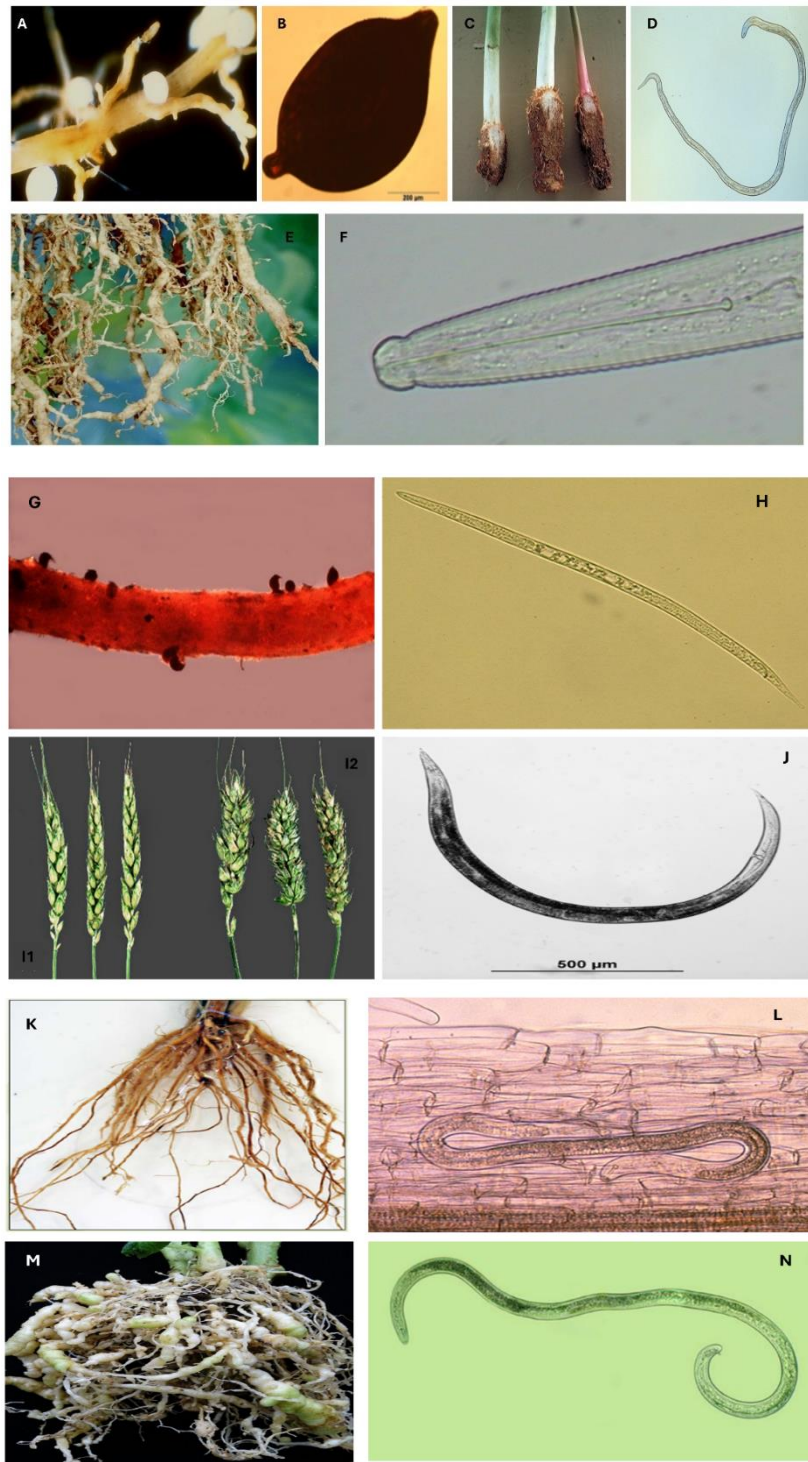


Figure 3. A, B- Cyst nematode and its Symptoms in the host plant. C, D- Root rot nematode and its symptoms in the host plant. E, F- Sting nematode and its effect on the host plant. G, H- Citrus nematode and its characteristic effect on the host plant. I (1, 2), J- Seed gall nematode and its effect on wheat. K, L- Lesion Nematode and the root affected by it. M, N- Knot formation in the root by Root-knot nematode. Picture Courtesy: (Google.com)

Lesion Nematode (*Pratylenchus* spp.)

Distribution:

Root lesion nematodes (RLNs), which belong to the genus *Pratylenchus*, are distributed globally and comprise approximately 97 recognized species.

Host Range:

Key hosts for RLNs include cereals, legumes, vegetables, fruits, ornamental plants, coffee, and peanuts. In temperate regions, twelve species are known to inflict significant damage, with eight being significantly detrimental to cereal crops (Fosu-Nyarko and Jones, 2016).

Symptoms:

Common symptoms in affected plants such as potatoes include yellowing leaves, stunted growth, and decay in roots and tubers (Esteves et al., 2015).

Duration of Life Cycle:

RLNs are migratory endoparasites whose life cycles range from 3 to 9 weeks and are influenced by specific species and environmental factors. For example, *P. penetrans* in red clover completes its cycle in 9 weeks. They reproduce through parthenogenesis and can endure harsh conditions in the soil for extended periods due to anhydrobiosis, making it possible for *Pratylenchus* spp. to survive for many years (Jones and Fosu-Nyarko, 2014).

Root Knot Nematode (*Meloidogyne* spp.)

Distribution:

Root-knot nematodes are found worldwide, with 98 identified species that cause about 5% of global economic losses (Khanal et al., 2016).

Host Range:

Their hosts comprise cover crops, fruit trees, weeds, ornamental plants, and agronomic crops (Khanal et al., 2016).

Symptoms:

These nematodes induce the development of galls or knots due to the swelling of root cells. Additional symptoms can include wilting, yellowing of leaves, nutrient deficiencies, and stunted growth (Ralmi et al., 2016).

Duration of Life Cycle:

Root-knot nematodes can be either migratory or sedentary endoparasites. They penetrate root zones to feed and have a life cycle that spans approximately 3-4 weeks under optimal conditions (Khan, 2015).

