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Utilization of Nematode Destroying Fungi for Management of Plant-Parasitic Nematodes - A Review

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Nematode destroying fungi are potential biocontrol agent for management of plant-parasitic nematodes. They inhibit nematode population through trapping devices or by means of enzymes and metabolic products. They regulate nematode behavior by interfering plant-nematode recognition, and promote plant growth. For more effective biocontrol, thorough understanding of the biology of nematode destroying fungi, targeted nematode pest and the soil ecology and environmental condition in the field is necessary. This review highlights different types of nematode destroying fungi, their mode of action as well as commercial products based on reports published in this area of research.

Keywords: Nematode destroying fungi; Trapping device; Endoparasitic fungi; Molecular metabolic product; Plant-parasitic nematodes.

Plant-parasitic nematodes with high population density cause economically significant yield reduction in most agricultural crops. About 12% of worldwide food production is lost due to plant-parasitic nematodes [1]. The global financial loss due to plant-parasitic nematodes may be as high as US$ 121 billion [2]. In India, the avoidable yield loss due to *Meloidogyne incognita* in vegetable crop is as high as 40.5% and annual loss in 24 crops due to economically important nematodes is estimated to the tune of Rs. 21068 million per annum [3].The development of new methods to control such nematodes is of major importance because the chemical nematicides are associated with environmental and health concerns. An alternative approach to manage plant-parasitic nematodes is the using of their natural enemies. Among them, the nematode destroying fungi, comprising a group of soil-living fungi, are natural enemies of plant-parasitic nematodes are of significant importance [4-7]. Use of nematode destroying fungi as biocontrol agent either alone or integrated with other nematode management strategies offer an environmentally sustainable method. Linford [8] attempted for the first time to reduce plant-parasitic nematode population in soils with nematode destroying fungi.

Nematode destroying fungi or nematophagous fungi consist of a wide and diverse range of fungi. They are pathogenic or parasitic, and some of them are predacious which infect and digest nematodes. Most nematode destroying fungi are saprophytic in soil, but in the presence of a host they change from a saprophytic to a parasitic phase, mostly found in soil with high organic matter content [9]. Approximately 700 species of nematode destroying fungi have been described so far [10].According to the mode of nematicidal action,

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Jatala [11] grouped nematode destroying fungi into: (a) Nematode-trapping or predacious fungi, (b) Endozoic or endoparasitic fungi. Endozoic or endoparasitic fungi are again subdivided into (i) egg parasites, (ii) parasites of cysts and females, (iii) parasites of vermiform nematode, (iv) parasites of all the stages of nematode. Nordbring-Hertz et al [12] and Yang and Zhang [13] grouped nematode destroying fungi into nematode-trapping fungi, endoparasitic fungi, opportunistic fungi or egg and cyst parasitic fungi and toxin producing fungi.

Classification of nematode destroying fungi

Based on morphological and molecular studies, the majority of nematode trapping fungi is hyphomycetes, within the Orbiliales (Orbiliomycetes or Ascomycota) besides Basiodiomycota and Zygomycota. The pioneering work was done by Drechsler [14]. Based on morphology of conidia (shape, septa and size) and conidiophores (branching, modifications of the apex), nematode-trapping fungi have been classified in a number of genera. This classification created a situation where species with diverse types of trapping devices have been assigned to one genus, while others with similar trapping devices can be found in different genera [15- 18]. Based on trapping devices, Rubner [19] revised the generic concepts of the predatory hyphomycetes Hagedorn and Scholler [20] and Scholler *et al*. [21] classified nematode-trapping fungi into four genera: *Dactylellina* characterized by stalked adhesive knobs including species characterized by nonconstricting rings and stalked adhesive knobs; *Gamsylella* characterized by adhesive branches and unstalked knobs; *Arthrobotrys* characterized by adhesive networks; and *Drechslerella* characterized by constricting rings. Li et al [22, 23] and Yang et al [24] provided a generic concept of nematode-trapping fungi based on morphological as well as multiple gene data. The adhesive knob is considered to be the ancestral type of trapping device from which constricting rings and networks were derived by passing through two pathways. In the first pathway adhesive knobs retained their adhesive material forming two-dimension networks and three-dimension networks. In the second pathway adhesive knobs lost their adhesive materials, forming nonconstricting rings and constricting rings.

Some of the endoparasitic fungi viz., *Catenaria anguillulae*, *Haptocillium* (formerly *Verticillium*), *Harposporium* or *Drechmeria* are placed in the Chytridiomycetes, Based on morphological and molecular characters, the teleomorph of *Harposporium* spp. has recently been transferred from *Atricordyceps* to *Podocrella* [25] and the genus *Verticillium* is transferred to the genus *Pochonia* [26].

