Chapter 10
Fungi: A Bio-resource for the Control of Plant Parasitic Nematodes

K. Kiran Kumar

Contents

10.1 Introduction

Plant parasitic nematodes are considered to be the major constraint on plant productivity, and they have been found to attack almost every part of the plant including roots, stems, leaves, fruits, and seeds. They are also responsible for invasion of secondary pests and pathogens by causing wounds in the host roots (Caboni et al. 2016). Global annual yield losses from plant parasitic nematodes have been estimated at 12.6% ($215.77 billion) for top 20 life sustaining crops (Abd-Elgawad and Askary 2015). Among different groups of plant parasitic nematodes, root knot (*Meloidogyne* spp.) and cyst nematodes (*Heterodera* and *Globodera* spp.) are economically important by forming complex feeding structures like giant cells and

K. K. Kumar (✉)
Department of Nematology, ICAR-Central Citrus Research Institute, Nagpur, Maharashtra, India

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syncytia in the roots of their hosts which act as a nutrient sink to the nematode. Apart from these, root-lesion nematodes (*Pratylenchus* spp.), burrowing nematode (*Radopholus similis*), stem nematode (*Ditylenchus dipsaci*), reniform nematode (*Rotylenchulus reniformis*), and several other plant parasitic nematodes causing economic damage to the crops (Jones et al. 2013).

Many traditional chemical pesticides such as fumigants, organophosphates, and carbamates have been used for the management of plant parasitic nematodes (Kour et al. 2020). However, the usage of harmful chemical pesticides cause environmental toxicity, health effects and further withdrawal of some pesticides has led to the development and adoption of non-chemical alternatives for the management of plant parasitic nematodes (Davies and Curtis 2011; Kumar et al. 2018). In addition, these chemicals do not affect the development of nematode eggs in soil, since the egg shell of nematode acts as a barrier which makes them resistant to chemical pesticides (Baron et al. 2019). Crop rotation and use of resistant cultivars have been used as the management strategies for plant parasitic nematodes. However, these practices are limited by the size of growing area, wide host range of nematode species, and high genetic diversity among or within nematode populations (Berlitz et al. 2014; Li et al. 2015).

Biological control, an alternative for the management of plant parasitic nematodes. The usage of biocontrol agents is increasing these days, due to their reduced environmental toxicity, target specificity, and safety to non-target organisms (Kumar and Singh 2015; Jiang et al. 2017). These biocontrol agents include fungi, bacteria, viruses, nematodes, and other invertebrates which have an antagonistic activity against plant parasitic nematodes. The market for biological nematicides has risen by nearly 20% from 2009 to the present, according to the Markets and Markets report, with most of the development in field crops. Nematicide sales amounted to just over $1 billion in 2014 and are anticipated to expand at a compound annual growth rate (CAGR) of 2.7% over the next 10 years to $1.3 billion over 20 years (Jiang et al. 2017).

Currently several biocontrol agents such as fungi and bacteria have been widely used as commercial products for the management of plant parasitic nematodes. Fungal antagonists have been considered as the most promising biocontrol agents and attention is being paid to the exploitation of fungi to control plant parasitic nematodes (Stirling 2011; Moosavi and Zare 2012; Lamovsek et al. 2013). Among different fungal biocontrol agents, the most widely studied species for nematode management include *Pochonia chlamydosporia*, *Purpureocillium lilacinum*, *Arthrobotrys oligospora*, *Trichoderma* spp. and *Verticillium* spp. (Rastegari et al. 2020a, b; Yadav et al. 2020a, b). This chapter reviews different categories of nematophagous fungi, mode of action, and knowledge of the interactions between nematodes and nematode trapping fungi and commercialization of different fungal products for the management of plant parasitic nematodes.

10.2 Nematophagous Fungi

This group of fungi has been widely used as biocontrol agents of plant parasitic nematodes due to their antagonistic, parasitic, and predatory action against different species. There are approximately 700 fungal species reported to be able to attack different life stages of nematodes (juveniles, adults, and eggs) (Li et al. 2015; Jiang et al. 2017). Over the decades, several researchers have worked on fundamental studies and their potential as biocontrol agents against different plant parasitic nematodes. Based on their infection mechanism, they are subdivided into four categories viz., nematode trapping fungi, endoparasitic fungi, egg and female parasitic fungi, and toxin producing fungi (Dackman et al. 1992; Nordbring-Hertz et al. 2006) (Table 10.1).

10.2.1 Nematode Trapping Fungi

These are soil borne fungi that have the ability to capture and kill nematodes by using trapping structures, including adhesive hyphae, adhesive knobs, constricting rings and non-constricting rings, and adhesive networks (Nordbring-Hertz et al. 2011; Jiang et al. 2017). The type of trapping structure formed mainly depends on the fungal species or strains of fungal species and both biotic and abiotic environmental factors (Nordbring-Hertz et al. 2006). Based on phylogenetic analysis results using ribosomal RNAs (rRNAs) and protein coding genes, these trapping devices could serve as indicators for generic delimitation among these fungi (Ahren et al. 1998; Scholler et al. 1999; Li et al. 2005). There are about 380 species of nematode trapping fungi have been reported from different regions of the world (Zhang et al. 2011). They are usually non-host specific and can infect all soil dwelling nematodes. All the known nematode trapping fungi belong to the order Orbiliales of the phylum Ascomycota (Zhang and Hyde 2014). These fungi can live both saprophytically on organic matter and as predatory by capturing tiny animals. However, they can shift from saprophytic to predatory lifestyle in the presence of nematode prey by the production of trapping structures (Li et al. 2011; Yang et al. 2012; Zhang and Hyde 2014). The application of these fungi for nematode suppression was accompanied by addition of large amounts of organic matter and in most cases the levels of nematode control were unpredictable (Stirling 1991).