Table 1. Plant Parasitic Nematodes and their host plants (Phani et al., 2021)

| Crop | Nematode species | Country | Reference |
|--------|------------------------------|-----------|----------------------------|
| Tomato | <i>Meloidogyne hapla</i> | Canada | Belair and Tremblay (1995) |
| Tomato | <i>Meloidogyne incognita</i> | China | Tingting et al. (2005) |
| Tomato | <i>Nacobbus aberrans</i> | Argentina | Vovlas et al. (2007) |
| Tomato | <i>Meloidogyne javanica</i> | Cyprus | Philis (1994) |

| | | | |
|------------------|--|--------------|--|
| Tomato | <i>Meloidogyne javanica</i> | Ethiopia | Beyan et al. (2019) |
| Tomato | <i>Meloidogyne javanica</i> | Greece | Tzortzakakis and Petsas (2003) |
| Tomato | <i>Meloidogyne incognita</i> , <i>M. arenaria</i> , <i>M. javanica</i> | India | Ramasamy and Ravishankar (2018) |
| Tomato | <i>Meloidogyne incognita</i> , <i>M. javanica</i> , <i>M. hapla</i> | Italy | Calabretta and Privitera (1985) |
| Tomato | <i>Meloidogyne</i> spp. | Italy | Fiume and Parisi (1995) |
| Tomato | <i>Meloidogyne</i> spp. | Italy | Assenza et al. (2000) |
| Tomato | <i>Meloidogyne</i> spp. | Italy | Lamberti et al. (2003) |
| Tomato | <i>Meloidogyne</i> spp. | Italy | Polizzi et al. (2004) |
| Tomato | <i>Meloidogyne incognita</i> , <i>M. javanica</i> | Italy | Minuto et al. (2006) |
| Tomato | <i>Meloidogyne incognita</i> | Italy | D'Errico et al. (2016) |
| Tomato | <i>Meloidogyne javanica</i> | Jordan | Muhammad et al. (1991) |
| Tomato | <i>Meloidogyne incognita</i> | Netherlands | Cools and Stolk (1984) |
| Tomato | <i>Meloidogyne</i> spp. | Portugal | Silveira and Gorges (1984) |
| Tomato | <i>Meloidogyne incognita</i> , <i>M. javanica</i> , <i>M. arenaria</i> | Russia | Khurramov (1990) |
| Tomato | <i>Meloidogyne incognita</i> | Saudi Arabia | Almaghrabi et al. (2012) |
| Tomato | <i>Meloidogyne</i> spp. | Spain | Ojinaga (2018) |
| Tomato | <i>Meloidogyne javanica</i> | Spain | Sorribas et al. (2003) |
| Tomato | <i>Meloidogyne incognita</i> , <i>M. javanica</i> | Syria | Toumi et al. (2014) |
| Tomato | <i>Meloidogyne incognita</i> , <i>M. javanica</i> | Turkey | Yucel et al. (2007) |
| Tomato | <i>Meloidogyne incognita</i> | Turkey | Kaskavalci (2007) |
| Tomato | <i>Meloidogyne ethiopica</i> (reclassified as <i>M. luci</i>) | Turkey | Aydinli et al. (2013); Geriř c Stare et al. (2017) |
| Tomato, cucumber | <i>Meloidogyne</i> spp. | Greece | Giannakou and Panopoulou (2019) |
| Tomato, cucumber | <i>Meloidogyne</i> spp. | Albania | Pertena et al. (2005) |
| Tomato, cucumber | <i>Meloidogyne</i> spp. | Greece | Giannakou and Anastasiadis (2005) |
| Tomato, cucumber | <i>Meloidogyne incognita</i> , <i>M. javanica</i> | Brazil | Charchar and Aragao (2005) |
| Tomato, cucumber | <i>Meloidogyne incognita</i> | Russia | Lashkova and Danilov (1982) |
| Tomato, cucumber | <i>Meloidogyne</i> spp. | Russia | Yarkulov (2000) |

| | | | |
|---|---|------------------------|----------------------------------|
| Tomato, cucumber | <i>Meloidogyne incognita</i> | Spain | Gine and Sorribas (2017) |
| Tomato, cucumber | <i>Meloidogyne arenaria, M. incognita</i> | Uzbekistan | Rizaeva (1983) |
| Tomato, cucumber | <i>Meloidogyne enterolobii</i> | Switzerland | Kiewnick et al. (2008) |
| Tomato, cucumber | <i>Meloidogyne javanica</i> | Russia | Trusevich (2004) |
| Tomato, cucumber | <i>Meloidogyne</i> spp. | Bosnia and Herzegovina | Kohnic et al. (2006) |
| Tomato, cucumber, chili, bell pepper | <i>Meloidogyne incognita, M. javanica, Helicotylenchus dihystera, Hoplolaimus columbus, Pratylenchus penetrans, Radopholus similis, Tylenchorhynchus claytoni, Xiphinema</i> spp. | Pakistan | Anwar et al. (2013) |
| Cucumber | <i>Meloidogyne</i> spp. | China | Xiao et al. (2006) |
| Cucumber | <i>Meloidogyne</i> spp. | Egypt | El-Haddad et al. (2003) |
| Cucumber | <i>Meloidogyne incognita</i> | Egypt | El-Rab (2000) |
| Cucumber | <i>Meloidogyne incognita</i> | Egypt | Amin et al. (2014) |
| Cucumber | <i>Meloidogyne</i> spp. | Brazil | Kohnic et al. (2006) |
| Cucumber | <i>Meloidogyne</i> spp. | Hungary | Toth (2019) |
| Cucumber | <i>Meloidogyne</i> spp. | Russia | Dobrokhotov (2000) |
| Cucumber | <i>Meloidogyne</i> spp. | Russia | Bedin and Tokarev (2004) |
| Cucumber | <i>Meloidogyne incognita</i> | Spain | Gine et al. (2017) |
| Cucumber | <i>Plant-Parasitic nematodes (unspecified)</i> | Spain | Echevarría et al. (2004) |
| Cucumber | <i>Plant-Parasitic nematodes (unspecified)</i> | Turkey | Engindeniz and Engindeniz (2006) |
| Tomato, lettuce | <i>Meloidogyne javanica</i> | Spain | Verdejo-Lucas et al. (2003) |
| Tomato, lettuce | <i>Meloidogyne</i> spp. | Germany | Graf et al. (2001) |
| Tomato, bell pepper, eggplant, cucurbits (melon, cucumber, courgette), lettuce, beet, bean, radish, | <i>Meloidogyne</i> spp., <i>Heterodera carotae, H. cruciferae, D. dipsaci, Pratylenchus</i> spp., <i>Tylenchorhynchus</i> spp. | France | Djian-Caporalino (2012) |

