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REVIEW

Nematophagous fungi for integrated management of *Meloidogyne* (Tylenchida): a review of taxonomic diversity, mechanisms of action and potential as biological control agents

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Abstract

Root-knot nematodes (RKNs) are classified under the genus *Meloidogyne* and are among the most devastating pests affecting strategical agricultural crops. They attack a wide variety of plant species, including vegetables, fruit trees and ornamental plants, causing root deformities and even lead to plant death in severe cases of infestation. These nematodes contribute to substantial crop yield loss and affect the quality of harvested products. Although synthetic nematicides are available for the control of these pest organisms, there is a growing emphasis on exploring sustainable and eco-friendly alternatives, such as nematophagous fungi like the genera *Purpureocillium*, *Arthrobotrys*, *Dactylellina*, *Orbilia*, and *Trichoderma*, among others. Here a review of literature on the matter is given, with a focus on the taxonomic classification of the most relevant fungal orders and genera, their diagnostic features, mechanisms of action, and potential as biological control agents (BCAs) against *Meloidogyne* species. Other relevant aspects addressed in this review include a brief description of the nematode genus *Meloidogyne*, along with the symptoms it causes in host plants, such as root gall formation, stunted growth, and yellowing of foliage, among others. It also describes integrated pest management (IPM) strategies such as crop rotation, resistant crops, soil solarization, trap crops, as well as currently used chemical control techniques. Biological control alternatives are also presented with particular emphasis on nematophagous fungi. Future research should focus on improving the formulae of biological agents based on nematophagous fungi under field conditions and understanding their ecological roles and interactions in soil microbiomes.

Keywords: Agricultural pests; *Arthrobotrys*; egg parasites; nematophagous fungi; plant parasites; root-knot nematodes.

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1. Introduction

Nematodes are multicellular organisms in the phylum Nematoda (kingdom Animalia) with the appearance of worms, generally measuring between 0.2 - 2.5 mm in length. They present different life and feeding habits, which vary depending on their environment and ecological niche. While many of them are free-living and feed on fungi, bacteria, protozoa or even other nematodes, others are parasites and infect plants and animals (Stirling, 2014). Nematodes perform a crucial role in soil food chains, as they act as microbial population controllers and, at the same time, become prey to many animals and soil organisms (Kudrin et al., 2015).

Plant-parasitic nematodes usually feed directly on plant tissue, through cell cytoplasm, root hairs or cortical cells (Decraemer & Hunt, 2013). These processes, in turn, lead to symptoms of necrosis, discoloration, tumors/galls, rotting and even death of the host plant (Howland & Quintanilla, 2023; Pulavarty et al., 2021). According to their feeding habits, plant-parasitic nematodes are grouped into ectoparasites, semiendoparasites and endoparasites (Decraemer & Hunt, 2013; Subedi et al., 2020). It is estimated that annual losses caused by plant-parasitic nematodes represent between 8.8% and 14.6% of the global agricultural production, which corresponds to a value between US$ 100 and US$ 157 billion per year (Ali et al., 2014). They affect the yield and quality in crops such as Amaranthaceae (sugar beet), Fabaceae (soybean), Poaceae (also known as Gramineae: rice, wheat, corn), Solanaceae (tomato, potato, peppers), among others (Sato et al., 2019). Considering the economic and social impacts of plant-parasitic nematodes on food and nutritional security (FNS), it is crucial to develop new environmentally safe alternatives for integrated pest management (IPM), in order to achieve sustainable economic efficiency and increase human welfare.

Fungi have already been successfully employed as BCAs of numerous pests and diseases of agricultural crops. Species of *Beauveria* and *Metarhizium* are used against insect pests (Amatuzzi et al., 2018; Duarte et al., 2016). Various species of *Trichoderma* are BCAs against various phytopathogenic fungi, including the genera *Fusarium*, *Pythium* and *Rhizoctonia* (Kumari et al., 2023; Maulana et al., 2024; Pérez-González et al., 2023). *Orbilia oligospora* (Fresen) Baral & E. Weber (syn. *Arthrobotrys oligosporus* Fresen.), *Metacordyceps chlamydosporia* (H.C. Evans) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora (syn. *Pochonia chlamydosporia* (Goddard) Zare & W. Gams) and *Purpureocillium lilacinum* (Thom) Luangsa-ard, Houbraken, Hywel-Jones & Samson (syn. *Paecilomyces lilacinus* (Thom) Samson), are applied for the control of plant-parasitic nematodes such as *Meloidogyne* spp. Göldi. Although this background is promising, there are still challenges to overcome, such as achieving mass production of these BCAs, educating farmers and developing more field scientific studies to demonstrate their efficacy (Shukuru et al., 2024). The present work is a systematic review of the current knowledge on nematophagous fungi and explores their potential as a sustainable alternative for the control of plant-parasitic nematodes.

2. The genus *Meloidogyne*

RKN belong to a group of sedentary (sessile) endoparasitic nematodes classified under the genus *Meloidogyne* (Figure 1). RKN species have a complex life cycle with different stages (Figure 2), including the immature eggs, eggs with J_1 larvae, J_2 second-stage larvae (infective stage), J_3 and J_4 (sedentary stage) and the adult females or males (reproductive stage, Sikandar et al., 2020).

Figure 1. Microphotographs of a species of *Meloidogyne*. A. Second-stage juvenile (J_2). B. Egg with first stage larva (J_1). C. Immature egg. D. Lateral view of a female *M. incognita* (J_4) extracted from roots of peppers (*C. annuum* L.). E. Anterior region of J_2 showing position of stylet (e), nodes (n), dorsal esophageal gland (deg) and median bulb (mb). F. Perineal pattern of *M. incognita* showing anus (a), vulval region (vr) and surrounding cuticular striae. Scale bars: A. 45 μm, B.-C. 20 μm, D. 90 μm, E. 15 μm.

