Nematophagous Fungi: Biology, Ecology and Potential Application

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Abstract

Nematodes and fungi are soil inhabitants. Both are essential for maintaining the stability of food-web and facilitation of the nutrient cycle. Interaction between nematodes and fungi is possible in multiple ways. Here, we supply a platform for nematophagous (nematode destroying) fungi (NF), their mode of action, and their importance in agricultural ecosystems. They are potentially important for sustainable agriculture and play a major role in integrated pest management programs. Nematophagous fungi belong to a broad taxonomic group, such as Ascomycota, Oomycota, Basidiomycota, and distinct groups of fungi. Nematophagous fungi are broadly distributed in terrestrial and aquatic ecosystems that contain high densities of nematodes. Depending on the mechanism that affects nematode, NF can be divided into four types. Here, we described the classification, taxonomy, occurrence, distribution and ecology, types of nematophagous fungi, and potential mechanisms of NF in the control of plant-parasitic nematodes.

Keywords

Plant-parasitic nematodes · Nematophagous · Biological control · *Arthrobotrys oligospora* · Egg parasites · Second-stage juveniles

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12.1 Introduction

In this materialistic world, increasing food production for feeding the ever-growing population is the major world demand, while earning more profit from agriculture is the grower's demand, who faces an occasional setback due to the serious outbreak of the diseases and keeps looking for an effective method to save his crop from destructive pathogens. Among them, one of the major limiting factors is plant-parasitic nematodes (PPNs) that continuously affected agricultural production by and large. Further, the nature of crops, varieties, nematode species, the population of primary inocula, and environmental factors influence the losses to a great extent. It is estimated that 12.3% of global annual losses of major crops are due to phytoparasitic nematodes (Sasser 1989). Such type of losses become intolerable for poor and developing countries including India. Plant-parasitic nematodes cause 18–25% losses in vegetables, 20–25% in pulses, 18–23% in oilseed crops, and 15–18% in cereals crops (Indian Economy 2004).

Management of plant-parasitic nematodes is largely dependent on the use of toxic pesticides, the majority of which are soil fumigants. Farmers are using toxic pesticides intensively for the last few decades in order to reduce such a magnitude of losses to sustained crop production. However, the residual effects of these pesticides on nontarget soil flora and fauna are of great concern. Further, long-term residual effects are responsible for eroding biodiversity, increasing resistance and resurgence in the pathogen, and causing pollution that poses health hazards to humans, animals, and the environment. Present circumstances of environmental awareness evoke urgent need to search for and establish compatible alternatives to these hazardous agrochemicals. The persistence of pesticides in soils, deterrents to ecosystems, environmental contamination, detrimental impact on human health, deterrents to ecosystems, and the creation of resistant pathogenic strains are all consequences of heavy pesticide use. In order to reduce the use of pesticides, researchers have intensified resistance breeding programs along with transgenic plants to control the losses caused by these notorious pathogens. However, several constraints limit the scope of the resistance breeding program, i.e., unavailability of suitable donor parents having a high degree of resistance, detection of the source of resistance, and transferring desirable traits into a cultivar using a resistance breeding program is a great challenge. Biological control of plant-parasitic nematodes offers a promising alternative to pesticides, which had attained lots of attention over the years. Under these circumstances, using microbe-based strategies for the control of plant-parasitic nematodes has been reported to be an environmentally friendly, safe, and residue-free approach (Singh et al. 2012a, b, 2013, 2019a, b). Several biological control agents of microbial origin have been evaluated and used to control the plant-parasitic nematodes in many crops. Among them, *Trichoderma asperellum*, *T. harzianum*, *T. virens*, *Bacillus subtilis*, *B. licheniformis*, *Pseudomonas fluorescens*, *Purpureocillium lilacinus*, *Arthrobotrys oligospora*, *Pochonia chlamydosporia*, *Dactylaria* spp., *Monacrosporium* spp., *Drechslerella dactyloides*, *Syncephalastrum racemosum*, *Hirsutella* spp., and *Duddingtonia* spp. were noted worthy and are used to manage nematodes worldwide (Singh 2013; Singh et al.