Nematode-trapping as well as endoparasites, *Hohenbuehelia* (anamorph *Nematoctonus*) are under Basidiomycota [27]. Another basidiomycete genus, *Pleurotus ostreatus* and *Coprinus comatus* constitutes the toxin-producing fungi [28].

Nematode- trapping or predacious fungi

Of the 200 parasites, predacious and pathogens of nematodes known so far, approximately 75% are nematode destroying fungi. Each group utilizes a different type of trapping device to adhere to or to attack nematodes (Table.1). They are found in all regions of the world, from the tropics to the Antarctica [29]. Most of them can grow both as saprophytes, decaying organic matters as substrates, and as parasites, using nematodes as nutrients [30]. The density of nematicidal fungi is highest in the upper 20 cm of the soil horizon and very few are found below 40 cm of depth [31]. Nematode-trapping fungi have been found **fossilized in amber** dated at 100 million years old and was mentioned in the Cretaceous age [32]. *A. oligospora* was described for the first time by Fresenius in 1852. Woronin reported that *A. oligospora* forms networks of hyphal slings or loops during 1870. Zopf [33] observe that a fungus trap a living animal. American mycologist, Drechsler [34] published a monumental paper that established 11 new species. Duddington [9] described predacious activity of many fungi against eelworm. Peterson and Katznelson [35], Garspard and Mankau [36], Persmark and Jansson [37] observed that nematode-trapping fungi were more frequent in the rhizosphere. *A. oligospora* colonized in epidermal cells may serve the purpose of trapping newly hatched juveniles of plant-parasitic nematodes.

Structures of nematode -trapping fungi

The trapping device of these fungi comprises the hyphal structure which is having an adhesive layer covering part or the entire surface [24]. The sparse mycelia of these fungi when come

into close contact with nematodes, it differentiates spontaneously into functional traps. The mycelial traps then penetrate nematode cuticle, kill and digest the nematodes' contents.

Adhesive hyphae / branch

Adhesive hyphae /branch consist of one or more cells to infect nematodes. The adhesive column is a short and erect hyphae consisting of a few swollen cells.

Adhesive knobs

The hypha having globose or subglobose cell either sessile or with an erect stalk produces adhesive knob. The knob can detach from the mycelia, travel along with the nematode and then penetrate nematode cuticle and infect the nematode. Usually infection involves one knob and several associated hyphal elements. Nematode cuticle are having several infection site. Adhesive knobs produce an infection peg and infection bulb. The infection bulb proliferates within the nematode body and thereafter digesting and assimilating the contents of nematode body. They break out through the nematode cuticle and produce external hyphal structure which resembles vegetative mycelium. The traps of *Monacrosporium ellipsosporum* are passive in action and nematode specific as well as stage specific [36].The adhesive knobs (*A. oligospora* and *A. dactyloides*) develop directly through the germination of the conidia, without a hyphal phase [38] .

Adhesive network

The vegetative hypha forms an erect lateral branch and then curving to fuse with the parent hyphae. Appressorias are developed from the hypae and penetrate the entangled nematodes and formation of an infection bulb and infection hyphae takes place which digest the contents of nematode body.

Mechanical structures

Constricting ring: The three ring cells are triggered to swell rapidly inwards as and when a nematode enters the ring and firmly loop the prey. An infection peg is produced by one of the three ring cells and a infection bulb develops after the infection peg has penetrated into the body cavity of nematodes [39]. Infection bulb digests and absorbs the nematodes internal contents, Ring inflation occur due to increased vacuolation, osmotic mechanism and presence of membrane bound inclusion in traps which may contribute to matrix for plasma membrane expansion on inner face of a trap. In presence of mild heat, pressure or Ca^{2+} [12], cells of the ring are effective in formation of loop.

Nonconstricting rings: The lateral branches from the vegetative hyphae thicken and curve and then fuses to the supporting stalk to form a nonconstricting ring. If a nematode, during its movement, thrusts its head inside the rings, it gets wedged in its efforts to force its way through and is held in the process. During the struggle of the nematode the ring often breaks off at the point of weakness near the stalk apex. The process may be repeated until several rings are wedged around the host. Detached rings are viable, the prey is then penetrated and the contents are consumed. There is no sticky material and the nematode is held purely by friction.

Other mechanical structures with nematicidal activity which can damage the cuticle of the nematode by their sharp projections have been reported.

Endozoic or Endoparasitic fungi

Endoparasitic fungi infect nematodes through special spores known as zoospores. The zoospores are swallowed by the nematode or adhere to their surface and the mycelia grow from spores within the nematodes (Table.2). **Endoparasitic fungi** are generally highly specific to nematodes, and are difficult to culture in artificial host in the absence of their host. Depending on the species, any nematode stages can be attacked. The conidia of *Hirsutella rhossiliensis* adhere to nematodes. After germination, fungal hyphae then penetrate the cuticle and utilize the internal contents for food. Before penetration, secretion of the toxin may immobilize the host. When the food source depleted; adhesive conidia emerge out of the cuticle.