| | | | |
|---|---|--------------------------------|-----------------------------------|
| spinach, basil, fennel, celery, strawberry | | | |
| Tomato, cucumber, pepper, eggplant, beans, banana, flower crops | <i>Meloidogyne</i> spp. | Mediterranean region (various) | Hanafi and Pappasolomontos (1999) |
| Tomato, beans, eggplant, zucchini | <i>Meloidogyne javanica</i> , <i>M. incognita</i> | Morocco | Janati et al. (2018) |
| Tomato, cucumber, eggplant, sweet pepper, green bean, squash | <i>Meloidogyne</i> spp., <i>Aphelenchoides</i> spp., <i>Tylenchorhynchus</i> spp., <i>Ditylenchus</i> spp., <i>Pratylenchus</i> spp., <i>Subanguina</i> spp., <i>Trichodorus</i> spp., <i>Hemicriconemoides</i> spp., <i>Paratylenchus</i> spp., <i>Helicotylenchus</i> spp., <i>Longidorus</i> spp., <i>Merlinius</i> spp. | Saudi Arabia | Almohithet et al. (2020) |
| Tomato, bell pepper, cucumber, tobacco | <i>Meloidogyne incognita</i> | USA | Kloepper et al. (2004) |
| Sweet pepper | <i>Meloidogyne incognita</i> | Spain | Ros et al. (2006) |
| Sweet pepper | <i>Meloidogyne incognita</i> | Spain | Guerrero et al. (2005) |
| Pepper | <i>Meloidogyne incognita</i> , <i>M. javanica</i> | Italy | Cartia et al. (1989) |
| Pepper | <i>Meloidogyne</i> spp. (mixed population of <i>M. incognita</i> , <i>M. javanica</i> , <i>M. arenaria</i>) | Turkey | Özarslandan et al. (2019) |
| Sweet pepper, carnation, cauliflower, tomato, eggplant, cucurbits | <i>Meloidogyne incognita</i> , <i>Helicotylenchus dihystera</i> , <i>Rotylenchulus reniformis</i> , <i>Pratylenchus</i> spp. | India | Chandel et al. (2010) |
| Cucumber, nightshade, tomato, melon, eggplant, pepper | <i>Meloidogyne arenaria</i> , <i>M. ethiopica</i> , <i>M. javanica</i> , <i>M. incognita</i> | Turkey | Aydinli and Mennan (2016) |

| | | | |
|---|---|----------|--------------------------------|
| Sweet pea | <i>Pratylenchus</i> spp. | Germany | Schreiner (1986) |
| French bean, cucurbits, tomato, crucifers, potato, capsicum | <i>Meloidogyne</i> spp., <i>Pratylenchus</i> spp., <i>Helicotylenchus</i> spp., <i>Mesocriconema</i> spp., <i>Tylenchorhynchus</i> spp., <i>Hoplolaimus</i> spp. | India | Singh and Khanna (2015) |
| Eggplant | <i>Meloidogyne</i> spp. | Italy | Cartia et al. (1996) |
| Eggplant | <i>Meloidogyne incognita</i> | Turkey | Çürük (2009) |
| Capsicum, tomato, chilli, okra, gherkin, muskmelon, watermelon, carnation, rose, gerbera, anthurium | <i>Meloidogyne incognita</i> , <i>M. javanica</i> , <i>Rotylenchulus reniformis</i> | India | Rao et al. (2015) |
| Cucumber, chilli, bell pepper, tomato | <i>Meloidogyne incognita</i> , <i>Pratylenchus</i> spp., <i>Rotylenchulus</i> spp., <i>Hoplolaimus</i> spp., <i>Helicotylenchus</i> spp., <i>Tylenchorhynchus</i> spp., <i>Ditylenchus</i> spp. | India | Patil et al. (2016) |
| Melon | <i>Meloidogyne arenaria</i> | Korea | Kim (2001) |
| Strawberry | <i>Xiphinema mediterraneum</i> , <i>Pratylenchus penetrans</i> , <i>Paraphelenchus pseudoparietinus</i> , <i>Helicotylenchus multicinctus</i> , <i>Aphelenchoides subtenuis</i> | Bulgaria | Nikolova et al. (1976) |
| Lettuce | <i>Paratylenchus</i> spp. | Belgium | Claerbout (2020) |
| Grape | <i>Pratylenchus</i> spp., <i>Tylenchorhynchus</i> spp., <i>Rotylenchulus</i> spp., <i>Tylenchus</i> spp. | India | Askary et al. (2018) |
| Sunflower | <i>Meloidogyne incognita</i> | Egypt | Rashad et al. (2011) |
| Cabbage | <i>Meloidogyne incognita</i> | India | Rana et al. (2018) |
| Strawberry | <i>Meloidogyne</i> spp., <i>Ditylenchus</i> spp. | Italy | Manzali (1994) |
| Sweet basil | <i>Aphelenchoides ritzemabosi</i> | Italy | Vovlas et al. (2005) |
| Soybean | <i>Rotylenchulus reniformis</i> | USA | Rodriguez-Kabana et al. (2003) |

| | | | |
|--|---|---------|--------------------------------------|
| Tomato, spinach, strawberry, melon | <i>Meloidogyne</i> spp. | Japan | Tanaka et al. (2000) |
| Tomato, pepper | <i>Meloidogyne</i> spp. | Greece | Prophetou-Athanasiadou et al. (2002) |
| Capsicum, tomato, cucumber, cabbage, carrot | <i>Meloidogyne</i> spp. | Hungary | Dabaj et al. (1994) |
| Capsicum, melon, tomato, lettuce | <i>Meloidogyne javanica</i> | Spain | Cenis (1984) |
| Greenhouse plants in botanical gardens | <i>Aphelenchoides fragariae</i> , <i>Ditylenchus destructor</i> , <i>D. dipsaci</i> , <i>Belondira paraclava</i> , <i>Helicotylenchus dehystra</i> , <i>Hemicycliophora parvana</i> , <i>Heterodera fici</i> , <i>Longidorus elongatus</i> , <i>Macroposthonia annulata</i> , <i>Paratrichodorus acutus</i> , <i>Meloidogyne incognita</i> , <i>Paratylenchus nanus</i> , <i>Pratylenchus crenatus</i> , <i>P. penetrans</i> , <i>Rotylenchus robustus</i> , <i>Tylenchorhynchus claytoni</i> , <i>T. dubius</i> , <i>Xiphinema americanum</i> | Ukraine | Gubin and Sigareva (2014) |
| Watermelon, cucumber, melon, tomato, eggplant | <i>Meloidogyne</i> spp. | Japan | Oda (1993) |
| Sweet pepper, tomato, cucumber, courgette, watermelon, eggplant, muskmelon | <i>Meloidogyne</i> spp. | Spain | Talavera et al. (2012) |
| Tomato, eggplant, carrot, radish, cucurbits | <i>Meloidogyne incognita</i> , <i>M. javanica</i> , <i>R. reniformis</i> , | India | Gowda et al. (2017) |