10.2.1.1 Adhesive Hyphae

These are mostly produced by lower fungi belongs to the genera *Stylopage* and *Cystopage* under phylum Zygomycota (Table 10.1). They cannot produce complex devices for capturing nematodes due to the absence of septa (Barron 1977). However, septate fungi such as *Arthrobotrys botryospora*, *Dactylaria psychrophila,*

Table 10.1 Different categories of nematophagous fungi

Category	Nematode trapping structure	Name of fungi	Phylum
Nematode trapping fungi	Adhesive hyphae	*Stylopage hadra*	Zygomycota
		Cystopage cladospora	Zygomycota
	Adhesive knobs	*Dactylellina ellipsospora*	Ascomycota
		Dactylellina drechsleri	Ascomycota
		Dactylaria candida	Ascomycota
		Monacrosporium haptotylum	Ascomycota
		Gamsylella querci	Ascomycota
		Gamsylella robusta	Ascomycota
		Gamsylella parvicollis	Ascomycota
		Nematoctonus sp.	Basidiomycota
	Non-constricting rings	*Dactylaria candida*	Ascomycota
		Dactylaria lysipaga	Ascomycota
	Adhesive knobs + non-constricting rings	*Dactylellina appendiculata*	Ascomycota
		Dactylellina haptotyla	Ascomycota
	Constricting rings	*A. dactyloides*	Ascomycota
		A. brochopaga	Ascomycota
		Drechslerella stenobrocha	Ascomycota
		Drechslerella brochopaga	Ascomycota
		Drechslerella dactyloides	Ascomycota
	Adhesive knobs + adhesive spores	*Nematoctonus concurrens*	Basidiomycota
	Adhesive networks	*Arthrobotrys oligospora*	Ascomycota
		Arthrobotrys musiformis	Ascomycota
		Arthrobotrys conoides	Ascomycota
		Arthrobotrys vermicola	Ascomycota
		Arthrobotrys superba	Ascomycota
		Dactylaria scaphoides	Ascomycota

(continued)

Table 10.1 (continued)

Category	Nematode trapping structure	Name of fungi	Phylum
Endoparasitic fungi	Adhesive conidia	*Drechmeria coniospora*	Ascomycota
		Hirsutella rhossiliensis	Ascomycota
		Hirsutella minnesotensis	Ascomycota
		Cephalosporium balanoides	Ascomycota
	Adhesive spores	*Nematoctonus concurrens*	Basidiomycota
		Nematoctonus haptocladus	Basidiomycota
		Nematoctonus leiosporus	Basidiomycota
	Ingested conidia	*Harposporium anguillulae*	Ascomycota
		Harosporium cerbri	Ascomycota
	Zoospores	*Catenaria auxillaris*	Blastocladiomycota
		Catenaria anguillulae	Blastocladiomycota
		Myzocytiopsis glutinospora	Oomycota
		Myzocytiopsis vermicola	Oomycota
		Myzocytiopsis enticularis	Oomycota
		Myzocytiopsis humicola	Oomycota
Egg parasitic fungi	Appresoria	*Pochonia chlamydosporia*	Ascomycota
		Purpureocillium lilacinum (=*Paecilomyces lilacinus*)	Ascomycota
		Acremonium (=*Cephalosporium*) sp.	Ascomycota
		Dactylella oviparasitica	Ascomycota
		Dactylella lysipaga	Ascomycota
		Lecanicillium psalliotae	Ascomycota
		Lecanicillium lecanii	Ascomycota
	Zoospores	*Nematophthora gynophila*	Oomycota
Toxin producing fungi	Toxic droplets	*Pleurotus ostreatus*	Basidiomycota
	Toxin, spiny structures	*Coprinus comatus*	Basidiomycota
Endophytic fungi		*Fusarium oxysporum*	Ascomycota
		Neotyphodium spp.	Ascomycota
		Acremonium	Ascomycota
		Penicillium oxalicum	Ascomycota

and *A. superba* can capture nematodes with adhesive hyphae under certain conditions (Chen and Dickson 2004). The infection begins with the capture organ being adhered by nematode. Within few minutes, the nematodes added to a fungal colony were captured and penetrated within 1 h by the trap forming cell hyphae. After 6 h, the whole nematode body was filled with hyphae. The dead nematode did not induce traps but developed a large number of thin hyphae around the nematode.

10.2.1.2 Adhesive Knobs

These are very effective trapping structures and nematodes are often attacked at more than one infection site (Barron 1977). These knobs are covered by a thin layer of adhesive materials and the infection process involves one knob and several associated hyphal elements. These adhesive knobs produce an infection peg and infection bulb. From this bulb, the infection hyphae proliferate within the nematode and digest the inner contents. The adhesive knobs are found in Ascomycota and Basidiomycota (Table 10.1). This group of fungi is unique in forming clamp connections on the secondary hyphae (Chen and Dickson 2004). The genomic studies of adhesive knob forming species, *Monacrosporium haptotylum* indicated the enrichment of small secreted proteins (SSPs) that were highly and differentially expressed during the interaction with nematode hosts (Meerupati et al. 2013).