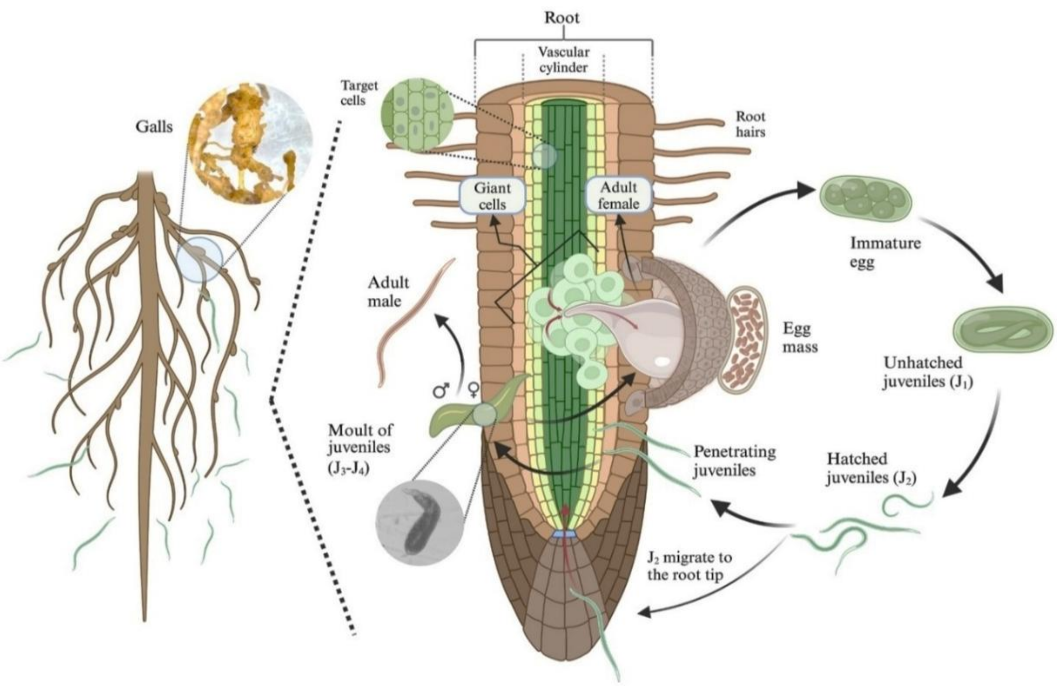

Figure 2. The life cycle of RKN starts with the eggs laying by the adult female in a gelatinous matrix (egg mass) close to or on the surface of plant roots. The eggs hatch into second stage juveniles (J_2), which constitute the infective stage. These juveniles migrate actively through the soil and penetrate the roots of plants through the root tip or natural openings (Wyss et al., 1992). Within the root, J_2s migrate into the vascular cylinder and establish a feeding site by inducing the formation of giant cells, specialized plant cells that provide nutrients to the nematode (Walia & Khan, 2023). Afterwards, J_2 become sedentary and undergo at least three more molts to mature into male or female adults (Sikandar et al., 2020). Over time, these giant cells contribute to the development of typical root galls. The nematode develops into an adult female, causing further gall formation as it matures and reproduces. The cycle continues when the female lays eggs in the gelatinous matrix, from which juveniles hatch to initiate a new infection (created by the first author with BioRender, BioRender.com/t97y137).

RKN are recognized as a pest of economic impact, causing damage during plant development and, thus, reducing their yield (Jones & Goto, 2011; Subedi et al., 2020). Currently *Meloidogyne* includes approximately 100 described species; however, only a few species represent important and common plant pests: *M. arenaria* (Neal) Chitwood, *M. enterolobii* Yang & Eisenback, *M. hapla* Chitwood, *M. incognita* (Kofoid & White) Chitwood, *M. javanica* (Treub) Chitwood (Azlay et al., 2023; Castagnone-Sereno et al., 2013; Jones et al., 2013; Subbotin et al., 2021).

2.1. Symptoms produced by *Meloidogyne* infestation

A common symptom of *Meloidogyne* infestation is the formation of galls at nematode feeding sites, which are usually restricted to the roots of infected plants (Elling, 2013). The second larval stage (J_2) is able to parasitize the roots of the host plant by penetrating the cells with the help of the stylet and cellulolytic and pectolytic enzymes (Jones et al., 2013). This process produces root knots or large bumps, which consist of multinucleated giant cells produced by infected plant tissue (Subedi et al., 2020; Trudgill & Blok, 2001). However, plants can suffer other problems such as chlorotic leaves (yellowing), stunted growth, wilting, atrophied roots (Figure 3) and, in severe cases, death due to lack of nutrient intake caused by the number of galls present in the root system (Elling, 2013; Jones et al., 2013; Priya et al., 2011).

3. IPM for plant-parasitic nematodes

When nematodes are present in a crop area, the strategy is to minimize the populations of these organisms as much as possible. Some practices used to reduce negative impacts, particularly those of *Meloidogyne*, include chemical control, crop rotation, soil solarization, the use of resistant crops, the trapping of crops and biological control (Azlay et al., 2023; Palomares-Rius et al., 2021; Sikandar et al., 2020; Subedi et al., 2020).

3.1. Chemical control

Crop protection against plant parasitic nematodes is carried out by fumigants and nonfumigants chemical, due to broad availability, easy application and solubility in water (Azlay et al., 2023; Degenkolb & Vilcinskas, 2016; Verdejo, 2005). Commonly used fumigant compounds for nematode control are 1,3-dichloropropene, methyl bromide, ethylene dibromide (EDB), as well as non-fumigants such as organophosphates fenamiphos, ethoprophos, cadusaphos and carbamates aldicarb, carbofuran and oxamyl, among others (Grabau et al., 2021; Khanal et al., 2022; Khanal & Desaeger, 2020; Liu & Grabau, 2022). Methyl bromide, ethylene dibromide and dibromochloropropane (DBCP) can have carcinogenic effects, deplete the ozone layer and in some cases become very expensive, and therefore are mostly inaccessible to small-scale producers, making it more difficult to manage this pest (Lilley et al., 2011; Onkendi et al., 2014). In some countries, the use of these products is restricted or banned by environmental protection laws, because of their harmful effects on the environment and human health (Requena, 2022). As a result, we focused on exploring the most effective management alternatives and strategies.

3.2. Crop rotation

This practice consists of sowing different plants in a section of the land before planting the main crop. These plants should be nonhosts or poor hosts of plant-parasitic nematodes from genera such as *Meloidogyne*, *Globodera*, or *Pratylenchus*, in order to decrease nematode populations in soil (Moosavi, 2020). This agronomic practice has shown effectiveness as it allows susceptible plants to grow and produce optimal yields (Chen & Tsay, 2006; Everts et al., 2006; Kratochvil et al., 2004; Sandoval-Ruiz & Grabau, 2023). However, in cases where RKN represents a significant pest, cover crops resistant to common *Meloidogyne* species should be incorporated, such as castor (*Ricinus communis* L.), crotalaria (*Crotalaria spectabilis* Roth), hairy indigo (*Indigofera hirsute* L.), maize (*Zea mays* L.), marigold (*Tagetes* spp.), and oat (*Avena sativa* L.), among others (Stirling, 2014).