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|---|---|----------|----------------------------------|
| | <i>Hoplolaimus</i> spp., <i>Tylenchorhynchus</i> spp., <i>Helicotylenchus</i> spp. | | |
| Rose, carrot, spinach, chrysanthemum, Broccoli, spring onion, cabbage, Chinese leek | <i>Aphelenchoides</i> spp., <i>Criconemella</i> spp., <i>Helicotylenchus</i> spp., <i>Meloidogyne</i> spp., <i>Paratrichodorus</i> spp., <i>Paratylenchus</i> spp., <i>Rotylenchulus</i> spp. | Japan | Yamamoto and Toida (1995) |
| Capsicum, cucumber, tomato, carnation, gerbera, rose | <i>Meloidogyne</i> spp., <i>R. reniformis</i> , <i>Pratylenchus</i> spp., <i>Aphelenchoides fragariae</i> , <i>Radopholus similis</i> , <i>Ditylenchus dipsaci</i> | India | Sharma et al. (2009) |
| Tomato, cucumber, pepper, carnation, gerbera, rose | <i>Meloidogyne</i> spp., <i>R. reniformis</i> , <i>Pratylenchus</i> spp., <i>Hoplolaimus</i> spp., <i>Tylenchorhynchus</i> spp., <i>Helicotylenchus</i> spp. | India | Sabir and Walia (2017) |
| Tomato, cucumber, eggplant, melon, squash, beans, lettuce | <i>Meloidogyne</i> spp., <i>Radopholus</i> spp., <i>Aphelenchoides</i> spp., <i>Ditylenchus</i> spp., <i>Pratylenchus</i> spp. | USA | Noling and Rich (2010) |
| Cut flowers and ornamentals | <i>Macroposthonia curvata</i> , <i>Xiphinema diversicaudatum</i> , <i>Ditylenchus dipsaci</i> , <i>Meloidogyne incognita</i> , <i>Aphelenchoides ritzemabosi</i> | Bulgaria | Choleva (1982) |
| Rose, gypsophila | <i>Mesocriconema sphaerocephaloides</i> , <i>Longidorus laevicapitatus</i> , <i>Paratylenchus obtusicaudatus</i> , <i>Nanidorus minor</i> | Ethiopia | Meressa et al. (2015) |
| Anthurium | <i>Radopholus similis</i> | Hawaii | Aragaki et al. (1984) |
| Carnation, gerbera | <i>Dazomet</i> , <i>chlorpyrifos</i> , <i>carbosulfan</i> , <i>carbofuran</i> , <i>Paecilomyces lilacinus</i> | India | Nagesh and Parvatha Reddy (2005) |

| | | | |
|-----------|---|-------|-------------------------|
| | (= <i>Purpureocillium lilacinum</i>), <i>Pochonia chlamydosporia</i> , neem cake | | |
| Carnation | <i>Pochonia chlamydosporia</i> | India | Rao and Shaylaja (2003) |
| Rose | <i>Heterodera daverti</i> | Italy | Lung et al. (1997) |
| Rose | <i>Meloidogyne</i> spp. | Kenya | Oloo et al. (2009) |

Mechanism of parasitism:

Plant parasitic nematodes (PPNs) have complex infection processes that enable them to colonize and exploit plant hosts effectively. The infection process generally involves the following stages:

Attraction to Host Plants:

Actively growing roots generate different gradients of both volatile and non-volatile, such as amino acids, ions, pH levels, and CO₂. Nematodes have specialized chemosensory structures called amphids that they use to locate these roots by sensing these gradients. This capacity to move toward root stimuli enhances their chances of encountering a host and reduces the duration without food (Perry, 1997). It is widely recognized that the cyst and root-knot nematodes' second-stage juveniles (J2) are drawn to the root tip, their favoured invasion site. Nonetheless, the elements that serve as "local attractants" have not been determined (Reynolds et al., 2011). These nematodes may react to an electrical potential gradient present in the root tip's elongation zone. The relative importance of electrical and chemical attractants in directing nematodes to the root tip remains unclear. Furthermore, the elevated temperature in the root elongation zone might also influence nematode perception.

Penetration and Feeding:

Nematodes can infiltrate plant roots by utilising their stylet, a structure resembling a needle, or by exploiting natural apertures like root tips or hairs. Invading host roots, sedentary endoparasitic nematodes create feeding sites inside the root tissue and feed internally. Recent and ongoing studies on the feeding habits of endoparasitic species have mainly concentrated on worms with cysts and knots in their roots. But other nematodes, such as *Nacobbus*, also produce feeding sites that serve as sinks for nutrients (Manzanilla-López et al. 2002). These nematodes could be studied more and more in the future, especially with the development of comparative genomics.

Both cyst and root-knot nematodes emit cell wall-degrading enzymes through their stylets, facilitating their movement by weakening or disintegrating plant cell walls. The subventral glands generate these enzymes. Root-knot nematodes also produce xylanase and polygalacturonase, in addition to the identified enzymes cellulases and pectate lyases (Davis et al., 2000; Gheysen and Jones, 2006).

Migration:

Nematodes travel across cells in search of their preferred feeding places after entry. Certain nematodes, such as *Meloidogyne spp.*, the root-knot nematode, can pass through plant cells and seriously harm the cells. Only the J2 and adult males of cyst and root-knot nematodes migrate. However, in species such as *Nacobbus*, only the mature female remains static; all juvenile stages, the male and the immature vermiform female, are migratory. *Pratylenchus* and *Radopholus* are two examples of migratory endoparasitic nematodes that infiltrate plant hosts through mobile stages before becoming sessile. Instead of creating permanent feeding sites inside the plant, these nematodes move about, feed on several cells, and seriously harm the plant's tissue (Port, 1980).