10.2.1.3 Adhesive Networks

This is the most common type of nematode trapping structure observed in *Arthrobotrys* spp. (Table 10.1). The trap may consist of a single ring or a three-dimensional network. *A. oligospora*, a model organism for understanding the interaction between fungi and nematodes, forms a three-dimensional adhesive network during infection process. The genomic and proteomic analyses of this fungus provide insights into nematode trap formation including G-protein coupled receptors, adhesive proteins, cell division cycle, peroxisome related proteins, and proteins involved in energy supplementation (Yang et al. 2011).

10.2.1.4 Constricting Rings

Among different trapping structures, constricting rings are probably the only ones that actually capture the nematodes and considered to be the lineal strategy after which other trapping structures evolved (Yang et al. 2007a; Liu et al. 2012). In general, trapping fungi that form constricting rings are more abundant in soils rich in organic matter and influenced by the population density of nematodes (Linford 1937; Gray 1985). However, the trapping mechanism is completely different in contrast to others. When a nematode passing into the ring, it stimulates the inner face of the ring such that the three cells comprising the ring inflate centripetally to about

three times and get trapped within 0.1 s. The pressure exerted by nematode on the ring during this process causes the activation of G-protein coupled receptors which leads to an increase in cytoplasmic Ca^{2+}, and activation of calmodulin that opens the water channels, and thereby inflates the ring trapping the nematode (Chen et al. 2001). The genome sequence of *Drechslerella stenobrocha* constricting ring forming fungus revealed that the downregulation of saprophytic enzyme genes and the upregulation of infection related genes during the capture of nematodes indicated a transition between saprophagous and predatory life strategies. This study also indicated that protein kinase C (PKC) signal pathway and Zn (2)-C6 type transcription factors were responsible for trap formation in *D. stenobrocha* (Liu et al. 2014). Following the capture an infection peg is produced by one of the three ring cells and a small globose infection bulb develops after the penetration of infection peg into the body cavity of the nematodes. Trophic hyphae quickly digest and absorb the internal contents of nematode leaving only the cuticle structures.

10.2.1.5 Non-constricting Rings

Non-constricting rings are generally produced by erect lateral branches produced from septate hyphae. When a nematode thrusts its head inside the non-constricting ring, it gets wedged and held by friction. During this, the ring often breaks at the point of weakness near the stalk apex and this process may be repeated until several rings are wedged around the host. Following capture, the fungi penetrate and consume the inner contents of the host (Zaki 1994). *Dactylaria candida* and *D. lysipaga* usually generally form non-constricting rings during infection process (Table 10.1).

10.2.2 Endoparasitic Fungi

These are a group of fungi that infect nematodes mainly by conidia (*Drechmeria coniospora*), ingestive spores (*Harposporium* spp.), adhesive spores (*Nematoctonus concurrens*) or zoospores (*Catenaria anguillulae*) (Table 10.1). Their spores either adhere to the nematode cuticle or swallowed by the host and then germinate inside the nematode body which finally result in the death of nematode. In *D. coniospora* surface proteins and chymotrypsin-like proteases were involved in the infection process (Lopez-Llorca et al. 2008; Jansson and Friman 1999). Although some of these like *Nematophthora gynophila* could parasitize a large number of nematodes viz., *Heterodera avenae*, *H. trifolii*, *H. schachtii*, *H. goettengiana*, *H. cruciferae*, etc., and their bioefficacy was dependent on adequate soil moisture and on the relative number of nematodes and endozoic units present in the soil. Besides, their obligate nature posed a problem for mass production (Kerry 1987).

10.2.3 Egg and Female Parasitic Fungi

The research on egg and female parasitic fungi has been initiated in the 1990s. These fungi use either appressoria (*Purpureocillium* spp., *Pochonia* spp.,) or zoospores (*Nematophthora gynophila*) to kill different life stages (Lopez-Llorca et al. 2008) (Table 10.1). The relationship between nematodes and these fungi was variable, but as some of the isolates were highly virulent, they were extensively used and are still available as formulations in the market, especially for sedentary endoparasites. However, it is important to ascertain the quality parameters, namely colony forming units (CFU), presence of contaminants of these formulations before application in the field for control of nematode population. Among different egg parasitic fungi, *P. chlamydosporia* and *P. lilacinum* are widely used as biocontrol agents.

10.2.3.1 Pochonia chlamydosporia

P. chlamydosporia is considered as potential biocontrol agent of endoparasitic nematodes due to their ability to colonize the rhizosphere of plants and cultivars, to produce chlamydospores in vitro and to infect eggs of endoparasitic nematodes such as root knot (*Meloidogyne* spp.) and cyst nematodes (*Heterodera avenae*, *H. glycines*, *H. schachtii*) (Manzanilla-Lopez et al. 2013; Dallemole-Giaretta et al. 2015). In addition, this fungus has shown activity against false root-knot nematode, *Nacobbus aberrans*, burrowing nematode, *Radopholus similis*, citrus nematode, *Tylenchulus semipenetrans,* and reniform nematode, *Rotylenchulus* spp. (Manzanilla-Lopez et al. 2013; Abd-Elgawad and Askary 2018). The specificity of this fungus towards sedentary endoparasitic nematodes is associated with the recognition of both quantitative and qualitative changes in root exudates patterns during nematode infection (Wang and Bergeson 1974). Crops such as beans, cabbage, crotalaria, kale, pigeon pea, potato, pumpkin, and tomato are considered as good hosts (200 CFU/cm^2 of root) for colonization of this fungus in the rhizosphere. Whereas, chilli, sweet potato, cowpea, rye, tobacco, and cotton are considered as moderate hosts (100–200 CFU/cm^2 of root) and poor hosts (<100 CFU/cm^2 of root) include aubergine, okra, soybean, sorghum, and wheat (de Leij 1992; Bourne et al. 1996).