3.3. Soil solarization

This is a nonchemical method where wet soil is covered with a transparent plastic sheet, creating hydrothermal conditions due to the ultraviolet rays emitted by the sun (Stapleton & DeVay, 1982). During this process soil temperature is raised between 2 – 15 °C in warm weather conditions, causing death of many microorganisms such as bacteria, fungi and nematodes, nevertheless, this method depends greatly on the combination of the soil temperature and the right time of application (Collange et al., 2011). Some studies have demonstrated that soil solarization is effective for controlling plant-parasitic nematodes (Bakr et al., 2013; Candido et al., 2008; Putri et al., 2021; Rudolph et al., 2023); however, this method is usually not profitable for large infested fields due to the high cost of polyethylene and the laborious treatment (Gaur & Dhingra, 1991).

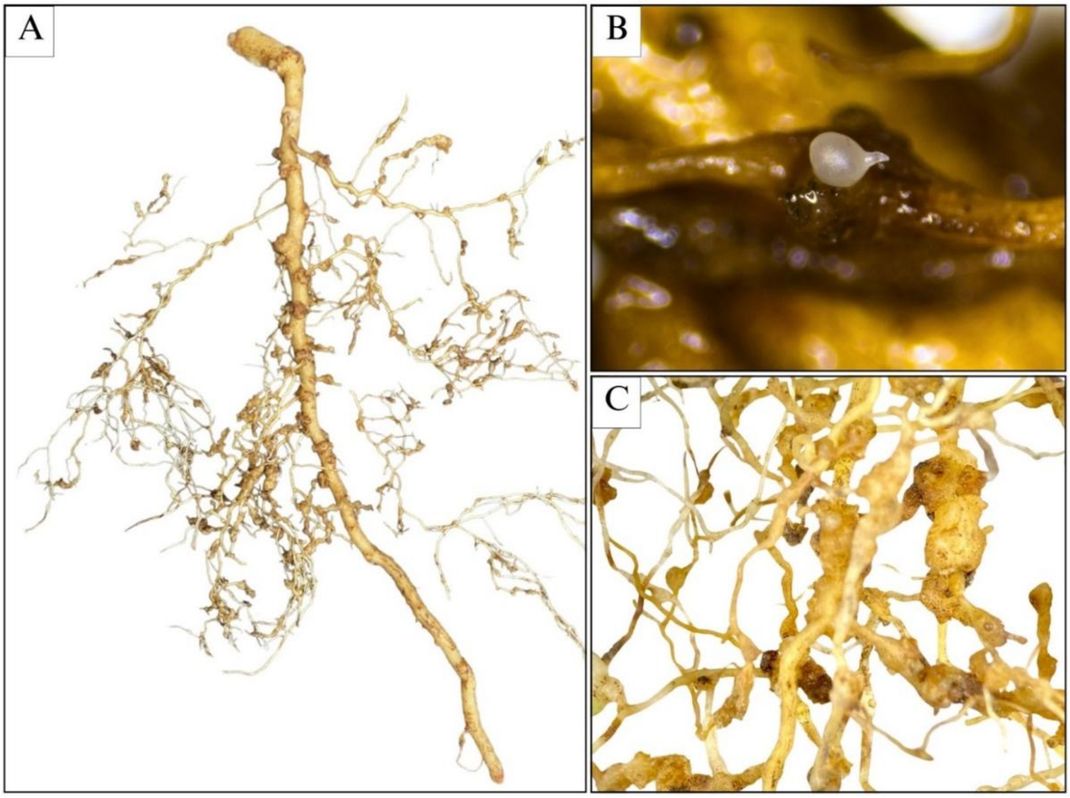

Figure 3. Pepper roots (*C. annuum* L.). A. RKN damage to bell pepper roots. B. Female extracted from the cortex (refer to Figure 2-D). C. Typical galling and hairy roots.

3.4. Resistant crops

Resistant crops play a crucial role in the management of plant-parasitic nematodes, offering one of the most effective and environmentally friendly methods for reducing losses caused by these pests (Lopes et al., 2019; Starr et al., 2002). Currently, advances in genetic engineering have revolutionized the field of agriculture, enabling the development of crops resistant to various soil-borne pathogens, including bacteria, fungi, and nematodes. For example, some crops, such as tomato, sweet potato and soybean, possess resistance genes for certain species of nematodes, although their protection is sometimes limited to individual pathotypes at species level (Fairbairn et al., 2007). These resistant varieties usually tend to perform better than plants that are susceptible to RKN (Subedi et al., 2020). Besides natural resistance genes, other employed strategies involve proteinase inhibitor genes (PIs), antinematode proteins, and RNA interference (RNAi) (Ali et al., 2017; Fuller et al., 2008). This method is often used in combination with other culture techniques, such as botanical extracts, BCAs, and/or chemical control, in order to make pest management more robust (Subedi et al., 2020).

3.5. Trap crops/trapping

The use of trap crops is a valuable tool for the control of plant pathogenic nematodes, which consists of planting susceptible or resistant host plants designed to mature and produce in a short period of time together with the main crop. This type of plant can attack with the production of secondary metabolites, contain and interrupt the life cycle of the pests of interest to reduce damage to the main crops (Samara, 2022). The susceptible plants must be destroyed at the adequate moment, in order to interrupt the reproductive cycles of the plant-parasitic nematodes (Halford et al., 1999; Scholte, 2000). Although trap crops represent an effective control method for plant-parasitic nematodes, it has not yet been welcomed by many farmers due to the time efforts and costs involved (Moosavi, 2020).

3.6. Biological control

A wide variety of soil microorganisms interact with nematodes and contribute to the regulatory systems that maintain the natural integrity of the soil food webs. When these biological buffering processes are altered, plant-feeding nematodes turn into pests. The use of BCAs can contribute to maintaining, restoring or enhancing the natural suppressive mechanisms present in all soils (Stirling, 2011). BCAs offer a low-risk, economical, natural, and often effective option against plant-parasitic nematodes (Borah et al., 2018). In this context, BCAs of plant-parasitic nematodes, including bacteria, antagonistic fungi, nematodes, viruses and microarthropods act as predatory organisms by reducing the population size of these pathogens (Stirling, 2014). However, according to Moosavi & Zare (2020), the number of organisms that could be useful for biological control is small; thus, understanding how suppressive processes work can be beneficial for managing the control of nematodes that affect plants. For this reason, researchers have been interested in seeking sustainable and environmentally friendly alternatives to chemical products, such as biological control, genetic modification of plants, and biological fumigants (Huang et al., 2016; Kumar & Singh, 2011; Nekoval et al., 2023; Peraza-Padilla et al., 2014; Sahebani & Hadavi, 2008; Sharon et al., 2007; Singh et al., 2012; Tazi et al., 2021; Varela-Benavides et al., 2017; Zhang et al., 2015).