Moulting:

The effects of the principal moulting hormone in insects, 20-hydroxyecdysone (20E), on *Meloidogyne javanica* were studied by Soriano et al. (2004). When exogenous 20E was applied, it caused J2 to become immobile and die. It also partially inhibited invasion and stopped spinach growth when it induced significant amounts of endogenous 20E. Nevertheless, the few J2 that did infiltrate did not show signs of aberrant moulting. There is no evidence that worms biosynthesise ecdysteroids, and efforts to identify 20E and its precursor, ecdysone, in *Meloidogyne incognita* and *Meloidogyne arenaria* have been fruitless (Chitwood et al., 1987). The genes involved in moulting in *Meloidogyne* may be revealed by the complete genome sequences of *Meloidogyne hapla* (Opperman et al., 2008) and *Meloidogyne incognita* (Abad et al., 2008).

Reproduction:

According to Evans' review, nematodes use a variety of asexual and sexual reproduction techniques (1983). *Meloidogyne* is one of the plant-parasitic nematodes investigated in great detail (Chitwood and Perry, 2009). The process of fusing haploid male (spermatocytes) and female (oocyte) gametes to create a diploid zygote that restores the 2n chromosomal complement is known as sexual reproduction (amphimixis). Sex ratios in species like *A. tritici* and *D. dipsaci* are genetically determined, with females being homogametic (XX) and males being heterogametic (XO or XY). There are no sex chromosomes in genera like *Globodera*, *Heterodera*, and *Meloidogyne*, and sex ratios may be affected by environmental variables. Moreover, females in some species, such as *Radopholus*, *Pratylenchus*, and *Heterodera*, can be impregnated by more than one male, leading to the genetic variety of the progeny.

Plant response to nematode infections:

Scientists and researchers have discovered several naturally occurring genes that contribute to developing plant nematode resistance. Nematode-resistant plants have not been successfully bred using conventional methods. In order to mitigate nematode infestations, RNA interference (RNAi) technology has become a dependable approach (Tamilarasan and Rajam, 2013). There are two primary forms of plant resistance to nematodes: passive and active resistance.

Anatomical, physiological, and pharmacological barriers influencing nematode infestation are passive resistance examples. Conversely, active resistance entails histological alterations that result in the nematode's death by forming necroses around it (Giebel, 1982).

It has been determined that some genes give resistance to particular nematodes. For example, the tomato (*Solanum lycopersicum*) Mi-1.2 gene is resistant against root-knot nematodes, while the HS1pro1 gene is resistant against sugar beet cyst nematodes. According to studies, isogenic plants are resistant to nematode pressures, up to 200,000 eggs per plant. Furthermore, potatoes' potato cyst nematode (*Globodera pallida*) is resistant to the GPa2 gene (Briar et al., 2016; Ralmi et al., 2016). Several metabolites, including tridecane, limonene, 2-isopropyl-3-methoxypyrazine, and methyl salicylate, can affect nematode mobility and prevent them from finding appropriate hosts (Sikder and Vestergard, 2020).

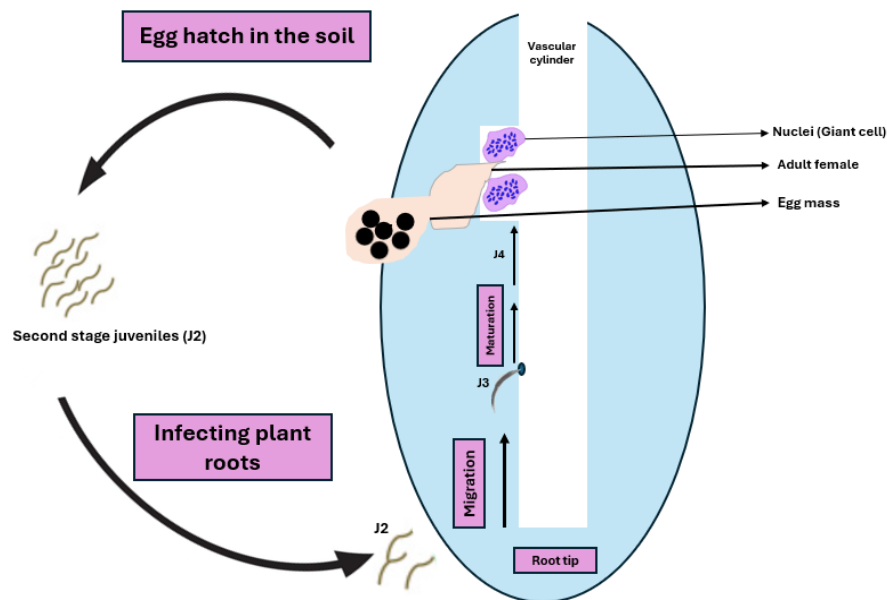


Figure 4. Mechanism of Parasitic root nematode

Impact of plant parasitic nematodes on crops:

With almost 4,100 species known to date, plant-parasitic nematodes represent a substantial financial barrier to agricultural crop production (Decraemer and Hunt, 2006). Crop loss caused by parasitic nematodes is estimated to be between \$80 and \$118 billion annually. These harmful nematodes, which comprise around 15% of all species found, primarily target the roots of important crops. This disturbance negatively impacts plant development, quality, and yields because it makes it difficult for plants to absorb water and nutrients. Because they parasitize plants, animals, and fungi, nematodes in the Tylenchida order are remarkable and ranked among the most important agricultural pests (Nicol et al., 2011).

Wheat:

With an annual production of about 758 million tons, wheat (*Triticum aestivum*) is the most important cereal crop in the world and is a mainstay for 40% of the world's population (FAO, 2017). Nonetheless, cereal cyst nematodes (*Heterodera spp.*) pose a significant danger to wheat yields, especially those belonging to the *Heterodera avenae* group, which comprises *H. avenae*, *H. filipjevi*, and *H. latipons*. These pests harm wheat and other important cereals, including oats (*Avena sativa*) and barley (*Hordeum vulgare*). These nematodes cause an estimated \$3.4 million in annual profit loss for wheat-growing regions in the United States, including Idaho, Oregon, and Washington (Smiley et al., 2010). According to Bonfil et al. (2004), *H. avenae* damage alone may produce yield losses in some areas that range from 30% to a disastrous 100%.

Rice:

Most of the world's population depends on rice (*Oryza sativa L.*), of which 480 million tons are produced worldwide (Childs et al., 2017). Plant-parasitic nematodes are one of the most important soil-borne pests that harm rice, which cause yield losses of 10–25% each year globally. The production of rice is impacted by more than 100 nematode species, with *Meloidogyne spp.* they are being common and incredibly detrimental to rice and other crops cultivated in temperate and tropical climates. *Meloidogyne graminicola* is one of the most damaging of them, with the ability to cut rice harvests by as much as 80% (Soriano et al., 2000). According to Pokharel et al. (2007), signs of infected plants include hook-shaped galls, slowed growth, fewer tillers overall, and poor development and reproduction.