Egg and cyst parasitic fungi

These are usually saprotrophic soil fungi found in plant roots. Nematode eggs of sedentary endoparasite, viz. *Globodera*, *Heterodera*, *Rotylenchulus*, *Tylenchulus*, and *Meloidogyne* are more vulnerable to attack by these fungi than those of migratory nematodes. The appressoria or globose mucilaginous knobs are formed when the fungal hyphae contacted the eggs [60]. During the early stage of infections, hyphae completely occupied the embryo in the egg and become vacuolated after the contents are consumed.

Penetration is facilitated by extracellular enzymes such as chitinases and proteases [24].The fungus can colonize nematode reproductive structure and affect their reproductive capabilities. These fungi have been found to be more prevalent in the root rhizosphere [61, 62]. *P. chlamydosporia* and the toxin-producing *P.djamor* [63] are present mostly as root colonizer. However the endoparasitic fungi *H. rhossiliensis* and *N. pachysporus* did not show root colonization [64-66].

Parasites of females/cyst

The white females of *Heterodera* spp. become infected after they rupture the root cortex and are exposed in soil. The infected females tend to lose turgor. The females donot turn brown and their entire content is replaced by zoosporangia in approximately 4 days at 13^0 C. In some of the white cysts where infection takes place after the commencement of egg laying, the fungus parasitized the eggs as well. In such cases, eggs with second stage larvae inside the eggshell are parasitized more than those eggs which are still in embryonic stage. The larvae, once invaded by the fungus, totally destroyed in 18-24 hrs. The total destruction of the young white females completed within 48-72 hrs. The spores are then spread in soil.

Hyphae of *Glomus fasciculatum* penetrated the female of *Heterodera glycine* cuticle and infected eggs shortly after it ruptured the root epidermis. Chlamydospores are also observed in *G.fasciculatum* within cysts [89].

Parasites of vermiform nematodes

Members of this group having adhesive spores and attached to cuticle, mouth, excretory pore, anus, or sensory organs prior to their germination and infections of the nematodes. After the production of germ tube the nematode cuticle was penetrated and growth of hyphae proceeded. They have generally limited mycelial growth outside the host. The nematode remained alive until the hyphae reached the vital organs.

Toxic fungi

The toxin producing fungi belong to widely divergent orders and families (Table.3). They attack their prey by secreting inhibitory metabolites (diffusible toxins), without any physical contact between the fungus and nematode [60, 93]. After immobilization of nematodes, the hyphae penetrate the nematode cuticle. The culture filtrates of these fungi are having strong proteolytic and chitinolytic activities, low molecular weight metabolites and some non-volatile oil components [81] to cause mortality of larvae or inhibit egg hatching. Toxic diffusible metabolites of the fungus either cause some alteration of egg shell make-up leading to aborted embryonic development. These deformed eggs varied in size and shape and do not hatch.

Mechanism of infection of nematode destroying fungi

Infection of nematodes starts with a recognition phase that is the chemotaxis of nematodes to fungal traps, or chemotaxis of zoospores to the nematode's natural openings [94]. Capture hyphae and vegetative hyphae have several ultrastructural differences. Capture hyphae have thicker cell walls than vegetative hyphae and their cells contain electron dense bodies. After contact, an extracellular material, or adhesive, is formed. The adhesive is a specific carbohydrate binding protein (lectin) which is present on trap surfaces [95, 96]. Some of the example are *A.oligospora* (N-acetylgalactose amine), *Dactylaria candida* (2-deoxyglucose), *Meria coniospora* (sialic acid), *A.conoides* (glucose/mannose), *Monacrosporium eudermatum* (I-sucrose) and *M.rutgeriensis* (2-deoxygluycose) [97, 98]. The adhesive on the traps of *A.oligospora* changes from an amorphous to a fibrillar appearance after contact with a nematode and the adhesive on conidia of *D. coniospora* are always appears fibrillar [99]. The adhesive on the appressoria of *P. chlamydosporia* and *P. rubescens* are glycoprotein in nature with mannose/glucose moieties [64]. Involvement of a Gal-NAc-specific lectin of *A. oligospora* in nematode recognition has been suggested by Nordbring-Hertz and Mattiasson [100]. The endoparasitic fungus *D. coniospora* infects nematodes with its conidia which adhere to the chemosensory organs of *Meloidogyne* spp., but do not penetrate. The fungus was capable of reducing root galling in tomato in a biocontrol experiment [77], indicating the involvement of chemotactic interference [99]. Conidial adhesion of *D. coniospora* was suggested to involve sialic acid-like carbohydrate [101] .*Monacrosporium ellipsosporum* adhesive knobs showed host specificity. This host recognition results in reorganization of the adhesive surface polymer on the fungus and adhesion of the nematode to the fungus which triggers the growth of hyphal