2013, 2017, 2019b; Wang et al. 2014; Huang et al. 2014; Gupta et al. 2015a, b). Predacious fungi are an important part of the soil's biodiversity. Interactions between predatory fungi and parasitic nematodes are widespread and dynamic in the soil. Several reviews and research publications have demonstrated the ability of nematophagous fungi (NF or NPF) to suppress plant-parasitic nematodes; however, they are scattered. Nematophagous (nematode-eating) fungi are found in both terrestrial and aquatic habitats and are diverse in nature (Pramer 1964; Nordbring-Hertz et al. 2006). More than 200 fungal species, which can develop specific trapping devices, belong to the NF group such as adhesive knobs, constricting rings, and adhesive networks to capture nematodes juveniles, eggs, and adults and then use various strategies to extract nutrients from their nematode prey (Jansson and Lopez-Llorca 2001; Nordbring-Hertz et al. 2006; Yang et al. 2007; Schmidt et al. 2007). Most of the nematode-trapping fungi can function as both saprophytes and parasites (Pramer 1964; Nordbring-Hertz et al. 2006). Nematode-trapping fungi develop sophisticated hyphal structures, such as hyphal knobs, hyphal branches or rings, and hyphal nets, by adhesion or mechanical capture (Nordbring-Hertz et al. 2006; Singh 2007; Singh et al. 2012b). They have an essential role in maintaining nematode population density via natural settings. Many egg-parasitic and trap-forming fungi may exist in soil saprophytically while endoparasites are obligate parasites. Considering the importance of the problem and the potentiality shown by previous workers, the present study was undertaken with the objectives to give an overview of the biology, ecology, and potential application of nematophagous fungi to sustain crop production in changing climatic scenarios.

12.2 Historical Background

The word "predacious" comes from the Latin word *preada*, which means "to grab out all valuables and things of a victim after they have been killed." Predacious fungi are distributed in all types of soils. These fungi are more significant in decomposing plant waste, and the organic matter supplied to the soil increases the number of predacious fungi. *Arthrobotrys oligospora* was first described as a common inhabitant of organic plant debris by Fresenius (1852). Woronin (1870) reported that the conidia of *A. oligospora* germinated on the old manure and some of the hyphae-produced net-like bails, although he did not know the functions of such bails. Sorokin (1876) created the genus *Catenaria* with the type species *C. anguillulae*. He found *C. anguillulae* parasitizing eelworms in a vessel, which were eventually killed. He also described that round zoospores were liberated from the sporangia through a discharge tube. Zopf (1888) was the first to record the predacious behavior of *A. oligospora*. Further, his studies show that the cuticle of the captured nematode is penetrated, and the fungus grew within the nematode body and consumed it by its hyphae. Thus, Zopf established the predatory relationship of a fungus on nematodes. Drechsler (1937) established a base for studies on predacious fungi responsible for capturing and killing nematodes. He described that the predacious fungi produced different trapping devices for the predation of nematodes. Such capturing devices include adhesive hyphae, adhesive branches, adhesive nets, and adhesive knots, whereas the nonadhesive organs include non-constricting rings and constricting rings. Some predaceous fungi produce sticky knobs that capture nematodes (Drechsler 1937; Barron 1977).

12.3 Occurrence and Distribution

Predacious fungi can be found as saprophytes in the soil or on decaying plant materials where they live saprophytically and/or feeding on plant-parasitic nematodes. The efficacy of capturing predacious fungi may be influenced by the nature of the soil and environmental conditions. The presence of nematodes in the soil and organic matter is necessary in maintaining the biodiversity of soil and increasing the population of predacious fungi. Most of the predatory species belong to either the Zoopagales or Moniliales, while endo-parasites are found in the lower fungi such as Chytridiales, Saprolegniales, Peronosporales, Lagenidiales, Mucorales, Entomophthorales, and in higher fungi Deutromycetes.

12.4 Classification

Fungi represent the fifth kingdom in the living organisms (Kendrick 2001). NPF are found in all lower and higher groups of fungi, such as Basidiomycetes, Ascomycetes, and Deuteromycetes in higher fungi and Chytridiomycetes, Oomycetes, and Zygomycetes in lower fungi. In distinct taxonomic groups of fungi, the habit of nematophagous fungi evolved separately. Barron (1992) reported that the habit of nematophagous fungi evolved from lignolytic (characterized by a unique ability to depolymerize and mineralize lignin) and cellulolytic fungi (hydrolyzing or having the capacity to hydrolyze cellulose) for adaptation to overcome nutrient competition in the soil.

In tandem with entomopathogenic species of *Verticillium*, which were relocated to the genus *Lecanicillium* based on both morphological and molecular features, egg-parasitic fungi previously placed within the genus *Verticillium* were recently shifted to the new genus *Pochonia* (Zare and Gams 2001; Zare et al. 2001). *Cordyceps* contains the teleomorphs of the *Pochonia* species. *P. chlamydosporia* and *P. rubescens* are the most well-known egg parasites, and other taxa reported to parasitize nematode eggs include *Paecilomyces lilacinus* and *Lecanicillium lecanii*. Based on the molecular evidence, Scholler et al. (1999) proposed the following classification: *Arthrobotrys* (adhesive three-dimensional networks), *Dactylellina* (stalked adhesive knobs or non-constricting rings), *Drechslerella* (constricting rings), and *Gamsylella* (non-constricting rings) (having adhesive branches and unstalked knobs).