Maize:

Across the globe, maize (*Zea mays*) is widely grown, with North America, Asia, and Europe producing the most (Nicol et al., 2011). Although there are more than 50 species of nematodes that are known to parasitize corn globally, the most harmful ones are the root-knot (*Meloidogyne spp.*), root lesion (*Pratylenchus spp.*), and cyst (*Heterodera spp.*) worms. The US has economic severe concern regarding the lesion nematodes (*Pratylenchus spp.*) and the maize cyst nematode (*Heterodera zaeae*). Nematode infections in maize usually show up as mild galling, chlorosis of the leaves, and poor plant development (Norton et al., 1983). Moreover, maize growth stunting associated with the needle nematode *Longidorus breviannulatus* may result in yield losses as high as 60%.

Potato:

As a member of the Solanaceae family, potatoes (*Solanum tuberosum*) are the third most significant crop in the world, with over 376 million tonnes being produced globally in 2013 (FAOSTAT, 2017). Particularly well-known for severely reducing potato crop yields are cyst nematodes. Originating in South America, *Globodera rostochiensis* and *Globodera pallida* also prey on other members of the Solanaceae family, including tomatoes and woody nightshade. These nematodes are thought to cause the United Kingdom to lose £50 million a year in losses and are considered quarantine pests in several nations, including the United States. The stem

worm *Ditylenchus destructor* and the root-knot nematodes (*Meloidogyne spp.*) also pose a significant threat to potatoes. Four species of root-knot nematodes impact potato output in the United States; the most important species is the Columbian root-knot nematode (*Meloidogyne chitwoodii*) (Santo et al., 1981). Furthermore, *D. destructor* is a primary host of the sweet potato (*Ipomoea batatas* L. Lam), with yield losses as high as 100% in certain production zones, including China, the world's largest producer (Zhang et al., 2006).

Sweet potato:

Cultivating sweet potatoes since prehistoric times, *Ipomoea batatas* (L.) Lam, has been an important plant throughout human history. It has been a staple food source for recorded history; its global production is estimated at 105 million metric tons. Sweet potatoes are the sixth most important food crop in the world. However, their cultivation has improved people's economic standing, particularly in underdeveloped countries where they are ranked the fifth most important crop (CIP International Potato Center, 2014). However, plant-parasitic nematodes cause the annual loss of about 10.2% of sweet potato yields (Decraemer et al., 2006). Of particular concern are root-knot nematodes (RKNs), which can cause symptoms like growth retardation, leaf yellowing, irregular flower output, and the creation of galls on roots. This causes the fleshy store roots to break and necrotize and reduce the absorption of nutrients and water. Because storage roots have a high economic value, growers are concerned about root breaking.

Symptoms of nematode infestation:

Nematodes that consume roots produce symptoms above ground that resemble different kinds of root injury. The leaves could wilt and lose their luster. Nematodes can cause long-term root stress, leaf yellowing and loss. Compared to healthy plants, new growth spurts typically have fewer, smaller leaves and are weaker overall. When there is a drought or low water levels, infected plants typically wilt more quickly than uninfected plants. The harm is usually unevenly distributed because nematodes are rarely dispersed equally throughout the soil. Nematode-caused root symptoms might differ widely. A few nematodes, such as root-knot and some foliar varieties, cause the tissues they feed on to develop abnormally. Others may cause patches of dead tissue to remain behind by preventing root growth or killing cells as they pass through the roots. Depending on the nematode species, damage might take the form of galls, stunted growth, or decaying roots. Often, infected roots have a darker appearance than healthy ones. Damage caused by nematodes to roots increases their vulnerability to bacterial and fungal infections, which can result in illnesses such as root rot and wilt. Furthermore, nematodes can spread certain viruses (Barker and Davis, 1996).

Management Strategies for Plant Parasitic Nematodes:

Developing environmentally safe and non-chemical methods has dramatically outpaced using chemical nematodes. These strategies include sanitation, soil management, and helpful biological

agents. Biological techniques exhibit considerable promise as substitutes for managing infestations of plant-parasitic nematodes (Collange et al., 2011). Biological Control Agents (BCAs), sometimes known as "biopesticides," are organisms or their byproducts that fight pests. In general, chemicals intended to protect plants that are not chemically created but instead come from natural substances or live organisms as a result of species co-evolution are referred to as biopesticides. It is advised to utilize them to manage bio-aggressors and control pests to protect the environment and biocenosis better. Plant-parasitic nematodes can be eradicated by biological agents, which include bacteria, fungi, actinomycetes, and other microbes. These agents are particular to their host. The most common bacteria and fungi in the soil ecosystem have an immense potential for controlling nematodes (Blyuss et al., 2019; El-Eslamboly et al., 2019). This review investigates the use of actinomycetes, bacteria, and fungi as plant-parasitic nematode control agents.

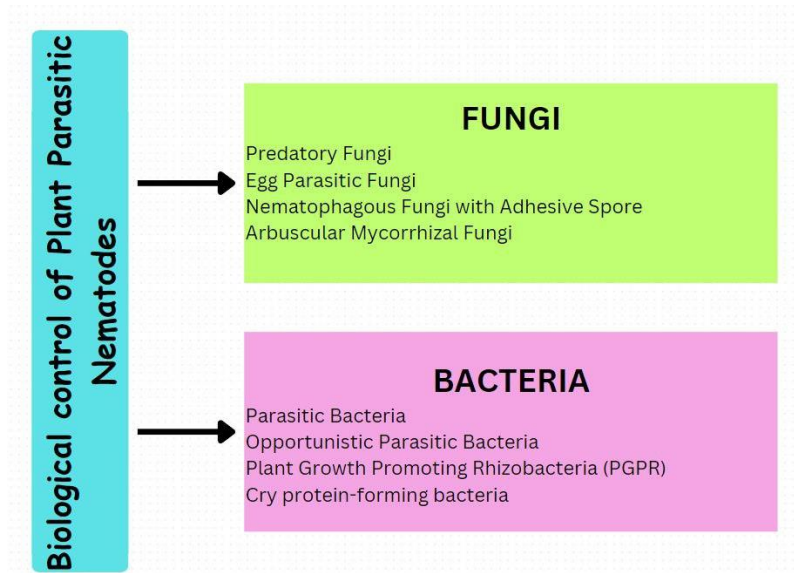


Figure 5. The mechanism of biological control of plant parasitic nematode

Fungi: A Biocontrol Agent Against Root-Knot Nematodes

Plant-parasitic nematodes, such as *Meloidogyne spp.*, the root-knot worm, are particularly vulnerable to attack by nematophagous fungi (Brand et al., 2004; Collange et al., 2011). The worm's cuticle is penetrated, organic soil debris is broken down and absorbed, and the nematode is invaded and digested as part of their infection mechanism (Huang et al., 2004). Nematode cuticles and egg walls are important components of fungal invasion. According to Huang et al. (2004), these nematode-feeding fungi predate the invasion of vital cuticle components like collagen, chitin, and fiber. Nematophagous fungi are categorised based on how they inhibit plant-parasitic nematodes (Cayrol et al., 1993).