Agricultural practices such as crop rotation and sowing resistant plants, in combination with BCAs, enhance the management of these pests (Azeem et al., 2020; Tian et al., 2024). However, the success of BCAs often depends on various parameters, such as the selection and use of the most effective BCAs, environmental factors and sanitary conditions of the soil (Afzal & Mukhtar, 2024).

4. Nematophagous fungi

Fungi have diverse survival strategies; some act as saprotrophs decomposing organic material, pathogens of plants or animals, others are endophytes or symbionts of some organisms and some act as predators attacking animals and obtaining nutrients from them. These essential feeding strategies of fungi contribute significantly to the exchange of energy and nutrients within the biological food chains (Liu et al., 2009). Nematophagous fungi comprises approximately 700 species that belong to different taxonomic groups within the kingdom Fungi (Table 1), specifically Ascomycota (Orbiliales, Hypocreales), Basidiomycota (Agaricales), Blastocladiomycota (Blastocladiales), Oomycota (Leptomitales, Peronosporales, Haptoglossales), and Zoopagomycota (Zoopagales, Khan et al., 2022; Soares et al., 2018). They are able to attack and consume living nematodes at various stages of their life cycle, including juveniles, adults, and eggs (Nordbring-Hertz et al., 2006). To do so they use highly specialized spores or mycelial structures known as traps, to snare nematodes or use hyphal tips to parasitize their eggs and cysts (Elkhateeb et al., 2023; Nordbring-Hertz, 2004). Nematophagous fungi are classified into four main categories on the basis of the way they interact with the host organism: 1) nematode-trapping fungi or predators, 2) obligate endoparasites, 3) opportunists or parasites of eggs, cysts and female nematodes, and 4) secondary metabolite or toxin producers (Elkhateeb et al., 2023; Gray, 1987; Kumar, 2020; López-Llorca et al., 2008).

4.1. Nematode-trapping fungi (NTF)

These fungi produce specialized hyphal structures denominated traps (Liang et al., 2019; Liu et al., 2009). These predatory structures play critical roles in the biology and behavior of fungi that specialize in the capture of nematodes (Liu et al., 2009). Several types of capture mechanisms have been described (Gray, 1987), such as unmodified and undifferentiated adhesive hyphae, hyphal branches forming three-dimensional adhesive nets, constricting rings, nonconstricting rings, adhesive branches which form two-dimensional adhesive nets, as well as sessile and stalked adhesive knobs (Figure 4) in which nematodes are captured (Figure 5A, K) by adhesion or mechanically (Devi, 2018; Nordbring-Hertz et al., 2006; Su et al., 2017). The mycelial traps capture and penetrate through the nematode cuticle or eggshell, killing them and digesting its content (Devi, 2018; Liu et al., 2009). Different biotic and abiotic factors can induce the formation of these structures, but the most important factor is the presence of live nematodes, which, by touching the mycelium, induce the formation of these structures and simultaneously serve as a source of additional nutrients for the fungus (Nordbring-Hertz et al., 2006). The formation of these traps also dependent on nematode type and number, acidity level (pH), temperature and available nutrients (Singh et al., 2012). Trap formation also involves the interaction of carbohydrate-binding proteins such as lectins and respective receptors in the nematode (Nordbring-Hertz et al., 2006).

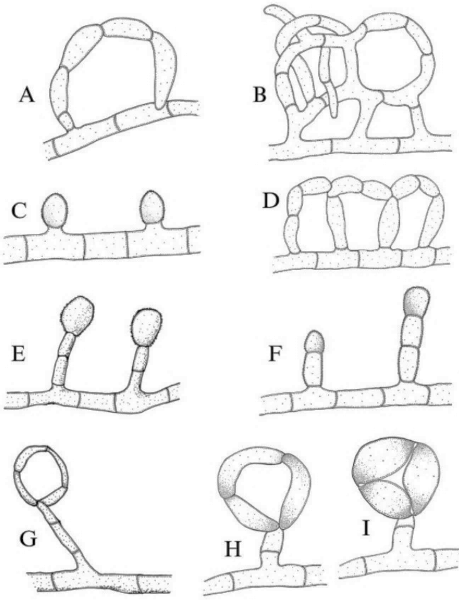

Figure 4. Diversity of nematode-trapping structures used by nematophagous fungi (Orbiliales). A. Simple-forming adhesive nets. B. Three-dimensional adhesive network. C. Sessile adhesive knobs. D. Two-dimensional adhesive net. E. Stalked adhesive knobs. F. Adhesive branches. G. Nonconstricting ring. H. Constricting ring open. I. Constricting ring closed.

Table 1

Taxonomic overview of the most frequent nematophagous fungi, structures of infection and mechanisms of action. The first name of the genus indicates the anamorphs phase, and the second after the slash indicates the telomorphs phase. Abbreviations: nematode-trapping fungi (NTF), endoparasitic fungi (EPF), egg- and female-parasitic fungi (EFP), toxin-producing fungi (TPF)

Division	Order	Genus	Infection structures	Mechanisms of action	References
Ascomycota	Helotiales	*Dactylaria*	Constricting ring	NTF	Singh et al., 2012
	Hypocreales	*Drechmeria*	Adhesive conidia	EPF	Wan et al., 2021
		Fusarium	Toxic metabolites	TPF	Kundu et al., 2016
		Harposporium/Podocrella	Ingested conidia	EPF	Dai et al., 2022
		Hirsutella/Ophiocordyceps	Adhesive conidia	EPF	Sun et al., 2024
		Lecanicillium/Cordyceps	Appressoria	EFP	Hajji-Hedfi et al., 2018
		Pochonia/Metacordyceps	Appressoria	EFP	Bontempo et al., 2014
		Purpureocillium/Cordyceps	Appressoria	EFP	Messa et al., 2020
		Trichoderma	Adhesive conidia	EPF	Peraza Padilla et al., 2014
	Orbiliales	*Arthrobotrys/Orbilia*	Adhesive networks	NTF	Tazi et al., 2021
		Dactylellina/Orbilia	Adhesive knobs and/or nonconstricting rings	NTF	Kumar, 2024
		Drechslerella/Orbilia	Constricting rings	NTF	Kumar, 2024
Basidiomycota	Agaricales	*Coprinus*	Toxin, "Spiny structures"	TPF	Luo et al., 2007
		Nematoctonus/Hohenbuehelia	Adhesive spores and adhesive "hourglass" knobs	EPF	Kennedy & Tampion, 1978
		Pleurotus	"Gun cells", injection	TPF	Youssef & El-Nagdi, 2021
Blastocladiomycota	Blastocladiales	*Catenaria*	Zoospores	EPF	Singh et al., 2013
Oomycota	Haptoglossales	*Haptoglossa*	"Gun cells", injection	EPF	Grover et al., 2021
	Leptomitales	*Nematophthora*	Zoospores	EFP	Kerry & Crump, 1980
	Peronosporales	*Myzocytiopsis*	Zoospores	EFP	El-Borai et al., 2011
Zoopagomycota	Zoopagales	*Cystopage*	Adhesive hyphae	NTF	Drechsler, 1941
		Stylopage	Adhesive hyphae	NTF	Drechsler, 1936