The taxonomy and phylogeny of endoparasitic fungi are far less well-understood (Fig. 12.1). Some, such as the zoosporic *Catenaria anguillulae*, are classified as Chytridiomycetes, while others are classified as *Haptocillium* (previously

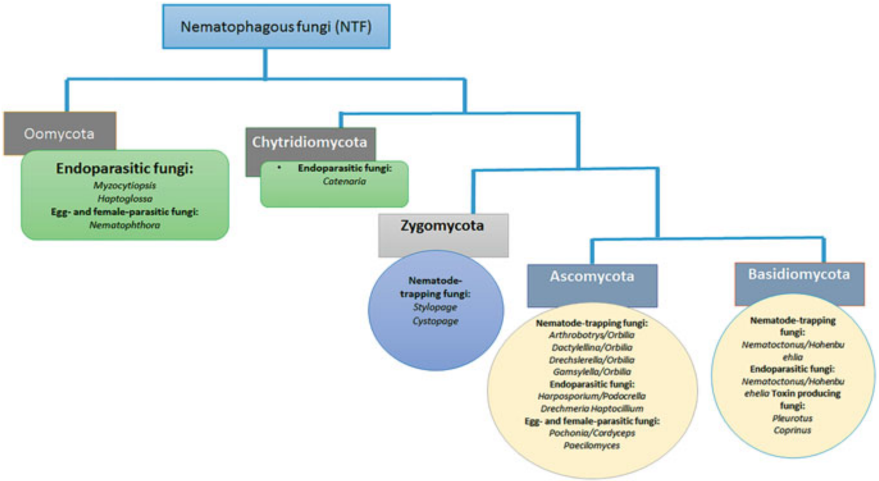

Fig. 12.1 Classification of nematophagous fungi

Verticillium), *Harposporium*, or *Drechmeria*. *Harposporium* spp. teleomorphs have lately been shifted to *Podocrella* from *Atricordyceps* (Chaverri et al. 2005). Pleurotus is a category of toxin-producing fungi that contains species such as the oyster mushroom *Pleurotus ostreatus*. Luo et al. (2004) reported that *Coprinus comatus* was recently discovered to have similar abilities, suggesting that nematophagy is more widespread among Basidiomycetes than previously thought.

12.5 Ecology

Nematophagous or nematode-trapping fungi (NF or NPF) are found in the soil. They are mostly found in the topsoil, meadows, leaf litter, mangroves, and some shallow aquatic areas. NF employ adhesive knobs, adhesive hyphal strands, and nets made of hyphal threads, hyphal loops, and non-constricting loops that capture nematodes. When the nematode is bridled, the NF hyphae enter the cuticle and eat the nematode's internal tissues (Zhang et al. 2014).

Arthrobotrys oligospora, a species of *Arthrobotrys*, is one of the most well-studied nematode-trapping fungi (Nordbring-Hertz et al. 2006). Strains of *A. oligospora* have been discovered in different soil conditions (Pfister and Liftik 2018; Money 1998). By creating intricate three-dimensional networks, *A. oligospora* enters the parasitic stage in the presence of nematodes to capture them. Nematode trapping triggers a chain of actions that include nematode adhesion, penetration, and immobilization (Nordbring-Hertz 2004; Nordbring-Hertz et al. 2006). The fungus' strong ability to capture nematodes makes it a promising candidate for controlling plant-parasitic worms. To catch nematodes mechanically, *A. oligospora* forms three-dimensional adhesive nets. The fungus actively seeks out its prey by creating chemical signals or olfactory cues that are similar to those used by worms to find food and mate (Yu'e et al. 2005; Zhang et al. 2015; Hsueh et al. 2017). Some nematophagous fungi produce toxins that render nematodes immobile. The hypha of the shaggy ink cap (*Coprinus comatus*) attacks the nematode *Panagrellus redivivus* as a spiny ball structure, which immobilizes and breaks the nematode cuticle, following which the hypha pierces the skin and digests the contents (Luo et al. 2007). The spores of the most endoparasitic fungi are attracted to and concentrated in the mouth region of soil nematodes. The hyphae proliferate throughout the nematode after penetration of the cuticle and absorption of nematode tissues. Conidia are contacted by the nematode in other fungal species and are infected in a similar fashion. *Harposporium anguillulae* having sickle-shaped conidia are consumed by the nematodes and lodge themselves in the esophagus or gut, where they destroy the tissues (Aschner and Kohn 1958).

The hypha flattens itself against the egg in egg-parasitic species, and the presence of appressoria indicates that infection is about to occur or has already occurred. After piercing the egg and devouring the developing juvenile worm, the hypha produces conidiophores and moves on to nearby eggs (Money 1998).