P. chlamydosporia infects nematode eggs through the development of appressoria at the hyphal tip and the presence of mucilaginous material between appressoria and surface of the egg shell appear to assist in egg shell penetration (Lopez-Llorca et al. 2002). A post infection bulb leads to the development of a mycelium within the egg and destruction of internal contents (Segers 1996; Kerry and Hirsch 2011). The fungus produce extracellular enzymes such as Serine proteases (VCP1) and chitinases which are involved in degradation of egg shells (Segers 1996). SCP1, a serine carboxypeptidase from *P. chlamydosporia* was immunolocalized in *M. javanica* eggs infected by fungus (Escudero et al. 2016).

The ability to produce chlamydospores in vitro without the addition of other energy sources lead to the consideration of this fungus as biocontrol agent. Hence application of chlamydospores at the rate of 5000 spores/g soil in aqueous suspension is recommended to test the efficacy of fungus but it may vary according to the strain and target nematode (de Leij et al. 1992; Stirling and Smith 1998; Bourne and Kerry 2000; Kerry and Hidalgo-Diaz 2004). Application of organic amendments may increase fungal abundance in soil and fungus remains in saprophytic phase but not necessarily increase in nematode parasitic activity (Atkins et al. 2003). Gene expression studies showed differences among several genes involved in cellular signals, transport or DNA repair, with a distinct cluster of genes commonly expressed during transition from saprophytic to parasitic phase of this fungus (Rosso et al. 2011). Niu (2017) reviewed that the secondary metabolites released from *P. chlamydosporia* and other species such as resorcylic acid lactone, pyranones, alkaloid, phenolics, etc. may act as virulence factors to plant and animal-parasitic nematodes parasitized by the fungus.

10.2.3.2 *Purpureocillium lilacinum* (=*Paecilomyces lilacinus*)

P. lilacinum is a soil inhabiting fungus reported from different parts of the world and widely used as potential biocontrol agent against plant parasitic nematodes (Vasanthi and Kumaraswamy 1999; Brand et al. 2010). This fungus infects eggs, egg masses, females, and cysts of many plant parasitic nematodes such as *Meloidogyne* spp., *Globodera* spp., *Heterodera* spp., *Tylenchulus* sp., and *Nacobbus* sp. The fungus first colonizes gelatinous matrix of different nematodes and penetrate the eggs with the help of appressoria or hyphae. In addition, the fungus produce several extracellular enzymes such as serine proteases, chitinases depending on the recognition of the host surface hydrophobicity and these were purified and characterized from different strains (Bonants et al. 1995; Lopez-Llorca et al. 2002; Khan et al. 2003; Huang et al. 2004; Khan et al. 2004). Enzymes produced by *P. lilacinum* strain 251 resulted in reduction of egg hatching in *M. javanica* (Khan et al. 2004). Similarly, the secondary metabolites produced by the fungi (Australian isolate), such as leucinostatins, have significant effect on the colonization of *M. javanica* eggs (Park et al. 2004).

In addition to control of plant parasitic nematodes, species of this fungus produce several metabolites which promote plant growth and defensive substances against biotic and abiotic stresses (Khan et al. 2012). Further, this fungus promote plant growth by performing Phosphorus solubilization in soil (Rinu and Pandey 2011; Lima-Rivera et al. 2016).

10.2.4 Toxin Producing Fungi

This group of fungi produces toxic metabolites which act as nematicidal toxins before the penetration of hyphae into nematode body through cuticle. The toxic effects on nematodes include reduced egg hatching, immobility, mortality, etc. The productions of toxins also help in preventing the consumption of fungal colonies by fungivorous nematodes and other invertebrates (de Freitas Soares et al. 2018). So far more than 200 compounds have been identified from nearly 280 fungal species (Li et al. 2007a; Li and Zhang 2014). The commonly included genera under this category are *Nematoctonus*, *Pleurotus,* and *Penicillium,* etc. (de Freitas Soares et al. 2018). These toxic metabolites include peptides, terpenoids, alkaloids, quinines, sterols, etc. (Li and Zhang 2014). Table 10.3 shows a list of toxic metabolites identified in different fungi and their effect on different nematode species. The discovery of these toxic metabolites further lead to the development of these chemicals as biocontrol agents against plant parasitic nematodes (Guo et al. 2012) (Table 10.2).

10.2.5 Endophytic Fungi

The approach of using endophytic fungi as biocontrol agents of plant parasitic nematodes has gained attention in recent years to rectify the difficulties involved in establishing an introduced organism in the rhizosphere environment. Endophytes have the benefit that they occur in the same ecological niche as endoparasitic nematodes but are not subject to competition from microorganisms in the soil and rhizosphere (Stirling 2011; Yadav et al. 2019a, b; 2020c). The most research work has focused on the strains of *Fusarium oxysporum* that reduce the infection and reproduction of burrowing nematode, *Radopholus similis* (Athman et al. 2007), root-knot nematode, *M. incognita* (Hallmann and Sikora 1994; Dababat and Sikora 2007), lesion nematode, *Pratylenchus goodeyi* (Waweru et al. 2014), spiral nematode, *Helicotylenchus multicinctus* (Waweru et al. 2014).