A. Predatory Fungi

Carnivorous fungi, sometimes predatory fungi, grow on the epidermis and consume other living things by ensnaring and feeding on them (Abd El-Rahman and Mohamed, 2014). These fungi, which belong to Basidiomycota, Ascomycota, and Mucoromycota, have over 200 species identified. Nematophagous fungi are those that eat plant-parasitic nematodes, which include a large number of these fungi. While certain fungus, such as *Arthrobotrys anchonia*, *Arthrobotrys dactyloides*, and *Dactylaria brochopaga*, build constrictive rings to capture nematodes, others, including *Arthrobotrys oligospora* and *Arthrobotrys superba*, use a network trapping method. Despite being saprophytic by nature, these nematophagous fungi can capture nematodes in the soil during their first larval stage or as free adults. Their importance is found in the peptides that are produced when extracellular proteases hydrolyze the cuticles of worms (Huang et al., 2004).

B. Egg-Parasitic Fungi

Nematode eggs can be infected and destroyed by egg-parasitic fungus. Numerous of this fungus can enter dead eggs and are saprophytic. *Verticillium*, *Pochonia*, and *Paecilomyces* species are a few examples. Two of the most potent egg parasites are *Pochonia chlamydosporia* and *Paecilomyces lilacinus*. Particularly *P. lilacinus* has been shown to control root-knot nematodes on tomatoes, eggplants, and other vegetable crops, including *M. incognita* and *M. javanica* (Verdejo-Lucas et al., 2002; Van Damme et al., 2005; Goswami et al., 2006; Haseeb and Kumar, 2006).

C. Adhesive Spore-Forming Nematophagous Fungi

Several classes of fungi use sticky spores to parasitize plant-parasitic nematodes. For example, biflagellate zoospores on the cuticles of nematodes can generate traps for oomycete fungi like *Myzocyttium lenticulare*, *Catenaria anguillulae*, and *Myzocyttium anomalum*. Zygomycete fungi, such as *Myzocyttium anomalum*, produce spherical conidia, which grow germinative filaments following attachment and create new conidiospores. The spores of deuteromycete fungi, including *Meria coniospora*, have a club form and adhere to the host through their anterior portion (Cayrol et al., 1992).

Bacteria: A Biocontrol Agent Against Root-Knot Nematodes

Bacteria are single-celled, microscopic organisms found in water, soil, acidic hot springs, and even radioactive waste (Fredrickson et al., 2008). In addition, they can coexist symbiotically or parasitically with plants and animals in the deep biosphere of the Earth's crust. A notable class of biological agents, microorganisms have been the source of several commercial treatments designed to manage phytonematodes (Hallmann et al., 2009). When managing plant-parasitic nematodes, *Bacillus* species stand out among the others. One well-known rhizobacterium, *Bacillus subtilis*, has gained global recognition as a biopesticide against phytopathogenic nematodes (Prakob et al., 2009). To regulate root-knot nematodes, bacteria use a variety of strategies, such as direct parasitism, antibiosis, and nutrient competition (Mendoza et al., 2008; Lee and Kim, 2016; Cawoy et al., 2011). Generating toxins, volatile organic compounds (VOCs),

and medications makes antibiosis very effective (Saraf et al., 2014). Furthermore, it is known that other rhizobacteria, including *Pasteuria*, *Pseudomonas*, and *Streptomyces*, can fight against nematodes that cause knotting in roots. Through seed treatment under pot settings, Bharali et al. (2019) discovered that bacterial bioagents were superior to fungal ones in controlling root-knot nematodes in black gram.

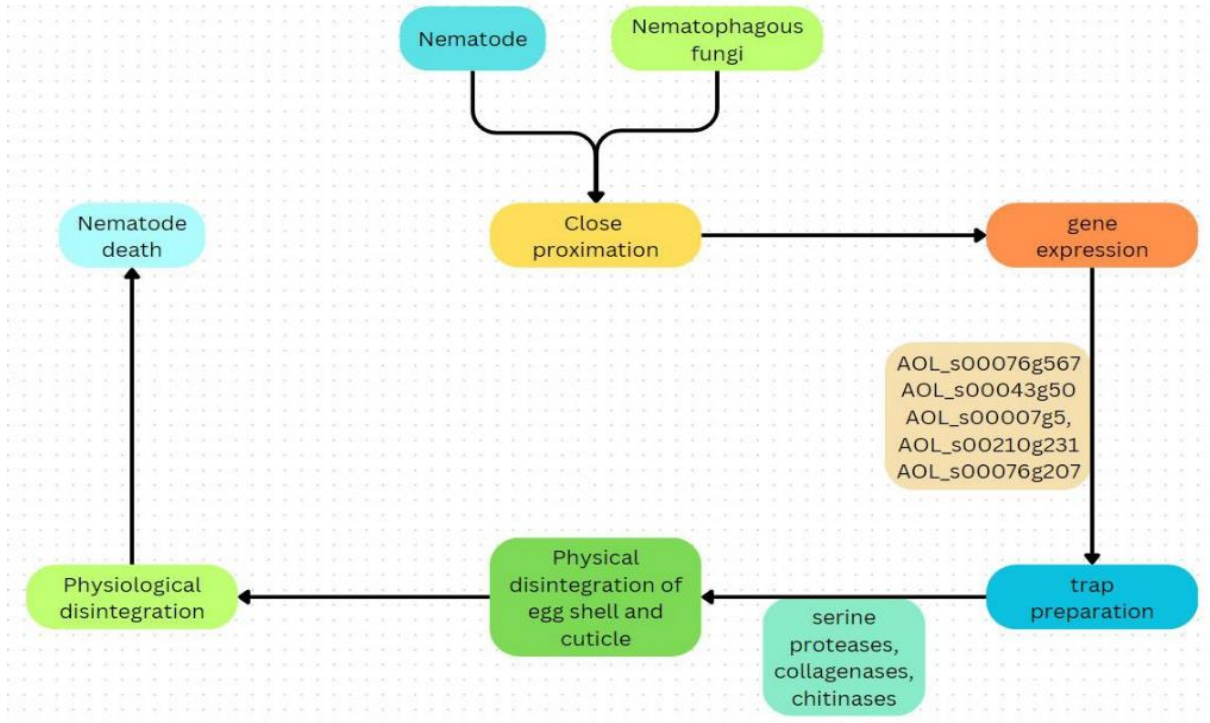


Figure 6. Diagrammatic representation of fungal antagonists of plant parasitic nematodes