12.6 Plant-Parasitic Nematodes have an Impact on Agriculture

Plant-parasitic nematodes are a serious constraint in agricultural crop production. These nematodes have been discovered in over 4100 different species (Decraemer and Hunt 2006). Crop loss is projected to cost between US$118 and 80 billion per year (Sasser and Freckman 1987; Nicol et al. 2011). The most economically important nematode species accounts for 15% of all identified nematode species. They directly target the plant roots of major crops, preventing nutrient uptake and water, resulting in decreased agronomic performance, overall yield, and quality of the crop. Surprisingly, just a small percentage of the nearly 4000 reported plant-parasitic nematodes cause major agricultural losses. In a survey, the principal genera of phytoparasitic nematodes identified to cause crop losses in the United States were *Meloidogyne*, *Heterodera*, *Hoplolaimus*, *Rotylenchulus*, *Xiphinema*, and *Pratylenchus* (Koenning et al. 1999).

12.7 Types of Nematophagous Fungi

Nematophagous fungi can be divided into four major groups (Fig. 12.2) depending on their mode of attacking nematodes (Jansson and Lopez-Llorca 2001):

1. Nematode-trapping fungi (previously sometimes called predacious or predatory fungi)
2. Endoparasitic fungi
3. Egg- and female-parasitic fungi
4. Toxin-producing fungi

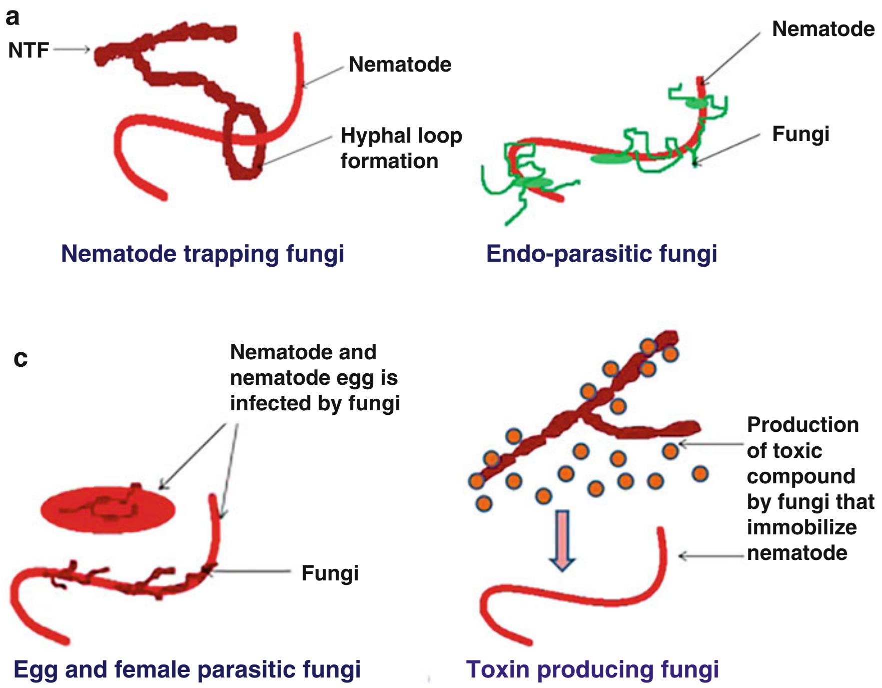

Fig. 12.2 Types of nematophagous fungi

The nematode-trapping fungi use hyphal trapping devices of various shapes and sizes to capture nematodes, such as sticky/adhesive three-dimensional nets, adhesive knobs, and nonadhesive constricting rings. Some “nematode-trappers” capture nematodes by an adhesive substance formed on their hyphae without any visible traps, e.g., *Stylopage* spp. Endoparasitic fungi use their conidia or zoospores to infect the nematodes. The propagules of fungi adhere to the cuticle of the nematode, and then spore contents are injected into them or spores are swallowed by the host. Most of them are obligate parasites and the entire vegetative stages of their life live inside the infected nematodes. The egg- and female-parasitic fungi are facultative parasites. They infect nematode females and their eggs, using appressoria or zoospores. Being facultative parasites, they grow on nematodes and parasitize the sedentary stages such as eggs. The toxin-producing fungi produce toxic compounds that can immobilize nematodes, prior to penetration by hyphae through the cuticle of the nematode. Parasitism of nematodes results in complete prey or egg digestion in all four nematophagous fungal groups, an action that provides the fungus with nutrients and energy for continuous growth.

12.8 Mechanism and Mode of Action of Nematophagous Fungi to Control Plant-Parasitic Nematode

Biological control of phytonematodes is described as a reduction in populations of nematodes caused by actions of living organisms other than those found naturally in the host plant, or by introduction of antagonist organisms into the environment (Kim 2015). More than 200 taxonomically distinct fungi have demonstrated the ability to kill live nematodes in all the stages of development such as juveniles, adults, and eggs (Nordbring-Hertz et al. 2006). Two types of barriers to fungus invasion are created by the morphology of nematodes. The eggshell is the first barrier, made up of three layers in root-knot and cyst nematodes: the outer vitelline (mostly proteins), the inner lipoprotein layer, and the chitin layer, and the cuticle is the second barrier. The parasitism, poisonous chemicals, and enzyme methods used by nematophagous fungi to infect nematodes can be separated into three categories (Fig. 12.3).

