

Effect of Nematophagous Fungi on Entomopathogenic Nematodes

Gitanjali Devi

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ABSTRACT

Entomopathogenic nematodes in the genera *Steinernema* and *Heterorhabditis* are important biological control agents against a wide range of insect pests. The third- stage juveniles of these nematodes survive in soil and can locate and infect an insect host. However poor survival of juveniles reduces the efficacy as well as their establishment in a host population. The survival of infective stage in soil depends on many abiotic and biotic factors. Soil contains organisms that may upset entomopathogenic nematodes and limit their use. Among these, nematode-parasitic fungi or nematophagous fungi i.e. nematode trapping fungi and endoparasites are important natural enemies of entomopathogenic nematodes in soil ecosystem. This review illustrates various mechanisms of nematophagous fungi that infect entomopathogenic nematodes as well as the survival mechanisms of entomopathogenic nematodes upon infection. As nematophagous fungi are important mortality factors for entomopathogenic nematodes, probable mechanism for prevention of fungal attack should be worked out for better bio-control option of insect pest.

Keywords Nematophagous fungi, Entomopathogenic nematodes, Interaction, Nematode-trapping fungi, Endo-parasitic fungi.

INTRODUCTION

A group of nematodes that are pathogens of insects are known as entomopathogenic nematodes (EPNs). The family Steinernematidae and Heterorhabditidae belong to this group of nematodes. Their pathogenic effect is conferred by their mutualistic interaction with facultative anaerobic bacteria. These bacteria (*Xenorhabdus* spp. associated with *Steinernema* spp and *Photorhabdus* spp. associated with *Heterorhabditis* spp.) are vectored from one insect host to another by the free-living 3rd stage juvenile stage (dauer) of these nematodes which are present in soil. They can locate and infect an insect host. Once inside the insect host, the nematodes release the bacteria into the insect's hemolymph, which kill the insect host. The bacteria degrade the insect's tissues and also provide food source for nematode which allow them to mature and multiply. One or two generations of this nematode produced within the insect cadaver. The progeny of the last generation reassociates with a few bacterial cells in a more specialize manner than their previous nutritional relationship as they move out from the insect cadaver into the soil where they will await another insect to parasitize. Thus these nematodes are recovered from soil as well as infected insects. These nematodes are important biological control agents and considered as valuable alternatives

Gitanjali Devi, Assistant Professor
Department of Nematology, Assam Agricultural University,
Jorhat 785013, Assam, India
Email : gitanjali.devi@aau.ac.in

to chemical pesticides of insect pests of economic importance. These nematodes can be mass produced and applied inundatively to control insect pests of soil as well as cryptic habitats. However, survival and persistence of these nematodes varies among different species and even strains. The performance of these nematodes in soil depends on many abiotic (e.g., temperature, moisture, soil texture, soil pH) and biotic (soil biota) factors (Kaya 2002). Soil biota are predators, parasites and pathogens, which reduces survival in soil, or reduces ability for host location or infection by dauers and their establishment and limit their use as biological control agents of insects (Jaffuel *et al.* 2016). Among these, nematophagous fungi (NF) or nematode destroying fungi are important soil biota that influences the efficacy of entomopathogenic nematodes in soil ecosystems (Shapiro-Ilan *et al.* 2012).

Nematophagous fungi are taxonomically diverse group. There are about 700 species of nematophagous fungi which can trap, kill and use them as nutrient source. Except few, most of them are facultative saprophytes (Jiang *et al.* 2017). About 160 species of fungi belongs to Zygomycota, Basidiomycota, and Ascomycota are able trap nematodes and digest them (Zhang *et al.* 2011, Yang *et al.* 2012, Jiang *et al.* 2017, Vidal-Diez de Ulzurrun and Hsueh 2018). Various morphological devices are employed in nematode capturing. All devices that mediate fungal-nematode interactions are either specialized hyphal structures or differentiated cells. Nordbring Hertz and Tunlid (2000) grouped these nematophagous fungi into three categories based on the mechanisms involved : Nematode-trapping that use specialized trapping structures, endoparasitic fungi through spore adhesion and invasive growth to break the nematode cuticle and colonize the nematodes' pseudocoeloms and toxic compound producing fungi that immobilize nematodes before invasion. Some opportunistic fungi also invade or colonize nematode eggs, females, or cysts with their hyphal tips. Many fungi have evolved to parasitize mobile stages of nematodes by stephanocysts and gun cells (Jiang *et al.* 2017, Su *et al.* 2017, Soares *et al.* 2018) and also using mechanical force produced by acanthocytes, spiny balls of the basidiomycetous fungi (e.g. *Stropharia rugoso annulata* and *Coprinus comatus*).

Endoparasitic fungi belonging to the Chytridiomycetes (*Catenaria* sp.), Oomycetes (*Myzocyttium humicola*), Zygomycetes (*Merisacrum asterospermum*), Deuteromycetes (*Harposporium anguillulae*), Basidiomycetes (*Nematoctonus* sp.) and Hyphomycetes (*Harposporium arcuatum*, *H. helicoides*, *Cephalosporium balanoides*) are obligate parasites as their whole life-cycle take place within the body of their hosts. They have generally limited mycelial growth or saprophytic phase in soil; generally exist as conidia or zoospores as infection structure in the environment.