Table 1. Nematode trapping fungi and infected nematodes

Nematode – trapping structure	Fungi	Taxonomic position	Nematode infected	Reference
Adhesive hyphae	*Stylopage hadraCystopage lateralis*	Zygomycota	*Rhabditis,Cephalobus,Acrobeles*	Drechsler [14,34]
Adhesive branches	*Dactylella cionopaga D.gephyropaga D.tylopage D.lobata Arthrobotrys oligospora/Orbilia*	Ascomycota	Plant-parasitic nematodes	Li et al.[23]Niu & Zhang [40]Singh et al.[41]
	Monacrosporium cionopagum	Ascomycota	*M.incognita*	Robinson & Jaffee, [42]Satou et al.[43]
Adhesive knob	*Nematoctonus/Hohenbuehelia*	Basidiomycota		Thorn & Barron [27]
	Dactylellina/Orbilia	Ascomycota		Yang et al.[44]
	D.haptotylaDactylella ellipsospora	Ascomycota	*Meloidogyne* spp.	Ahren et al.[45]Timper & Brodie[46]
	Monacrosporium haptotylum		*Pratylenchus penetrans*	Ahren et al.[47]Friman[48]Liu et al.[49]
	Monacrosporium ellipsosporum		*Aphelenchus avenae*	Dowsett&Reid[50]
	Dactylaria candidaD.brochopaga D. scaphoides			
	A. oligospora A. dactyloides	Ascomycota		Nordbring-Hertz et al.[12]
Adhesive network	*A.oligosporaA.musiformis*	Ascomycota		Nordbring-Hertz et al. [12]
	Dactylaria scaphoides	Ascomycota		Dowsett&Reid[50]
Constricting ring	*Drechslerella* / *OrbiliaDrechslerella stenobrocha*	Ascomycota		Higgins & Pramer, [51] Dijksterhuis et al. [52]Nordbring-Hertz *et al*.[12] Liu et al.[53]
	Dactylaria brochopagaDactylella bembicoides	Ascomycota	*Meloidogyne graminicola*	Singh et al.[54] Kumar & Singh [55]
	Arthrobotrys conoides A.dactyloides Monacrosporium ellipsosporum	Ascomycota	*Xiphinema index*	Gaspard & Mankau [56]
Non-constricting ring	*Dactylaria candidaD. lysipaga*	Deuteromycetes	*Ditylenchus dipsaci, Globodera rostochiensis*	Galper et al. [57]Liu et al.[49]
	Dactylellina/Orbilia	Ascomycota		Yang et al[44]
Spiny ball	*Coprinus comatus*	Basiodiomycota	*M.arenaria*	Luo et al. [28,58,59]
Canthocytes	*Stropharia rugosoannulata*	Basiodiomycota	*Bursaphelenchus xylophilus*	Luo et al. [58,59]

Table 2. Endoparasitic fungi and infected nematodes

Endoparasitic fungi	Fungi	Taxonomic position	Nematode infected	Reference
Adhesive conidia	*Haptocillium* /*Cordyceps* (*Drechmeria coniospora)*	Ascomycota	*Caenorhabditis elegans*	Jansson [67] Quandt et al. [68] Lebrigand et al.[69]
	Hirsutella rhossiliensis	Ascomycota	*Heterodera spp.*	Jaffee & Zehr [70] Chen et al. [71]
	Hirsutella minnesotensis			Chen & Liu[72]
	Harposporium/*Podocrella*	Ascomycota		Yang & Zhang[13]
	Hyphoderma	Basidiomycota	Mycophagous nematode, *Rotylenchulus, Trophonema*	Tzean &Liou[73] Zhang et al. [74]
	Trichothecium	Ascomycota	*M.incognita*	Ciancio et al. [75]
	Triposporina	Ascomycota		Zhang et al. [74]
	Tridentaria	Ascomycota		Zhang et al. [74]
	Zoophagus	Zygomycota		Zhang et al. [74]
Adhesive buds	*Myzocytium humicola*	Oomycota	Rhabditis	Barron & Percy[76] Zhang et al. [74]
adhesive knob	*Nematoctonus*/*Hohenbuehelia* *Nematoctonus concurrens*	Basidiomycota		Zhang et al. [74]
	Myzocytiopsis	Oomycota		Jansson et al. [77]
	Haptoglossa	Oomycota		Barron[78] Nordbring-Hertz et al.[79]
	Catenaria	Chytridiomycota		Zhang et al. [74]
	Pochonia	Ascomycota		Zhang et al. [74]
	Paecilomyces / Cordyceps	Ascomycota		Zhang et al. [74]
	Nematophthora	Oomycota		Zhang et al. [74]
	Meria(Drechmeria)	Ascomycota		Jansson et al. [77]
Egg and cyst parasitic fungi	*Fusarium*	Ascomycota	*H.schachtii*	Westphal [80] Westpha&Becker[81]
	Cephalosporium	Ascomycota		Jansson et al. [82]
	Verticillium chlamydosporium (*Pochonia chlamydosporia)*	Ascomycota	*H.schachtii* *M.arenaria*	Siddiqui & Mahmood[83]
	V.bulbillosporum *V.balanoides* P.rubescens			Durschner Pelz &Atkinson[84]
	Mortierella nana	Zygomycota		Jansson et al. [82]
	Paecilomyces lilacinus	Ascomycota	*Meloidogyne* spp	Tranier et al.[85]