Production of Anti-Nematode Compounds of plants:

In response to the invasion of plant-parasitic nematodes (PPNs), plants release secondary metabolites. For instance, the presence of the phenolic compound chlorogenic acid in a variety of plants, such as those in the Solanaceae family (Hung and Rohde, 1973; Pegard et al., 2005), rice (Plowright et al., 1999), and carrots (Knypl et al., 1976), suggests that these plants share a defence mechanism against PPN infections. Although there is a strong correlation between PPN resistance levels and chlorogenic acid production, the compound itself only exhibits mild nematode activity against *Meloidogyne incognita* (D'Addabbo et al., 2013) and moderate activity against the false root-knot nematode *Nacobbus aberrans* (López-Martínez et al., 2011). The reason for this poor connection could be that plants are particularly poisonous or unstable when it comes to the metabolized metabolites of chlorogenic acid, which may have increased nematicidal activity. Orthoquinone, which is poisonous to PPNs, can be produced through chlorogenic acid hydrolysis to quinic and caffeic acid (Sato et al., 2019). However, more research is required to determine the precise functions of orthoquinone and caffeic acid in PPN resistance.

Phenylphenalenone anigorufone is another phenolic molecule that builds up at the sites of infection of the burrowing worm *Radopholus similis* in a resistant cultivar of banana (*Musa* sp.) (Dhakshinamoorthy et al., 2014). The development of massive lipid-anigorufone complexes within the bodies of *R. similis* renders anigorufone highly nematicidal. Additionally, this substance is an antifungal phytoalexin triggered by infection with the harmful fungus *Fusarium oxysporum* (Luis et al., 1997). Notably, anigorufone inhibits succinate dehydrogenase in the mitochondrial respiratory complex II, which results in the death of the human protozoan parasite *Leishmania* (Luque-Ortega et al., 2004). However, the precise harmful mechanism of anigorufone in PPNs and its connection to the creation of lipid-anigorufone complexes are still unknown.

As nematicides, nemastatic substances (which impede movement but do not kill), repellents, egg hatching inhibitors, flavonoids, a broad class of secondary metabolites, are essential for PPN resistance (Chin et al., 2018). Flavonols (kaempferol, quercetin, myricetin), isoflavonoids, and pterocarpan (medicarpin, glyceollin) are notable anti-nematodal flavonoids. While myricetin, quercetin, and kaempferol operate as hemostatic agents and repellents to juvenile *M. incognita*, kaempferol suppresses the hatching of *R. similis* eggs (Wuyts et al., 2006). Furthermore, medicarpin suppresses *Pratylenchus penetrans* motility in a concentration-dependent way (Baldrige et al., 1998). Patuletin and patulitrin also show anti-nematodal properties. According to Faizi et al. (2011), quercetin and rutin have nematicidal effects on the infectious juveniles of *Heterodera zae*.

Plants that are resistant to infection frequently release specific flavonoids. Glyceollins, for instance, are soybean-specific prenylated pterocarpan phytoalexins that react to infection and are produced by soybean varieties resistant to *Meloidogyne incognita* (Davis et al., 1989). Notably, it has been demonstrated that glyceollin inhibits *M. incognita*'s mobility. Resistant soybean cultivars accumulate higher concentrations of glyceollin than by susceptible ones. In resistant roots, glyceollin I, one particular isomer, tends to concentrate in tissues close to the nematode's head (Huang and Barker, 1991). This implies that the buildup of glyceollin is directed towards the site of infection.

Apart from phenolic chemicals, marigold and asparagus are other plants that have been found to have nematode-antagonistic qualities. The nematicidal activity of marigold roots is demonstrated by their ability to successfully penetrate the nematode's hypodermis and release α -terthienyl, a chemical that causes oxidative stress (Faizi et al., 2011). Similarly, asparagus yields asparagusic acid, which can prevent *Globodera rostochiensis* and *Heterodera glycines* from hatching (Chitwood, 1992).

The Brassicaceae family of plants is known for its broad-spectrum antibacterial activities against plant-parasitic nematodes (PPNs). Examples of these plants are those that yield isothiocyanates and indole glucosinolates. As well as being poisonous to both RKNs and the semi-endoparasitic nematode *Tylenchulus semipenetrans*, isothiocyanates are known to impede the hatching of both cyst nematodes (CNs) and root-knot nematodes (RKNs) (Zasada and Ferris,

2004). The cytochrome P450 enzymes CYP79B2, CYP79B3, and PAD3 control the formation of camalexin, an indole alkaloid glucosinolate phytoalexin, in *Arabidopsis* (Mikkelsen et al., 2000). While camalexin-deficient *pad3* mutants are more susceptible to RKNs than wild types, *Arabidopsis* mutants lacking in these enzymes, such as *cyp79b2/b3*, exhibit higher vulnerability to CNs (Shah et al., 2017). Although there is no evidence of direct toxicity, some indole glucosinolates, such as camalexin, appear to affect PPNs.

In addition to nemastatic substances and nematicides, plants may defend themselves by interfering with PPN chemotaxis. Nematode attraction to roots can be decreased by ethylene, a hormone released in response to wounding and pathogen invasion (Booker and DeLong, 2015). PPNs seem less drawn to *Arabidopsis* mutants that overproduce ethylene, but more drawn to those treated with ethylene-synthesis inhibitors or ethylene-insensitive mutants (Fudali et al., 2013).

Conclusion:

Around the world, parasitic nematodes seriously threaten agricultural production, affecting crop yields and quality. The harm they cause, which is frequently overlooked, highlights the need for thorough and integrated pest control methods. The several strategies plants use to ward off these nematodes such as chemical deterrents and physical barriers have been covered in this chapter. Ensuring food security requires effective control of parasitic nematodes, particularly considering the world's expanding population and rising food demands. We could mitigate the negative consequences of these pests by studying the intricate relationships that nematodes have with their host plants and using this information to create effective management measures.

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