Trichoderma spp. are endophytic and mycoparasitic fungi that have been described as biocontrol agent against plant parasitic nematodes (Zhang et al. 2014; Li et al. 2015; Dandurand and Knudsen 2016). *Trichoderma* parasitizes nematode eggs by the secretion of chitinolytic enzymes encoded by two genes chi 18-5 and chi 18-12 (Szabó et al. 2012). In addition, trypsin like protease (PRA1) and serine protease (SprT) were also observed against *Meloidogyne* juveniles during infection by the fungi (Suarez et al. 2004; Chen et al. 2009). Further, Szabó et al. 2013 reported that comparative analysis of protease expression profiles in *T. harzianum* revealed 13 peptidase encoding genes, suggesting that these genes might play an important role in infection process by the fungi. In addition to direct antagonism, nematophagous activity has also observed on eggs of *M. incognita*, *M. javanica*, *M. arenaria,* and *M. exigua* (Windham et al. 1989; Eapen et al. 2005; Sharon et al. 2007; Spiegel et al. 2007; Ferreira et al. 2008).

Table 10.2 Nematicidal toxic metabolites identified in nematophagous fungi

Toxin	Fungi	Test nematode	Reference
Secalonic acid D, Oxalin	*Penicillium anatolicum*	*Globodera rostochiensis*, *Heterodera avenae* spp	Steyn (1970)
	Penicillium vermiculatum, Penicillium oxalicum	*Globodera rostochiensis, Globodera pallida*	
	Penicillium chrysogenum	*Meloidogyne javanica*	
trans-2-decenedioic acid	*Pleurotus ostreatus* NRRL 3526	*Panagrellus redivivus*	Kwok et al. (1992)
S-coriolic acid	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
Linoleic acid	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
p-Anisaldehyde	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
1-(4-Methoxyphenyl)-1,2-propanediol	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
2-Hydroxy-(4′-methoxy)_ propiophenone	*Pleurotus pulmonarius*	*Caenorhabditis elegans*	Stadler et al. (1994a)
Dihydropleurotinic acid	*Nematoctonus robustus*		Stadler et al. (1994b)
Pleurotin	*Nematoctonus robustus*		Stadler et al. (1994b)
Leucopleurotin	*Nematoctonus robustus*		Stadler et al. (1994b)
T2 toxin, Moniliformin, Fusarenone, Neosolaniol, Verrucarina,	*Fusarium solani*	*Meloidogyne javanica*	Ciancio (1995)
Cheimonophyllon E; 5α,8α-epidioxyergosta-6,22-dien-3-β-ol; 5-hydroxymethyl-furancarbaldehyde	*Pleurotus eryngii* var. *ferulae* L14	*Bursaphelenchus xylophilus*	Li et al. (2007b)
5-methylfuran-3- carboxylic acid; 5-hydroxy-3,5-dimethylfuran-2 (5H)-one	*Coprinus comatus*	*Meloidogyne incognita* and *Panagrellus redivivus*	Luo et al. (2007)

The future market for fungal products may be improved by commercializing several virulent strains for nematode pests. Zhao et al. (2013) reported that the culture filtrates of new fungal species, *Simplicillium chinense* (strain-Snef5) showed potential effect against soybean cyst nematode, *Heterodera glycines*, root-knot nematode *M. incognita*, white tip nematode *Aphelenchoides besseyi* and *Caenorhabditis elegans*. Whereas, *Trichoderma* sp. KAV1 and *C. rosea* KAV2 showed 100% mortality to second stage juveniles of *M. incognita* and *M. javanica*

under in vitro conditions (Migunova et al. 2018). Further, the fungal isolate, *Mortierella globalpina* proved pathogenic to *M. chitwoodi* in vitro using trapping structures and subsequently reduced root galls in vivo on the roots of tomato (*Solanum lycopersicum* var. Rutgers) (DiLegge et al. 2019). Recently, Du et al. (2019) reported inhibition rate of 84.61%. 78.91% and 84.25% and 79.48% for adult females, juveniles, egg mass, and gall index of *M. incognita* under greenhouse experimental conditions at a concentration of 3×10^8 cfu mL-1 *Phanerochaete chrysosporium* (strain B-22) in tomato.

10.3 Nematode-Fungal Interaction

The infection process of nematophagous fungi to nematodes involves a variety of virulence factors which have been studied by various techniques such as electron microscopy, bioassays, and several biochemical, physiological, immunological, and molecular techniques (Thorn and Barron 1984; Murray and Wharton 1990; Singh and Yadav 2020). In general, the interaction of fungi with nematode species involves five different stages, viz., recognition, attraction, adhesion, penetration, and digestion.

10.3.1 Recognition

The mechanism of host recognition by fungi is not completely understood. However, few reports suggested that lectin, a carbohydrate binding protein plays an important role in nematode–fungal interaction (Borrebaeck et al. 1984; Rosenzweig and Ackroyd 1983; Nordbring-Hertz and Mattiasson 1979; Nordbring-Hertz and Chet 1986). For example, the interaction between *A. oligospora* and nematode was mediated by GalNAc-(*N*-acetyl-D-galactosamine) specific lectin which binds to carbohydrate on the nematode surface (Nordbring-Hertz and Mattiasson 1979). Whereas, Hsueh et al. (2013) reported that ascarosides, a group of glycolipids constitutively secreted by soil dwelling nematodes could trigger the trap formation in *A. oligospora*. This type of ascaroside induced morphogenesis is conserved in several closely related species of nematophagous fungi and occurs under nutrient stress conditions (Jiang et al. 2017).