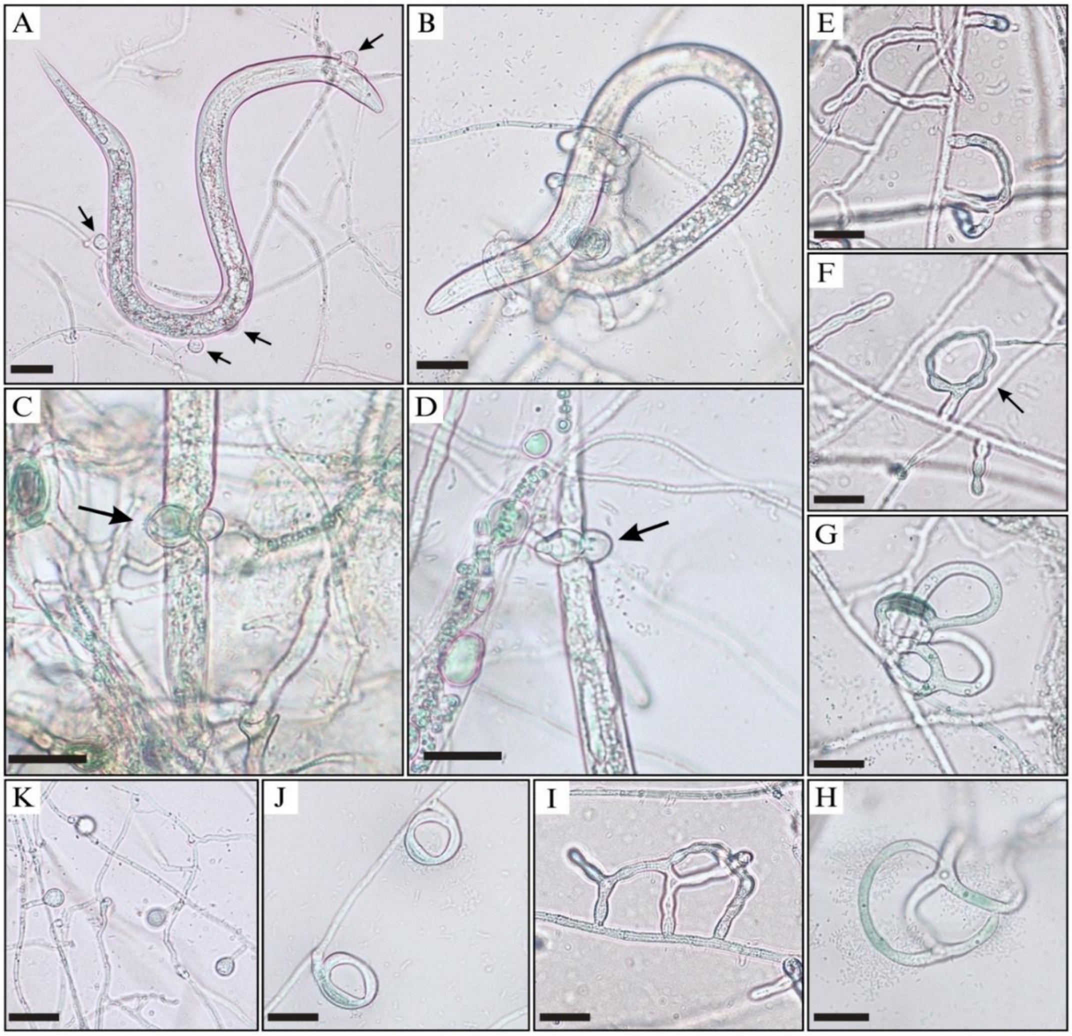

Figure 5. Microphotographs of capture structures of nematode-trapping fungi isolated and evaluated in antagonist essays against Meloidogyne spp. A. J_2 captured by stalked adhesive knobs (arrows). B. J_2 captured by three-dimensional adhesive network. C, D. J_2 captured and killed by constricting rings at the anterior and posterior ends. E. Simple-forming adhesive nets. F. Nonconstricting ring (arrow). G, H. Three-dimensional adhesive network. I. Two-dimensional adhesive net. J. Constricting rings open. K. Stalked adhesive knobs. Scale bars: 20 μm.

NTF comprise a wide variety of taxa with different capture structures; for example, species of *Stylopage* have adhesive hyphae, *Orbilia oligospora* forms adhesive networks, species of *Drechslerella* develop constrictor rings, and species of *Gamsylella* have adhesive branches and unstalked knobs.

Singh et al. (2012) in India used five isolates of *A. oligosporus* were used to test their predatory ability against *Meloidogyne graminicola* (Golden & Birchfield) larvae *in vitro*. Compared with the other isolates, the isolate VNS-1 captured significantly more nematodes than other isolates and killed 57.8% of *M. graminicola* (J_2) after 8 days.

Kumar (2024) tested nine strains of NTF, including *Orbilia brochopaga* (Drechsler) Baral, E. Weber, Bin Liu & Z. F. Yu (as syn. *Drechslerella brochopaga* (Drechsler) M. Scholler, Hagedorn & A. Rubner), *Arthrobotrys dactyloides* Drechsler (as syn. *D. dactyloides* (Drechsler) M. Scholler, Hagedorn & A. Rubner), *Dactylellina gephyropaga* (Drechsler) Ying Yang & Xing Z. Liu (as syn. *Dactylella gephyropaga* Drechsler), *Dactylellina phymatopaga* (Drechsler) Yan Li (as syn. *D. phymatopaga* Drechsler) and some species of *Arthrobotrys*, to measure their effectiveness in the biological control of *M. incognita*. The four species showed the highest mortality rates of juveniles with 73.2% – 99.8% within 5 days after inoculation (Kumar, 2024). The species *A. conoides* Drechsler, *A. eudermata* (Drechsler) M. Scholler, Hagedorn & A. Rubner, *A. musiformis* Drechsler, *A. oligosporus* and *A. thaumasius* (Drechsler) S. Schenck, W.B. Kendr. & Pramer resulted in a moderate decrease in root-knots with 45.3% – 53.4%, females with 55.5% – 61.1%, and eggs and juveniles with 52.9% – 60.1% compared to the control group (Kumar, 2024).