	(*Purpureocillium lilacinum*)		*Radopholus similis,* *Heterodera* spp, *Globodera* spp,	
	Acremonium bacillosporum	Ascomycota	*Pratylenchus* spp	Stirling[86]
	Dactylella oviparasitica	Ascomycota	*Meloidogyne spp.,* *Acrobeloides* sp., *Heterodera schachtii* ,	Stirling[86]
	Monacrosporium lysipagum *M.haptotylum*	Ascomycota	*Tylenchulus semipenetrans*	Ahren et al.[45]
	Catenaria anguillulae	Chytridiomycota	*M.graminicola*	Singh et al.[87]
	Trichoderma harzianum *T. viride* (*T.asperelloides*) *T. asperellum* (*T.asperelloides*)	Ascomycota	*M.javanica*	Sharon et al. [88]
	Nematophthora	Oomycota		Siddiqui& Mahmood [83]
Parasites of females/cyst	*C.auxillaris*	Chytridiomycota	*H.schachtii*, *H.avenae*, *H.cajani*, *H.zeae*	Zhang et al. [82]
	C.vermicola	Chytridiomycota	*H.avenae*, *H.cajani*, *H.zeae*, *H.graminis*, *H.mothi H. sorghi*	Zhang et al. [74]
	Dactylella oviparasitica	Ascomycota	*T.semipenetrans* *Nacobbus aberrans*	Zhang et al. [74]
	Nematophthora gynophila	Oomycota	cyst nematodes	Zhang et al. [74]
	Glomus fasciculatum *G.microcarpum* *G.mosseae*	Glomeromycota	Root-knot nematode	Kantharaju et al. [89]
	Pochonia/Metacordyceps	Ascomycota		Morgan-Jones et al. [90, 91] Freire & Bridge[92] de Leij & Kerry[63]
	V.chlamydosporum	Ascomycota	*H.avenae*	Zhang et al. [74]
	Chaetomium cochloides *Exophiala pisciphilla* *Fusarium oxysporum* *F.solani* *Phytophthora cinnamon* *Trichosporon beigeli*	Ascomycota	*H.glycines*	Stirling[86]
	Pythium spp.	Oomycetes Basidiomycota Oomycetes		
	P.lilacinus		*M.incognita* *T.semipenetrans* *Nacobbus aberrans*.	Tranier et al.[85]

					Stirling[86]
Parasites of vermiform nematodes	*Catenaria* sp.	Chytridiomycetes			Stirling[86]
	Myzocytium humicola	Oomycetes			
	Merisacrumn asterospermum	Zygomycetes			
	Harposporium anguillulae	Deuteromycetes			
	Nematoctonus sp.	Basidiomycetes			
	H.arcuatum,	Hyphomycetes			
	H.helicoides,				
	Cephalosporium balanoides				
	Meria coniospora	Ascomycota	*Panagrellus redivivus*, *Aphelenchoides fragariae* , *Ditylenchus destructor*, *M.*spp.	Jansson et al. [77]	
	H. arcuatum	hyphomycetes			Stirling[86]
	Caternaria anguillulae	Chytridiomycetes	*Xiphinema rivesi*		Stirling[86]
	Lagenidium caudatum		*X.americanum*,		
	Aphanomyces sp.				
	Teptolegnia spp.				
uniflagellate zoospores	*Catenaria vermicola*	Chytridiomycetes	*H.avenae*, *H.sorghi* , *H.cajani*		Stirling[86]

branches into the nematode to initiate its digestion. Once inside the body of the nematode, the fungus swells up to produce a globe-shaped vesicle, also named as mortiferous excrescence, infection bulb, post-infection bulb. From this bulb, hyphae proliferate in both directions and consume the host's contents.