10.3.2 Attraction

Nematodes are attracted by the culture filtrates and living mycelia of several nematophagous fungi (Li et al. 2015). The volatile compounds such as monoterpenes (α-pinene and β-pinene) and a terpenoid (camphor) produced by an endoparasitic fungus *Esteya vermicola* hypothesized to be involved in the interaction of pinewood nematode, *Bursaphelenchus xylophilus* to *E. vermicola*. Fungi which have more

parasitic ability, i.e., endoparasitic fungi are more effective in attracting nematodes than saprophytic fungi and it was tested in soil microcosms (Tunlid et al. 1992; Dijksterhuis et al. 1994; Nordbring-Hertz et al. 2006). In the same way, the volatile compounds produced by host plant roots could also play a role in the interaction of nematode and fungi (Zhao et al. 2007).

10.3.3 Adhesion

The adhesion of nematodes to the spores and trapping structures is an essential requirement in the infection process. The presence of extracellular fibrillar layer with residues of neutral sugars, uronic acid and proteins on the surface of adhesive traps, spores and appresoria mediates the adhesion of fungi to the nematode cuticle surface (Tunlid et al. 1991; Whipps and Lumsden 2001; Su et al. 2015).

10.3.4 Penetration and Digestion

During this stage the nematophagous fungi penetrate the host by mechanical pressure and the activity of several extracellular hydrolytic enzymes that can degrade the polysaccharides and proteins of the nematode cuticle and egg shells. These extracellular enzymes include proteases, collagenases, and chitinases that have identified in different nematode trapping fungi, which act as key factors in the penetration process. After penetration, the nematode is digested by the fungus.

10.4 Extracellular Enzymes

Extracellular hydrolytic enzymes such as proteases, chitinases, and collagenases produced by nematophagous fungi play an important role in nematode cuticle penetration and host cell digestion (Åhman et al. 2002; Huang et al. 2004; Morton et al. 2004). Among these, proteases produced more rapidly in higher concentrations by nematophagous fungi than collagenases and chitinases. So far, more than 20 serine proteases have been detected, characterized, and cloned from different nematode trapping and egg parasititc fungi by several researchers (Tunlid et al. 1994; Yang et al. 2007c, 2008). Lopez-Llorca (1990) first isolated serine protease P32 from *Pochonia rubens* (*Verticillium suchlasporium*). With the availability of genomic data, the number of genes encoding serine proteases have been identified in different nematophagous fungi (Table 10.3).

Chitinases are the enzymes usually produced by nematophagous fungi to penetrate the nematode eggshell during infection (Gortari and Hours 2008). The first chitinase (Chi43) was purified from *P. chlamydosporia* and *P. suchlasporia* (Tikhonov et al. 2002). So far, 20 chitinases have been purified or cloned from

Table 10.3 Serine proteases purified/cloned in nematophagous fungi

Fungi	Protease	Testing nematode	Fungal activity against nematode	Reference
Pochonia rubescens	P32	*Globodera pallida*	Degradation of proteins in nematode eggs	Lopez-Llorca (1990)
Pochonia chlamydosporia	VCP1	*Meloidogyne incognita*	The purified enzyme hydrolysed proteins in situ from the outer layer of the egg shell and exposed its chitin layer	Segers et al. (1994)
Arthrobotrys oligospora	PII	*Panagrellus redivivus*	76.8% immobilized nematodes after 20–22 h of treatment	Tunlid et al. (1994)
Paecilomyces lilacinus	pSP-3	*Meloidogyne hapla*	Significantly affect the development of eggs	Bonants et al. (1995)
Arthrobotrys oligospora	Aoz1	*Panagrellus redivivus*	Immobilization of nematodes	Zhao et al. (2004)
Clonostachys rosea	Lmz1 (Serine like protease)		Immobilization of nematodes after 24 h of treatment	Zhao et al. (2005)
Lecanicillium psalliotae	Ver112	*Panagrellus redivivus*	81% of cuticle degradation after treating with ver112 for 12 h	Yang et al. (2005)
Clonostachys rosea	PrC	*Panagrellus redivivus*	80 ± 5% of J2 were immobilized and degraded after treating with PrC for 48 h	Li et al. (2006)
Monacrosporium microscaphoides	Mlx	*Panagrellus redivivus*	Immobilization of nematodes after 24 h of incubation in purified protease and nematode cuticle degradation	Wang et al. (2006a)
Dactylella shizishanna	Ds1	*Panagrellus redivivus*	>60% of nematodes were killed and degraded after being treated with crude extract or the purified enzyme for 12 h	Wang et al. (2006b)
Hirsutella rhossiliensis	Hnsp	*Panagrellus redivivus*, *Heterodera glycines*	100% mortality of *H. glycines* J2 was observed in 100 µl crude enzyme solution after incubation for 12 h	Wang et al. (2007)

(continued)

Table 10.3 (continued)