4.2. Endoparasitic fungi

This group of fungi parasitizes nematodes through adhesive or ingested spores, such as conidia or zoospores (Barron, 2004; Kumar, 2020). The spores attach to the nematode cuticle or are consumed by the nematode and then germinate inside its body, eventually leading to the death of the nematode (López-Llorca et al., 2008; Moosavi & Zare, 2020). In some species, these spores adhere to the larval cuticle or eggshell via the formation of specialized hyphal cells called appressoria (López-Llorca et al., 2008; Sharon et al., 2007). To penetrate through the nematode cuticle, the fungal hyphae excrete a variety of fungal enzymes, such as serine proteases, chitinases and collagenases (Liang et al., 2010; Yang et al., 2007). The internal mycelium digests the contents of the nematode and then emerges from it, sporulating on the surface and, thus continuing with a new cycle of infection (Gams & Zare, 2003).

Approximately 50 species are known as endoparasites, they have a wide host range and are mostly obligate parasites (Degenkolb & Vilcinskas, 2016; Moosavi & Zare, 2020). Some of the fungi that belong to this group attack by ingested spores (Figure 6), such as species of the genus *Harposporium* (teleomorph: *Podocrella*), or spores that adhere to the host such as species of the genus *Drechmeria* and *Hirsutella*, or form zoospores such as species of *Catenaria* (Figure 7) (López-Llorca et al., 2008). Species of the genus *Nematoctonus* have predatory and endoparasitic habits (Dürschner-Pelz, 1987). Unlike predatory species, which use their hyphae as capture tools by developing adhesive knobs called hourglass-shaped cells, endoparasitic species have developed a more indirect mechanism by using conidia as specialized traps (Gray, 1987). In recent years, species of the genus *Trichoderma* have also been the focus of attention as BCAs against different types of pests. It is not considered a nematophagous fungus because it does not form traps to capture and parasitize nematodes (López-Llorca et al., 2008). However, their mechanisms of action have been described as direct parasitism via mycelial invasion and indirect parasitism through the production of nematotoxins (Peraza Padilla et al., 2014; Szabó et al., 2012; Viterbo et al., 2007; Zhang et al., 2014).

Sun et al. (2024) compared the parasitic activity of *Hirsutella rhossiliensis* Minter & B.L. Brady strain HR02 on three different nematode species including *B. xylophilus*, *C. elegans*, and *M. incognita*. The results showed that parasitism was significantly higher in *M. incognita*, exceeding a rate of 90%, after 16 hours of fungal inoculation, compared to the other two nematode species.

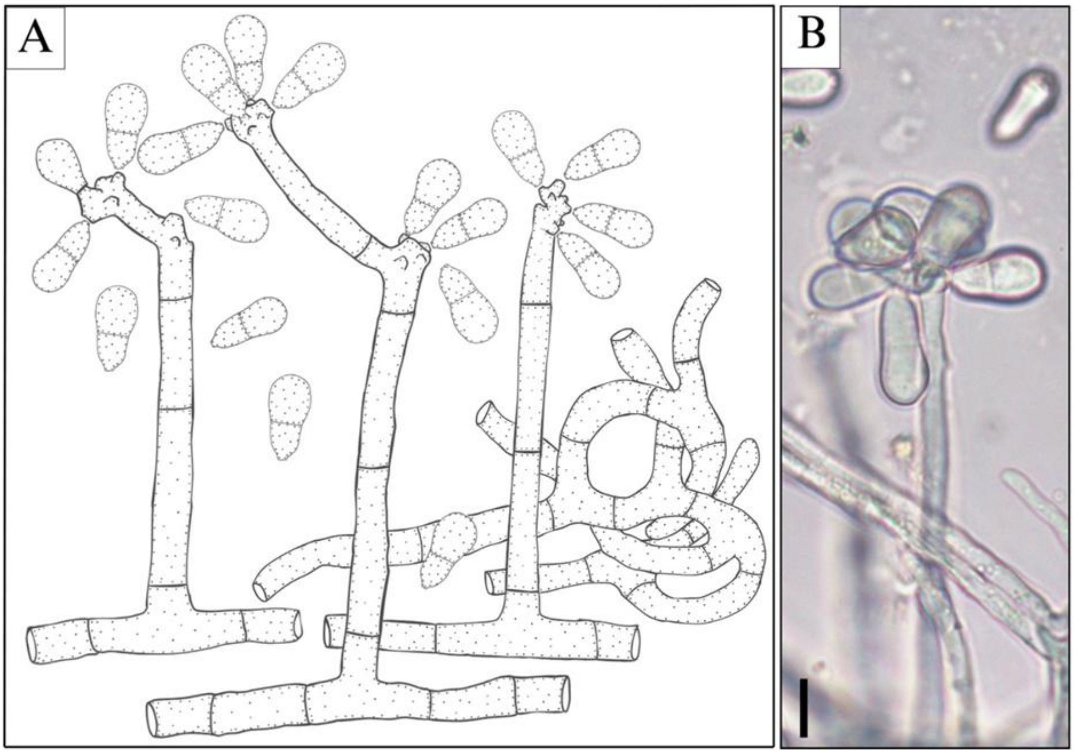

Figure 6. Nematode-trapping fungus of the genus *Arthrobotrys* sp. isolated from the coffee plantation at the IDIAP Experimental Station, Río Sereno, Panama. A. Drawings of conidiophores and the formation of traps. B. Microphotograph of conidiophores from a pure culture. Scale bar: 20 μm.

A similar study, carried out with *H. rhossiliensis*, showed a higher capacity for infection and damage in *M. incognita* than in the other nematode species used in the study (Cayrol et al., 1986). Application of conidia of *Drechmeria coniospora* (Drechsler) W. Gams & H.-B. Jansson at a concentration of >10^5 and *Panagrellus redivivus* juveniles as vectors infected with *D. coniospora* resulted in a significant reduction of *M. incognita* and *M. javanica* populations in tomato plants (Jansson et al., 1985).