Different nematophagous fungi infect nematodes and their eggs in a similar, general way. Infection of nematode eggs by *Pochonia rubescens*, as well as the zoospores of *Catenaria anguillulae*, which infect vermiform worms, demonstrate this. *P. rubescens* begins penetrating nematode eggs by contacting the egg with its hyphae and then forming an appressorium. The appressorium forms an extracellular matrix (ECM) or adhesive, which is disclosed by lectin Concanavalin A labeling. The fungus uses both mechanical and enzymatic components to enter the worm eggshell from the appressorium. Because the nematode eggshell is mostly made up of chitin and proteins (Bird and Bird 1991), chitinases and proteases are vital during the penetration of eggshell (Lopez-Llorca 1990a, b; Tikhonov et al. 2002). Eggshells are degraded as a result of proteolytic action.

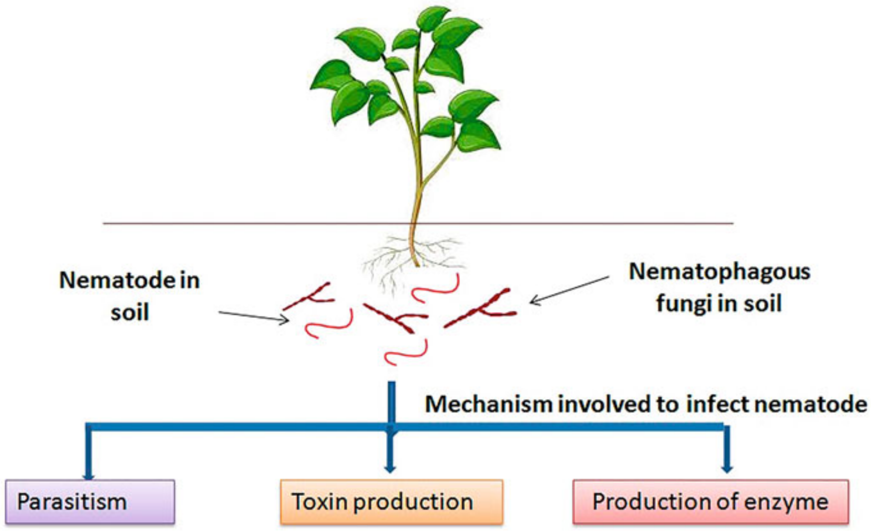

Fig. 12.3 Key mechanisms involved in the nematophagous fungi

12.8.1 Chemotaxis and Adhesion (Host Recognition, Host Specificity, and Infection)

The recognition phase of nematode begins, which includes chemotaxis of the host toward fungal traps, hyphae, or zoospore chemotaxis toward the host's natural apertures (Jansson and Nordbring-Hertz 1979; Jansson and Thiman 1992). It is unknown which chemicals are involved in the chemotactic events (Jansson and Friman 1999; Bordallo et al. 2002). After contact with a nematode, the adhesive on *A. oligospora* traps changes from amorphous to fibrillar, in contrast to the adhesive on *D. coniospora* conidia, which always appears fibrillar (Jansson and Nordbring-Hertz 1988). Lopez-Llorca et al. (2002) suggested that the adhesion on the appressoria of *P. rubescens* and *P. chlamydosporia* can be identified using the lectin Concanavalin A, indicating that it is a glycoprotein having glucose/mannose moieties. *A. oligospora*'s Gal-NAc-specific lectin and *D. coniospora*'s sialic acid-specific lectin have both been implicated in worm recognition (Nordbring-Hertz and Mattiasson 1979; Jansson and Nordbring-Hertz 1984). Infection events eventually trigger a signaling cascade that is required for nematode prey penetration and colonization (Tunlid et al. 1992). An extracellular substance is generated after contact, which keeps the fungus attached to the nematode surface. Proteins or carbohydrates are typically found in the adhesives of nematophagous fungi (Tunlid et al. 1991a, b). Carbohydrates on nematode surfaces are engaged in the lectin-binding recognition stage, but they also appear to play a role in nematode chemotaxis (Zuckerman and Jansson 1984; Jansson 1987). Major nematode sensory organs, such as inner labial papillae and amphids, are positioned around their mouth in the labial and cephalic region (Ward et al. 1975). Zuckerman (1983) and Zuckerman and Jansson (1984) proposed that carbohydrates play a role in nematode chemoreception. Lectins (Concanavalin A binds with mannose/glucose residues, and Limulin binds with sialic acid) could block the chemoreceptors, leading bacterial-feeding nematodes to lose their chemotactic behavior to microbial exudates (Jeyaprakash et al. 1985). Further, nematode chemotaxis was reduced when enzymes (mannosidase, sialidase) obliterated the terminal carbohydrates (Jansson et al. 1984), demonstrating the importance of carbohydrate moiety in nematode chemotaxis. An endoparasitic nematophagous fungus, *D. coniospora*, uses conidia to infect nematodes that cling to the host's chemosensory organs (Jansson and Nordbring-Hertz 1983). Both Limulin treatment of nematodes and sialic acid treatment of spores reduced conidial adhesion, implying that a sialic acid-like carbohydrate is involved (Jansson and Nordbring-Hertz 1984). Furthermore, it is evaluated that nematode adherent with spores lost their capacity to respond chemotactically to all the attracting sources, including hyphae, conidia, or bacteria, implying a link between chemotaxis and adhesion via carbohydrates on the surface of nematode (Jansson and Nordbring-Hertz 1983). *D. coniospora* conidia stick to *Meloidogyne* spp. chemosensory organs, but they do not penetrate and cannot infect the worms.