Fungi	Protease	Testing nematode	Fungal activity against nematode	Reference
Arthrobotrys conoides	Ac1	*Panagrellus redivivus, Bursaphelenchus xylophilus*	Immobilization of 60–80% *P. redivivus* population after treated with crude enzyme for 24 h. Whereas, 40–50% of *B. xylophilus* nematode population was immobilized after 24 h of treatment	Yang et al. (2007b)
Dactylella varietas	Dv1	*Panagrellus redivivus* and *Caenorhabditis elegans*	50–100% tested nematodes were killed and degraded after being treated with either the crude extract or the purified enzyme for 12 h	Yang et al. (2007c)
Monacrosporium cystosporium	Mc1	*Panagrellus redivivus, Bursaphelenchus xylophilus*	70–80% of *P. redivivus* were immobilized after being treated with the crude and the purified proteases for 24 h, but only 50–60% of *B. xylophilus* were immobilized	Yang et al. (2008)
Cordyceps sinensis	Csp1	*Hepialus* spp.	Loosening and degradation of cuticle in larvae	Zhang et al. (2008)
Cordyceps sinensis	Csp2	*Hepialus* spp.	Loosening and degradation of cuticle in larvae	Zhang et al. (2008)
Hirsutella rhossiliensis	Hasp	*Heterodera glycines*	The mortality of J2 was significantly higher in purified hasp solutions (43 ± 5% mortality at 4 U/ml and 53 ± 4% mortality at 8 U/ml) than in the buffer control (22 ± 2%)	Wang et al. (2009)
Monacrosporium thaumasium	Mt1	*Angiostrongylus vasorum*	23.9% reduction in the number of L1 larvae, compared with control	Soares et al. (2012)
Duddingtonia flagrans	Df1	*Cyathostomin*	58% reduction of L3 larvae, after 24 h of treatment compared with control	Braga et al. (2012)
Esteya vermicola	Evsp	*Bursaphelenchus xylophilus*		Wang et al. (2015)

Table 10.4 Chitinases purified/cloned in nematophagous fungi

Nematophagous fungi	Chitinase	Testing nematode	Fungal activity against nematode	Reference
Pochonia chlamydosporia (=*Verticillium chlamydosporium*) *P. suchlasporia* (*V. suchlasporium*)	Chi43	*Globodera pallida*	Treated eggs showed surface damage	Tikhonov et al. (2002)
Paecilomyces lilacinus (strain 251)	Plc			Khan et al. (2003)
Lecanicillium lecanii (*Verticillium lecanii*)	Chi2			Lu et al. (2005)
Lecanicillium psalliotae	LpChi1	*Meloidogyne incognita*	Inhibition of egg hatching by 38.2% after 3 days of treatment	Gan et al. (2007a)
Clonostachys rosea (=*Gliocladium roseum*)	CrChi1			Gan et al. (2007b)
Paecilomyces variotii	Chi 32	*Meloidogyne incognita*		Nguyen et al. (2009)
Paecilomyces variotii	Chi 46	*Meloidogyne incognita*		Nguyen et al. (2009)
Pochonia chlamydosporia	PcChi44	*Meloidogyne incognita*	Scars on the surface and peeling of eggshells was observed for about 24 h after treatment	Mi et al. (2010)

various nematophagous fungi (Li et al. 2015). Table 10.4 showed a list of chitinases either purified or cloned from different nematophagous fungi and their activity on different species of nematode eggs under in vitro conditions.

Collagenases are another group of enzymes which are suspected to play a role in nematode infection. Initially Schenck et al. (1980) reported that eight nematophagous fungi could secrete collagenases. Later Tosi et al. (2002) reported that *Arthrobotrys* genus could produce collagenases.

10.5 Commercialization

The development of a biocontrol agent needs several steps aimed at isolation in pure culture and screening by different bioassay tests under in vitro, in vivo, and ex vivo conditions (Montesinos 2003). For commercialization of any product, the bioagent must be produced in a large scale, formulated by means of biocompatible additives to improve the storage capacity of the product. Further, quality control, registration of the particular formulated product and implementation are required (Ravensberg 2011).

In case of nematophagous fungi, various species have been tested for their efficacy in control of plant parasitic nematodes. However, only a few species have been commercialized for large scale multiplication and field application. Table 10.5 demonstrates a list of commercial products of nematophagous fungi produced by various companies under different trade names. Among these, the formulations of

Table 10.5 Commercial products of fungal biocontrol agents developed against plant parasitic nematodes

Fungal species	Trade name	Formulation type	Target nematode	Producer/country
Purpureocillium lilacinum (=Paecilomyces lilacinus)	Bioact	Water dispersible granule, water dispersible powder	Root-knot nematodes, cyst nematodes, reniform nematode, burrowing nematode, citrus nematode, golden cyst nematode and lesion nematode	Bayer Crop Science/ USA
	PL Gold	Granulate, WP		BASF Worldwide/ Germany
	PL 251	Water dispersible granule		Biological Control Products/South Africa
	Biocon	WP		Asiatic Technologies, Inc./Philippines
	Shakti Paecil	WP		Shakti Biotech/India
	Yorker	WP		Agriland Biotech Limited/India
	Pl plus	Wettable powder		Biological Control Products/South Africa
	Miexianning	Talc		Agricultural Institute, Yunnan Academy of Tobacco Science/ China
	Melocon	Water dispersible granule		Prophyta GmbH/ Germany; Certis/ USA
	Nematofree	WP		International Panaacea Ltd./India
	Paecilo	WP		Agri life/India
	Gmax bioguard	Talc		GreenMax AgroTech/ India
	Green Nemagon	Liquid		
	Bio-Nematon	Liquid/ powder		Imported from T. Stanes and company limited, India by Gaara company, Egypt
	Biostat			LAM International/ USA