In a related study, *D. coniospora* successfully reduced galling in tomato and alfalfa plants roots infected with *M. hapla*, however, this was not reflected in the quantity of J_2 stages present per gram of soil (Townshend et al., 1989). The 5-hydroxymethylfuran-2-carboxylic acid extracted from *Drechmeria coniospora* strain YMF1.01759 had a nematicidal effect against *M. incognita* juveniles, at all concentrations (400, 200, and 100 µg/mL), and also inhibited egg hatching (Wan et al., 2021). Females of *M. javanica* were highly susceptible to *Catenaria anguillulae* Sorokīn after 48 hours after inoculation with a 90% mortality rate and 7 days after inoculation with a 100% mortality rate (Singh et al., 1996). In an in vitro study *C. anguillulae* strain CAS-101 presented the maximum capture recorded after five days of inoculation of *M. graminicola*, and under greenhouse conditions decreased the number of root galls and juveniles in wheat plants after 45 days of inoculation decreased to significant levels (Singh et al., 2013).

Species of *Trichoderma* are considered effective mycoparasites and nematotoxicants with promising potential for the biological control of *Meloidogyne* (Nandeesha, 2020; Peraza Padilla et al., 2014; Sahebani & Hadavi, 2008). They are able to inhibit the hatching of eggs and juveniles by attacking their cuticle or membrane and then parasitizing them (Sharon et al., 2007).

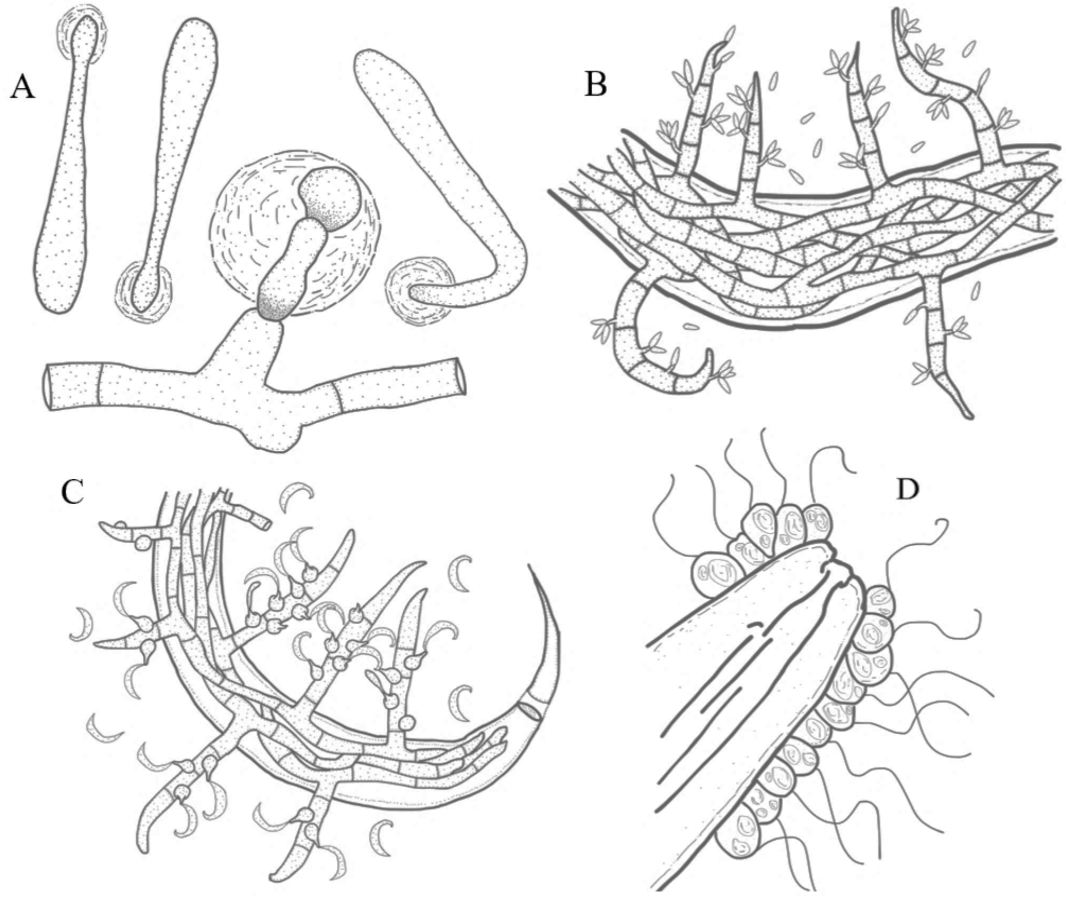

Figure 7. Fungal structures of endoparasitic fungi. A. Capture structure of *Hohenbuehelia leiospora* (syn. *Nematoctonus leiosporus*): conidia and hourglass-shaped adhesive knob surrounded by spherical sticky mucilage. B. *Drechmeria coniospora*: conidiophores and conidia emerging from an infected nematode. C. Species of *Harposporium*: bundle-shaped conidia and conidiophores emerging from an infected nematode. D. *Catenaria anguillulae*: zoospores encysted in the buccal part of a nematode.

Zhang et al. (2015) showed that under in vitro conditions a strain of *T. longibrachiatum* Rifai at a concentration of 1.5 × 10^7 conidia/mL was able to inhibit the movement and parasitize J_2 juveniles of *M. incognita*, causing mortality greater than 88% at the end of the 14 days following treatments. In another experiment under in vitro conditions, a *T. harzianum* Rifai BI strain showed a significant effect on the hatching of *M. javanica* eggs (Sahebani & Hadavi, 2008). Whereas the maximum hatching percentage in the control was on the third day, in the treatments hatching was about 20% lower and delayed on the sixth day. In that sense, *T. harzianum* BI not only reduced *M. javanica* egg production but also increased egg fragility and mortality (Sahebani & Hadavi, 2008).

In a recent study, several indigenous nematophagous fungal strains were evaluated for their potential as BCAs against *Meloidogyne enterolobii* in dry bean (*Phaseolus vulgaris* L.) cultivation, both with and without compost incorporation. Among the tested fungi, *Trichoderma ghanense* Yoshim. Doi, Y. Abe & Sugiy exhibited the highest egg parasitism rate with 86%, while *Talaromyces minioluteus* (Dierckx) Samson, N. Yilmaz, Frisvad & Seifert showed the highest parasitism of second-stage juveniles (J_2) at 95%. This provides a very encouraging alternative and ecologically complementary management of *Meloidogyne* in dry bean production (Ramatsitsi et al., 2024).

4.3. Egg and female parasitic fungi

These fungi are facultative parasites of mature and immature eggs, as well as the sedentary female stages of certain nematodes (Lamovšek et al., 2013). Generally, their mode of action involves the initial contact of the hyphae or zoospores with the cuticle or membrane of the egg, the subsequent formation of appressoria or cysts respectively, and the growth of the internal mycelium, which eventually depletes the content of the egg or the female body (López-Llorca et al., 2008). During the absence of suitable hosts these facultative parasites can survive as saprotrophic organisms in the rhizosphere without difficulty (Devi, 2018; Moosavi & Zare, 2020). Fungi in this category are relatively easy to mass cultivate and are more effective at infection because their host is sessile (Moosavi & Zare, 2020).