12.8.2 Differentiation and Signaling

When recognizing the surface of the host, or even synthetic surfaces, most harmful fungi distinguish appressoria. Appressoria formation in plant pathogenic fungi infecting leaves has been examined in depth (Lee et al. 2003; Basse and Steinberg 2004). St. Leger (1993) proposed a signaling hypothesis for the insect pathogen *Metarhizium anisopliae* during appressorium production, based in part on knowledge of plant pathogenic fungi. Appressoria on their hosts are differentiated by nematophagous fungi, particularly egg parasites (Lopez-Llorca and Claugher 1990). The signaling pathways that lead to nematode infection by nematophagous fungus are poorly understood. Using expressed sequence tag (EST) techniques, it was recently demonstrated that genes involved in the creation of infection structures and fungal morphogenesis were expressed during trap formation in the nematophagous fungus *Dactylellina haptotyla* (syn. *Monacrosporium haptotylum*) (Ahren et al. 2005). As a response to chemical and tactile inputs, fungi-infecting vermiform nematodes differentiate multiple trapping organs. The three ring cells that make up the trapping mechanism are inflated by the constricting ring traps. When a nematode comes into contact with the inner ring wall, an unknown mechanism causes the nematode to inflate and close, which takes around 0.1 s.

12.8.3 Nematodes Cuticle and Eggshell Penetration by NPF

Nematophagous fungi penetrate the worm cuticle or eggshell after a solid adhesion to the host surface. Both enzymatic and physical mechanisms appear to be used by the nematophagous fungus to penetrate host surfaces, as in many other cases of fungal penetration. Because the nematode cuticle is mostly made up of proteins (Bird and Bird 1991), proteolytic enzymes are necessary for penetration of the nematode cuticle. The PII serine protease of *A. oligospora* has been characterized, sequenced, and cloned (Ahman et al. 1996). The protein presence, such as nematode cuticles, increases PII expression (Ahman et al. 1996). The subtilisin PII has a molecular mass of 32 kDa and belongs to the subtilisin family (Fig. 12.4).

Another serine protease (Aoz1) was recently identified from *A. oligospora*, having 38 kDa molecular mass and 97% similarity with PII (Zhao et al. 2004). Other fungi have been isolated and characterized, including *Arthrobotrys microscaphoides* (Mlx) (Wang et al. 2006a, b) and *Arthrobortys shizishanna* (Ds1) (Wang et al. 2006a, b), both of which show significant similarities to the *A. oligospora* serine (Wang et al. 2006a, b).

Protein and chitin are structured in a microfibrillar and amorphous form in nematode eggshells (Clarke et al. 1967). As a result, extracellular enzymes that degrade such polymers were sought. Lopez-Llorca (1990a, b) identified, purified, and characterized P32, a 32 kDa serine protease from the egg parasite *P. rubescens* for the first time. P32 suppression by polyclonal antibodies and chemicals reduced the penetration and egg infection, despite pathogenesis being a complex process involving many variables (Lopez-Llorca et al. 2002). An extracellular protease