(continued)

Table 10.5 (continued)

Fungal species	Trade name	Formulation type	Target nematode	Producer/country
Pochonia chlamydosporia	Xianchongbike	Liquid	Root-knot nematodes, cyst nematodes, false root-knot nematode, reniform nematode	Laboratory for Conservation and Utilization of Bio-resources, Yunnan University/ China
Pochonia chlamydosporia (IMI SD 187)	KlamiC®	Granulate		CENSA/Cuba
P. chlamydosporia (Pc-10)	Rizotec®			Rhizoflora, Viçosa (Brazil)
	PcMR-1 strain	Liquid		Clamitec, Myco solutions, lda/ Portugal
Arthrobotrys robusta	Royal 300		Unspecified	France
Arthrobotrys irregularis	Royal 350		Root-knot nematodes	France
Myrothecium verrucaria	DiTera®	Dry flowable	Root-knot nematode, cyst nematode, root-lesion nematode, stubby-root nematode, citrus nematode, burrowing nematode, sting nematode	Valent Biosciences Corp/USA
Trichoderma harzianum	Romulus	WP	Root-knot nematodes, cyst nematodes	Dagutat Biolab/South Africa
	Ecosom-TH	Wettable powder, liquid, lyophilized		Agri Life SOM Phytopharma Limited/India
	Commander	Unknown		HTC Impex Private Limited/India
	Trichobiol	WP		Control Biológico Integrado; Mora Jaramillo Arturo Orlando—Biocontrol/ Colombia
Trichoderma viride (strain 2684)	Trifesol	WP		BioCultivos S.A., Bogotá, Colômbia

(continued)

Table 10.5 (continued)

Fungal species	Trade name	Formulation type	Target nematode	Producer/country
Trichoderma lignorum	Mycobac	Unknown		Laboratórios Laverlam/Colombia
Beauveria bassiana strain GHA	Botanigard	ES/WP	Root-knot nematodes	
B. bassiana strain GHA	Mycotrol	ES	Root-knot nematodes	
Verticillium lecanii	Mycotal	WP	Root-knot nematode (*Meloidogyne incognita)*	
Consortium (*Bacillus subtilis, Trichoderma* spp., *Paecilomyces* spp. and extracts of *Tagetes* sp.)	Nemaxxion Biol	Liquid	Root-knot nematodes	GreenCorp/Mexico.
Consortium (*Arthrobotrys* spp., *Dactylella* spp., *Paecilomyces* spp., Mycorrhiza (*Glomus* spp.), and bacteria (*Bacillus* spp. and *Pseudomonas* spp.))	Rem G			Green Solutions/Italy

P. chlamydosporia, *P. lilacinum*, and *A. robusta*, *A. irregularis* have been widely used for nematode management in vegetables and fruit crops.

Although, nematophagous fungi provides several advantages over traditional products, the Commercialization of these bioproducts lags far behind due to inconsistent performance, quality control issues, limited shelf life of product, slow rate of kill, lack of field persistence of some formulations, difficulties in scale-up production, expensive and time consuming registration process and marketable issues, etc. (Moosavi and Askary 2015; Venkatesan and Pattar 2017). There is a need to focus on improving the formulation and manufacturing technologies that reduce costs and enhance shelf life of the commercial product.

The development and success of a biocontrol agent for plant parasitic nematodes require a better knowledge on the biology and ecology of the nematophagous fungi and the nematode, its host cultivar, method and time of application, and the various biotic and abiotic factors regulating the efficacy of biocontrol agent, the root diffusates differ markedly between plant species and cultivar which influences the proliferation of fungi (Tunlid and Ahrén 2001; Morton et al. 2004; Davies 2005). In addition, several soil microbes or their metabolites compete with the introduced bioagents for scarce energy sources. These can significantly affect the efficacy of

the agent even when added to soil in a pre-colonized substrate. For example, egg masses of *Meloidogyne* spp. harbored 122 bacteria and 19 fungi, 23% and 74% of which, respectively, were antagonistic to *P. chlamydosporium* (Kok and Papert 2001). *Bacillus* sp. strain H6 isolated from a fungistatic soil produced iturin like compounds from that caused swelling in the conidia and germ tube of nematophagous fungi (Li et al. 2007a). Such sensitivity of a biocontrol agent to antagonism by an isolate of another microbe varies with the isolate (Montfort et al. 2006).

10.6 Conclusion and Future Prospects

Over the past 50 years, the number of scientists involved in research on the biocontrol of nematodes has increased significantly. Although several biocontrol agents for nematodes have been reported, only few organisms were developed as commercial bioagents. Surveys and empirical tests are being replaced by quantitative experimentation and basic research at genomic levels is being undertaken. Such information is essential for a realistic appraisal of the impact of microbial agents on nematode pests and for monitoring the spread and survival of the releases organisms. Our research efforts need to be directed towards identifying the factors governing their proliferation in soil and to remove the constraints wherever feasible. With the application of molecular biology, the molecular mechanisms of the interaction between nematode and fungal species can be understood, which further helps to develop new screening procedures of nematophagous fungi to control plant parasitic nematodes.

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