Predacious fungi grow and reproduce saprotrophically until come in contact with nematodes. The change induced in fungal structure is stimulated by a metabolic product of nematode known as nemin [102]. Nemin appears to contain several amino acids viz. valine, aspartic acid, glutamic acid, leucine, isolleucine, serine and arginine and specific peptides of low molecular weight [52].Peptides may be inducing changes in the lipid metabolism of the fungi which may lead to membrane structural changes associated with trap formation in *Arthrobotrys oligospora* [103]. PII is a serine protease purified from *A.oligospora* that could digest proteins present on the nematode cuticle [104]. PII belongs to the subtilisin family of serine proteases and has a molecular mass of 32 kDa. The expression of PII is increased by the presence of proteins, including nematode cuticles [105]. Another serine protease from *A. oligospora* (Aoz1), with a molecular mass of 38kDa showing 97% homology with PII was recently described [106]. Another serine protease (P32) of molecular mass of 32 kDa was purified and characterized from the egg parasite *P. rubescens* [107]. Ahman *et al.* [108] reported that over expression of the PII gene resulted in a higher virulence. *P. chlamydosporia* produces an extracellular protease (VcP1) which is immunologically related to P32 [109,110]. VcP1-treated eggs were more infected than untreated eggs suggesting a role of the enzyme in eggshell penetration by egg-parasitic fungi. A chymotrypsin-like protease from conidia of the endoparasite *D. coniospora* [111] and a collagenase produced by the nematode-trapping *Arthrobotrys tortor* [112] has been detected. Several chitinolytic enzymes like 43 kDa endochitinase (CHI43) of *Pochonia rubescens* and *P. chlamydosporia* have been suggested [113]. By using mass spectrometry, 26 cell-wall proteins were identified and included glycosyl hydrolases, oxidases, pectin lyases and proteases which are being upregulated in traps as compared to vegetative mycelium in *A. oligospora* [114] Ascarosides, sugar ascarylose linked to a

Table 3. Toxin producing fungi and infected nematodes

Toxic metabolite	Fungi	Nematode infected	Reference
LeucinostatinsSerine protease, Chitinase	*Purpureocillium lilacinum* *Paecilomyces* sp.	*M.javanica, M. incognita, P. redivivus ,Bursaphelenchus xylophilus*	Park et al.[143] Liu et al.[144]
T2 toxin, Moniliformin, Fusarenone, Neosolaniol, VerrucrinA,	*Fusarium solani*	M.javanica	Ciancio[145]
Secalonic acid D, Oxalin	*Penicillium anatolicumP.sp. P.vermiculatumP.oxalicum P.chrysogenum*	*G.rostochiensisH.avenaeM.spp. G.rostochiensis,G.pallida M.javanica*	Steyn [146]

fatty-acid chain are constitutively secreted by nematodes, trigger trap formation in nematode-trapping fungi [115,116].

Trap formation is also influenced by cultural conditions and defined low nutrient medium (LNM) giving the most rapid and pronounced induction in *A.oligospora* and *A.dactyloides*. Trap formation by *A.conoides* was higher in rich nutrient medium of corn meal agar (CMA) than LNM [117].

The development of traps is a complex process involving cytoskeleton assembling, enhanced cell wall biosynthesis, increased glycerol synthesis and accumulation, as well as peroxisome biogenesis [118]. Recently, using expressed sequence tag (EST) techniques, it was detected that genes involved in formation of infection device and fungal morphogenesis were expressed during trap formation of *Dactylellina haptotyla* (syn. *Monacrosporium haptotylum*) [47].

The penetration of *M.incognita* females by *Paecilomyces lilacinus* (*Purpureocillium lilacinum*) is generally through the anal or vulval openings [119].They colonizes the gelatinous egg matrix of *Meloidogyne* and penetration of nematode eggs is completed through appressoria [11, 120]. Both mechanical and enzymatic activities may be involved in the penetration. Culture filtrates containing a peptidal antibiotic P-168 of *P. lilacinum* have been shown to be toxic to nematodes and other soil microorganisms [121-123]. The ultrastructural changes observed in egg shell are splitting of vitelline layer into 3 discrete membranes which appear unevenly thickened, the chitin layer become vacuolated and the lipid layer disappears. Similar disorganization of the larval cuticle occurs and larvae become necrotic. In heavily colonized larvae, the external cortical layer is contorted .These are due to the presence of chitosanase [124]. *P.lilacinus* is a good root colonizers [125] and rhizosphere competitor, and has been tested widely and shown to suppress nematode population densities and increase plant yields [126].