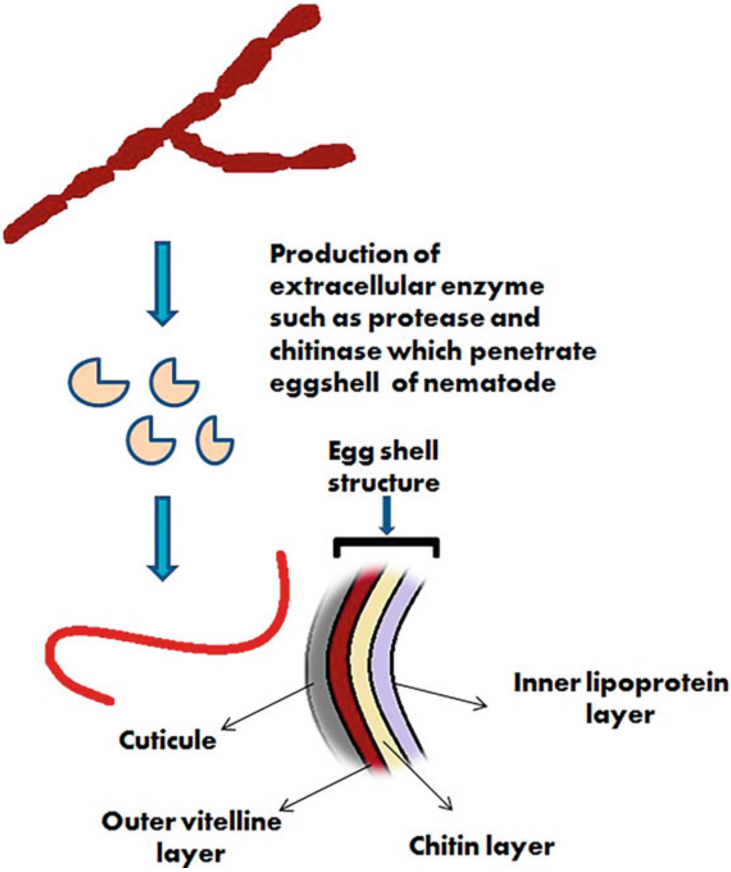

Fig. 12.4 Eggshell penetration by NPF

(VcP1) is produced by *P. chlamydosporia*, which is linked to P32 and similar entomopathogenic fungal enzymes (Segers et al. 1994). Eggs treated with VcP1 enzyme were more easily infected than non-treated eggs, implying that the enzyme plays a role in eggshell penetration by fungi that feed on eggs. Recently, a serine protease (Ver112) from *Lecanicillium psalliotae* was isolated and described, exhibiting approximately 40% homology with *Arthrobotrys* proteases (PII and Aoz1) and have 60% homology with egg-parasitic serine proteases (Yang et al. 2005a, b). Non-nematophagous fungi such as *Clonostachys rosea* and *Trichoderma harzianum* are additional sources of nematicidal serine proteases (Suarez et al. 2004; Li et al. 2006). Huang et al. (2014) reported that *Pochonia rubescens* and *Pochonia chlamydosporia* both have chitinolytic enzymes that have been discovered. A 43 kDa endochitinase (CHI43) was one of those responsible for the majority of the activity (Tikhonov et al. 2002). Damage to eggshells was more widespread when treating *G. pallida* eggs with both P32 and CHI43, which indicated that the two enzymes work together to destroy eggshells (Tikhonov et al. 2002). A hydrolytic enzyme chitosanase from the egg-parasitic fungus *P. lilacinus* was recently identified and described (Chen et al. 2005).

12.9 Potential Application

For many years, nematophagous fungi have been tested for biological control of plant-parasitic nematodes, but the strategy had limited success due to the lack of understanding of these species' ecology (Stirling 1991) (Table 12.1).

The colonization of plant roots by endophytes is a significant element. By induced resistance or by the production of secondary metabolites, NF may protect plants from several fungal diseases and plant-parasitic nematodes. Plant growth can also be boosted by nematophagous fungi participating in the nutrient intake or modifying plant growth regulators. As a result, endophytic colonization must be taken into consideration while looking for nematophagous fungi as biocontrol agents. Combining numerous forms of nematophagous fungi, such as egg-parasitic and nematode-trapping fungi, that kill nematodes at different phases of their lives, could be a key requirement. When choosing the right fungi for biological control of plant-parasitic nematodes, interactions with other soil fungi, including plant-parasitic and biocontrol agents, are also crucial factors to consider. Larriba et al. (2015) demonstrated the egg-parasitic fungus *Pochonia chlamydosporia* having potential for biological control of plant-parasitic nematodes. They act as an endophyte in both monocot and dicot plants and have shown plant growth promotion in a variety of crops. Nematophagous fungus *Pochonia chlamydosporia* promotes growth of barley (*Hordeum vulgare*) plants by endophytic colonization of roots and provides defense against stresses. Escudero and Lopez-Llorca (2012) stated that endophytic colonization of tomato roots by *P. chlamydosporia* is important for plant growth and may influence root-knot nematode management.

12.10 Future Prospects

Plant-parasitic nematodes cause major yield and monetary losses in agriculture all over the world. The utilization of nematophagous fungi as endophytes is a potential technique for the biocontrol of nematodes in the soil. Larriba et al. (2015) observed that at the molecular level, plants colonized endophytically having growth-promoting effect by *P. chlamydosporia*, paving the way for more research into the fungus' ability to mitigate the negative effects of biotic and abiotic factors on plant crops. Bioproducts formulated with these NF have various advantages over chemical nematicides for more sustainable agriculture, including ease of application, environmental safety, little impact on soil biota, and no residues in harvested products. However, when producing a commercial bionematicidal product, there are various aspects to be kept in mind as it is a living system. As a result, new technology such as

Table 12.1 Some fungal biocontrol agents for the management of plant-parasitic nematodes