Species of the genus *Purpureocillium* and *Metacordyceps* are used worldwide in the biological control market due to their great effectiveness in parasitizing eggs and other stages of various species of nematodes (Lamovšek et al., 2013). In an experiment conducted under in vitro conditions, bacterial strains of *Bacillus subtilis* and *Pasteuria fluorescens*, as well as fungal strains of *Purpureocillium lilacinus* and *Trichoderma harzianum* were evaluated for their nematicidal activity against juveniles of *M. incognita* (Nandeesha, 2020). The results revealed that the maximum mean mortality was recorded for *P. lilacinum* with 67.77%, followed by *T. harzianum* with 54.89%, *P. fluorescens* with 50%, and *B. subtilis* with 48.89%. The four evaluated species were outstanding as good BCAs against the J_2 stage of *M. incognita* (Nandeesha, 2020). Huang et al. (2016) studied the nematicidal and ovicidal potential of *Bacillus cereus*, *Purpureocillium lilacinum* and *Syncephalastrum racemosum* Cohn ex J. Schröt. In the study *P. lilacinum* and *S. racemosum* at a concentration of 50% with 4.5 × 10^8 spores per mL acted as the best control agents for inhibiting the hatching of *M. incognita* eggs.

Metacordyceps chlamydosporia (syn. *Pochonia chlamydosporia*) is used as a BCA, due to its high efficiency in parasitizing nematode eggs and females. It releases a cascade of degradative enzymes, including serine proteases and chitinases, which play an important role in the degradation of the outer layer of eggs (Khan et al., 2022). According to Aminuzzaman et al. (2013), the *P. chlamydosporia* strain WZ07-1F-3 managed to parasitize 96.0% of *M. incognita* eggs, decreasing the hatching rate to 68.8% and causing the death of 47.2% of the juveniles. In Panama, De Lisser (2022) tested a commercial strain of *P. chlamydosporia* (Nema-Kell SC) under field conditions in rice crops and evaluated its efficacy on phytopathogenic nematode populations. The results indicated that this strain with a treatment dose of 0.75 mL reduced approximately 63% of juveniles (De Lisser, 2022).

4.4. Toxin-producing fungi

This group attacks nematodes by immobilizing them via the secretion of toxins or inhibitory metabolites, subsequent penetration of the cuticle and digestion of body contents (López-Llorca et al., 2008). More than 200 compounds with nematicidal activity have been described from this group of fungi so far, including alkaloids, peptides, terpenoids, sterols, aliphatic compounds, quinones, among others (Li & Zhang, 2014). Species of Basidiomycota are the predominant producers of nematotoxins, especially wood decomposers which often lack certain nutrients such as nitrogen (Khan et al., 2023; Soares et al., 2018).

Species of *Pleurotus* are popular edible mushrooms valued for its high protein and nutrient contents

(Rosado et al., 2003). Some species secrete potent lethal toxins that immobilize and kill nematodes, for example *Pleurotus ostreatus* (Jacq. P. Kumm.) produces microdroplets of trans-2-decenedioic acid, which causes the immobilization of nematodes (Kwok et al., 1992). Erazo et al. (2020) showed that *P. ostreatus* effectively reduced the number of galls caused by *M. incognita* on tomato plants under greenhouse conditions and there was no significant difference compared with the chemical control. Nyangwire et al. (2024) observed that *P. ostreatus* caused a 95% mortality of *M. incognita* at 72 h of exposure in an aqueous suspension. Furthermore, different dilutions of the fungus filtrate were applied in vitro and in pots of watercress showing a 95% of mortality at 48 h and a gilling index (GI) in the plants of 0.70 on doubling the *P. ostreatus* inoculum, respectively (Nyangwire et al., 2024). Other studies have demonstrated that *Coprinus comatus* (O.F. Müll.) Pers. is capable of immobilizing and trapping *Meloidogyne* juveniles by spiny balls (Luo et al., 2004, 2007).

Toxin producing fungi are also found among Ascomycetes, for example some nonpathogenic strains of *Fusarium oxysporum* Schltdl. can have lethal effects on *Meloidogyne* juveniles via the production of bioactive secondary metabolites such as ethyl acetate, 2-methylbutyl acetate, 3-methylbutyl acetate, 2-methylpropyl acetate, fusarubin, and anhydrofusarubin (Kundu et al., 2016; Terra et al., 2018).

5. Conclusions and prospects

Plant-parasitic nematodes are a problem of scale for medium and small farmers due to their adaptation capability to different environments, their quick reproduction and potential damage, resulting in significant economic losses. In low-income countries, these consequences directly affect FSN. The genus *Meloidogyne* can be a challenge as an object pest within strategic crops in traditional agricultural systems; however, understanding its physiology, interaction with the host plant, mechanism of action and early action can enable effective IPM of these organisms.

The use of synthetic fumigants and nonfumigants can lead to a negative impact on the environment, affecting soil biodiversity, water and contamination, inducing resistance in plant-parasitic nematodes and threatening human health. Therefore, the integration of sustainable alternatives in conjunction with innovative approaches, such as the use of genetic engineering or BCAs, is promising. Knowledge about nematophagous fungi has grown in recent years due to taxonomic and molecular studies. As revealed in this article, different groups of nematophagous fungi can have positive effects on the control of RKNs, therefore, BCAs are promising for the IPM.

The future relevance of nematophagous fungi hinges on limited research and development, thus, it is worthy of further findings at the level of biodiversity, taxonomic and molecular studies, formulations that ensure their viability and efficacy over long periods in vitro and in vivo. However, it is important to mention that without proper soil management, the use of ecofriendly agronomic practices (crop rotation, resistant plants, trap crops, among others), knowledge transfer through educational tools, workshops and farmers' training, and the development of economical and accessible formulations, the efficacy and sustainable use of these pest-controlling microorganisms in both conventional and modern cropping systems can be compromised.

The application of new technologies such as microencapsulation for controlled release into the substrate, liquid and dry bioformulations for easy transport and long-term storage, the use of genetic and biotechnological methods to optimize the attack on target organisms, can contribute significantly to reduce costs and losses for farmers. Finally, we propose that nematophagous fungi are a potential alternative to synthetic agricultural chemicals in the management of plant parasitic nematodes, and that they may be more effective in promoting sustainable agriculture by replacing hazardous chemicals and reducing the environmental and health effects of their residues.

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Declaration of Competing Interest

The authors declare that there are no conflicts of interest related to this review work.

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