Penetration of *P. chlamydosporia* to eggshells occurs through lateral branches of mycelium; penetration peg (appressoria) develops and leads to the disintegration of the vitelline layer , dissolution of the chitin and lipid layers of nematode cuticle [91,127-130]. Both proteases and chitinases are involved in infection process. Proteases of nematode parasites have been characterized from *V. suchlasporium* [131] and *P. chlamydosporia* [129]. Studies of different isolates of *P. chlamydosporia* have also shown that they produce a range of different subtilisins [132]. There are reports of difference of virulence of isolates of *V. chlamydosporium*, collected from the same soil to root-knot population; even variations of virulence exist within root-knot populations [117]. *P.rubescens* starts with contact of the hyphae with the egg of root-knot nematode and formation of an appressorium. The appressorium of the fungus penetrates the nematode eggshell by means of both mechanical and enzymatic components. On the appressorium an extracellular material (ECM), or adhesive, is detected that can be labeled with the lectin Concanavalin A (Con A), indicating that it contains glucose/mannose residues. The ECM contains the protease P32 that can be immunologically detected using both fluorescent stains and colloidal gold. This proteolytic activity

causes the degradation of eggshells. In pot experiments *P. chlamydosporia* increased plant growth, suggesting a growth promoting effect by *P. chlamydosporia* [133].

The uniflagellate zoospores of *C. anguillulae* become attracted to natural orifices (mouth or excretory pores) of the nematode. Upon contact with the nematode natural orifices, the zoospores show an 'amoeboid movement' before encystment takes place. During encystment a cell wall is formed covered by an adhesive. The encysted zoospore forms an infection peg which

Table 4. Commercial products of Nematode destroying fungi

Commercial product	Formulation	Fungi	Reference
BIOACT®WG	Water-dispersiblegranulate	*Purpureocillium lilacinum*	Davies and Spiegel [175]
BIOACT®WP	Water-dispersible powder		
PL Gold	Wettable powder		
PL 251	Water-dispersiblegranulate		
BIOCON	Wettable powder		
Shakti Paecil	Wettable powder		
Yorker	Wettable powder		Davies and Spiegel[175]
Miexianning			
Pl Plus®	Wettable powder		
Melocon®	Water-dispersiblegranulate		Davies and Spiegel [175]
Green Nemagon	Liquid formulation		Moosavi & Askary [178]
Bio-Nematon			Kabaluk et al.[179]
BIOSTAT(r)			Tranier et al.[85]
KlamiC®	Granulate	*Pochoniachlamydosporia*	Davies & Spiegel [175]
PcMR-1 strain	Liquid		
Xianchongbike	Liquid		
Romulus	Wettable powder	*Trichoderma harzianumT*	Moosavi &
Ecosom-TH	Wettable powder,liquid, lyophilized	*. virideT. lignorum*	Askary [178]
Commander Fungicide			
Trichobiol	Wettable powder		
Trifesol	Wettable powder		
Mycobac			
Trianum(r)		*T. harzianum*	Tranier et al.[85]
Trifender		*T.asperellum*	Biro-Stingli & Toth [180]
DiTera®	Dry flowable	*Myrothecium verrucaria*	Warrior et al.[181] Lamovsek et al.[182]
Royal 300	fresh mycelium on	*Arthrobotrys robusta*	Cayrol et al.[183]
Royal 350	organicsubstrates	*Arthrobotrysirregularis*	Cayrol [184, 185]
	Alginate-based	*Monacrosporium ellipsosporum*	Jaffee & Muldoon[186]
	formulations	*Monacrosporium cionopagum*	Jaffee & Muldoon[186]
	encapsulationin	*Dactylella candida*	Stirling & Mani[187]
	alginate	*Arthrobotrysdactyloides*	Stirling & Mani[187]
	granular	*H. rhossiliensis*	Lackey et al.[188]
	microencapsulation		Patel et al[189]
REM G(r)	Granulate	consortium	Tranier et al.[85]
Abamectin	microcapsule	*M.incognita*	Beixing et al.[190]

penetrates the nematode cuticle. The fungus digests the nematode contents and the zoospores are released which can infect new nematodes.

Some actinomycetes are known to produce compounds with nematicidal properties. Macrocyclic lactones designated Avermectins have been isolated from mycelia of *Streptomyces avermitillis* [134]. They are antagonists of GABA as opposed to the acetylcholinesterase inhibition by organophosphates and carbamates and their potential efficacy is greater than the current nematicides. Avermectins (B_2a) have been reported to reduce oxygen uptake of larvae of *M.javanica*, *M.arenaria* and *M.incognita* under laboratory condition.