Name of fungi	Mixed with	Effective for nematode	Crop/ plant	References
P. chlamydosporia	Carbofuran + neem cake	*M. incognita*	Okra	Dhawan and Singh (2009)
Paecilomyces lilacinus	Groundnut cake, neem cake, castor cake, mahua cake, and linseed cake	*M. javanica*	Brinjal	Ashraf and Khan (2010)
T. viride	Compost	*Meloidogyne* spp.	Gotukola (*Centella asiatica*)	Shamalie et al. (2011)
T. viride	Neem cake	*M. incognita*	Tobacco	Raveendra et al. (2011)
Pochonia chlamydosporia	Combination of *P. fluorescens*, *T. viride*, and carbofuran	*Globodera* spp.	Potato	Muthulakshmi et al. (2012)
T. harzianum	Combination of neem cake and *P. fluorescens*	*M. incognita*	Brinjal	Singh et al. (2013)
T. harzianum	Carbofuran	*M. incognita*	French bean	Gogoi and Mahanta (2013)
P. chlamydosporia	Mustard cake and neem cake	*M. incognita*	Brinjal	Parihar et al. (2015)
T. harzianum	Lantana camara	*M. incognita*	Tomato	Feyisa et al. (2015)
T. harzianum	Carbofuran	*M. incognita*	Brinjal	Devi et al. (2016)
T. harzianum	Carbofuran and neem cake	M. incognita	Pea	Brahma and Borah (2016)
P. chlamydosporia	Neem cake	*Heterodera zeae*	Sweet corn	Baheti et al. (2017)
Paecilomyces lilacinus	Neem cake and Karanj leaves	*Heterodera zeae*	Sweet corn	Baheti et al. (2017)
P. fluorescens	Carbofuran	*Meloidogyne graminicola*	Rice	Narasimhamurthy et al. (2017)
Arthrobotrys oligospora, *Candellabrella musiformis*, and *Dactylella eudermata*	Carbofuran	*Meloidogyne incognita*	Tobacco	Hastuti and Faull (2018)
Drechslerella dactyloides	–	*Meloidogyne incognita*	Tomato	Singh et al. (2019a, b)
Dactylaria brochopaga	–	*Meloidogyne incognita*	Tomato	Singh et al. (2019a, b)
Duddingtonia flagrans	–	*Meloidogyne incognita*	–	Xiaoyu Mei et al. (2021)
Arthrobotrys oligospora	–	*Meloidogyne incognita*	Tomato	Soliman et al. (2021)

real-time quantitative PCR is used to quantify and track the biocontrol agent after its application into the soil. Biocontrol agents can be genetically modified to have their efficacy increased by increasing the expression of genes implicated in nematicidal activity or pathogenicity (Zhang et al. 2020a, b). To improve aggression and virulence against nematodes, expression of heat shock factors, UV protectants, immunological modulators, destroying enzymes of cuticle, and genetic modification techniques can be used. Several studies established the efficacy of applying a combination of treatments to manage plant-parasitic nematode populations under diverse conditions, including various cultural techniques (such as soil amendment and soil solarization), biological agents, and chemical nematicides (Zhang et al. 2014). Finally, the unpredictability of nematode antagonists against PPN in field circumstances, as well as their limited efficacy, are key barriers to using biocontrol agents to manage plant-parasitic nematodes. The intrinsic mechanisms governing ecosystem stability in field circumstances may be one of the causes for the disparities between the results of laboratory trials and field trials. Understanding interactions between nematodes and nematophagous fungi in native niches aids in the development of better applications for long-term crop protection approaches. The effects of combining various partners, such as NF, plant-pathogen mycoparasites, and plant growth-promoting microorganisms, could provide useful information for the development of biocontrol agents to reduce the impact of nematode and fungal pathogens on agriculturally important crops (Luns et al. 2018; Baron et al. 2020).

12.11 Conclusion

Nematophagous fungi are common soil organisms that may infect, attack, and consume nematodes at any stage of their development, including adults, juveniles, and eggs. To infect their nematode hosts, they use trapping organs, spores, and appressoria. In addition to infecting nematodes, nematophagous fungi can infect other fungi as mycoparasites and colonizing plant roots endophytically. Because of their various capacities, nematophagous fungi, in particular, may be a promising candidate for the biological management of plant root diseases. The use of nematophagous fungi as a substitute for synthetic chemicals used in the production of nematicides is fascinating. Obtaining bionematicides efficiently is a goal and a prerequisite for all agricultural researchers seeking sustainability in the system. Depending on the pathogenicity factor, some information is still lacking. Some NF enzymes such as serine proteases, chitinases, and toxins function as virulence factors and are especially interesting in the parasitic worm infection process. Some NF strains' success implies that they have different host preferences. Finally, we suggest that NF is a potential alternative to synthetic pesticides in the management of plant-parasitic nematodes, and that they may be more effective in making agriculture sustainable by replacing hazardous chemicals and mitigating the effects of their residues on the environment.

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