Trichoderma is a ubiquitous soil fungus and root colonizes.The highly branched conidiophores of *Trichoderma* produce conidia that can attach to different nematode stages. Fungal coiling and appressorium like structures are formed for penetration of the nematode cuticles or eggshells, *Trichoderma harzianum* and *T. viride* (*T.asperelloides*) colonizes eggs and juveniles of *Meloidogyne* spp. and the antagonistic or parasitic effect are brought about by glycolytic and chitinolytic enzymes and peptaibiotics[135-137].*Trichoderma harzianum* are sources of serine proteases with nematicidal activity [138,139]. Application of *Trichoderma* resulted in reduced nematode galling and improved plant growth and induces resistance to root-knot nematode [140,141].

Arthrobotrys dactyloides has been shown to produce a nematotoxin, the active ingredient being ammonia. Some of the nematicidal metabolites produced by Ascomycetes namely oligosporon, 42 ,52 -dihydrooligosporon, talathermophilins A and B, phomalactone, aurovertins D and F, paeciloxazine, a pyridine carboxylic acid derivative, and leucinostatins has been detected. Blumenol A is one type of metabolite which acts as a nematode attractant [142].

Isolation, mass production, commercialization and field application

Westphal [80], Borneman and Becker [160] developed several techniques by which it is determined whether a soil includes antagonistic organisms against plant-parasitic nematodes or not. Baiting technique and sprinkle-plate method are some of the techniques to isolate fungi [161,162,163]. For egg parasitic fungi, egg masses are to be isolated, subculture and identified. A PCR-based detection technique revealed many fungi that are closely related to nematode trapping fungi and eggs parasitic fungi [164]. For development of a potentential biocontrol agent the common strategy has been to mass-produce the fungi either on solid or liquid substrates followed by application. The nematode-trapping fungi are easy to grow in the laboratory [52, 165] while zoopagales cannot be cultured on artificial media[166]. It is possible to control the development of traps by modifying the growth condition and the medium composition. Growing *A. oligospora* in aerated liquid cultures in a low-nutrient media containing soya peptone supplied with small amounts of the amino acids phenylalanine and valine allows significant trap formation [167].Growing *Monacrosporium haptotylum* in this system makes the knobs detach from the mycelium due to the air bubbling from the bottom and the knobs can be separated from the mycelium by filtration [168]. Methods that produce the highest number of propagules are not essentially those that generate the most efficacious [169,170]. Mass culture should be done after testing their potentiality as biocontrol agent through *in vitro* and pot experiments. A promising candidate is the one that can produce numerous resistant spores or structures with an acceptable shelf-life and applicable with routine agricultural machinery [171]. Fungal biocontrol agents that are unable to develop resting structures may be applied as vegetative cells, hyphae or conidia. These structures are more vulnerable and need more complex formulations [172]. The important factors in producing specific propagules include carbon source, osmotic potential, temperature and pH [173]. A proper formulation assists in delivering an optimal population density of biocontrol agent at the most appropriate site and time as well as improving the efficiency [172-175]. Some nematophagous fungi have been formulated as encapsulated pellets made from calcium alginate to aid in their dispersal in the field. To deliver the infectious fungi to growers, potent infectious fungi must be commercialized [174]. Several research workers and entrepreneurs have tried to discover, develop and commercialize but in practice only a few bio products have successfully been introduced to the market (Table. 4). However, for more development of the commercial product, thorough understanding of the complexicity of

soil ecology (soil temperature, soil moisture, soil texture and structure, soil microflora) in agricultural fields is required. Quality control is an important component of all commercial products. The cost of registering a product which includes a variety of tests required proving the safety and efficacy of a product is also a significant concern. The application technology should be devised depending on biocontrol agent type, mode of action and cropping system, compatibility with existing farm practices and safety, besides low price [173,176]. Most bionematicides in the market are in the form of liquid or wettable powder formulations, which are implemented in furrow or through drip irrigation systems [175]. Kerry [177] suggested the application of organic manures in combination with nematophagous fungi and application of biocontrol agents with the planting material.

CONCLUSION

Better knowledge about the mode of action of nematode destroying fungi or microbe-nematode interactions is a prerequisite for the development of biocontrol agent for management of plant-parasitic nematodes [130, 191]. Furthermore, knowledge about the genes that regulated during pathogenicity and survival of the introduced fungus could help for the development of new control agents [175]. Besides health and safety, some of the aspects viz., identification of the nematode species to be controlled ,soil receptivity to selected spores of these fungi, demand for the product, potential market size and on existing competing products, must be considered before a nematode destroying fungus can be registered as an agricultural biocontrol agent [172].

For a sustainable nematode management we have to intensify the search for environmentally beneficial and cost-efficient alternatives. Nematode destroying fungi will provide a promising bionematicides, and in turn improve plant growth. Using as a component in integrated pest management we can increase crop yields and ultimately help in production of more food to feed the growing population.

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