Habitats of nematophagous fungi

Population density of nematophagous fungi depends on nematodes. In the deciduous woodland, nematophagous fungi are isolated from upper 10–30 cm of soil. The net-forming trapping fungi and endoparasites were isolated from all depths in soil (Gray 1988). Those fungi forming constricting rings, adhesive branches and adhesive knobs, are found on the upper litter and humus layer. Though the species of nematode-trapping fungi vary with depth, a high level of nematode-trapping activity, the species producing constricting rings has been recorded more than the knob-forming species from the rhizosphere area depending on plant and soil types and nematode population level (Jansson and Lopez-Llorca 2001). Distribution and abundance of *A. oligospora* is more frequent suggesting its vast ability to adapt and grow in varied environmental conditions (Wachira *et al.* 2009). The net-forming species are independent of soil fertility, even at low K level ; they are isolated from soils (Warcup 1967). Although nematode antagonists are found in virtually all soils , their densities may be less than that in the high *H. rhossiliensis* soil. Locations vary in the abundance of nematode antagonists and this may lead to inconsistent control of insects by entomogenous nematodes. Thus, the efficacy of these nematodes may be more consistent in nurseries and greenhouses, where fumigation and steaming of soil have removed most other organisms, than in undisturbed habitats. Therefore soil's suitability for EPN application depends on soil fungal communities.

Mode of action of nematophagous fungi

The pathogenic mechanisms of nematophagous fungi during the infestation process are different (Jiang *et al.* 2017, Vidal-Diez de Ulzurrun and Hsueh 2018).

Nematode-trapping fungi (NTF)

Nematode-trapping fungi produce special hyphal structures called traps. These traps are derived from sparse mycelia to capture and infect nematodes. Different fungal species can produce one or more types of different trapping devices, including constricting rings and different types of adhesive traps (sessile adhesive knobs, stalked adhesive knobs, adhesive nets, adhesive columns and nonconstricting rings). Nematode-trapping fungi are usually not host specific and can trap all soil-dwelling nematodes (Jansson and Lopez-Llorca 2004, Jiang *et al.* 2017). The traps produced by nematode-trapping fungi make these fungi attractive to nematodes (Hsueh *et al.* 2017). Nematodes can be attracted by molecules secreted by their pathogens through their olfactory neurons and receptors (Hsueh *et al.* 2017, Wang *et al.* 2018, Yang *et al.* 2018, Zhen *et al.* 2018). Several morphology-regulating arthrosporol metabolites were recently characterized from *A. oligospora* (Liang *et al.* 2019 ; Xu *et al.* 2015). Nematophagous fungi can detect and respond to ascarosides, which are small molecules secreted by many species of soil-dwelling nematodes as molecular signal to recognize prey and trigger trap formation (Chen *et al.* 2013, Hsueh *et al.* 2013). A metabolic product or a group of substances from the nematode *Neoaplectana glaseri*, collectively called 'nemin', a peptide of relatively low molecular weight or possibly a single amino acid caused morphogenesis and induced trap formation in nematode-trapping fungi. Nitrate and nematodes can act synergistically to induce trap formation in *A. oligospora* (Liang *et al.* 2016, 2017). Nematodes' response to d-limonene may make them less likely to respond to other environmental stimuli, such as to attractants released by nematophagous fungi. Prey recognition by the fungus has been attributed to a molecular interaction of certain proteins on the fungal surface with sugar molecules on the nematode cuticle. In many nematophagous fungi, cuticle recognition via a lectin-carbohydrate relationship has been

established (Nordbring-Hertz and Jansson 1984, Jansson and Nordbring-Hertz 1988). This is because of presence of extensive layers of extracellular polymers on the surfaces of trapping devices for adhesion and infection. Fungi pierce the cuticle by forming a penetration tube, with a combination of mechanical pressure and extracellular hydrolytic enzymes, such as serine proteases (PII, Aoz1, Ac1, Ds1, Dv1, Mlx, Mc1, collagenase, and chitinase (Yang *et al.* 2014, Kuo *et al.* 2020). Liang *et al.* 2011 showed that *A. oligospora* produced extracellular proteases during its infection of nematodes. Collagenase was isolated from *Arthrobotrys amerospora* (Blaxter and Robertson 1998, Swe *et al.* 2011). Several nematophagous fungi have been reported to produce nematotoxins that immobilize or kill nematodes. *A. oligospora* is capable of paralyzing the nematodes by producing a chemical substance, nematotoxin (Niu and Zhang 2010, Xu *et al.* 2015). Nematode content is converted to lipid droplets; these fungi obtain nutrients from the nematodes for their growth and reproduction (Liu *et al.* 2009). In 2011, the first genome of a nematophagous fungus *A. oligospora* was sequenced (Yang *et al.* 2011). Recent genome comparisons and surface structural analyses revealed evidence for expansion of adhesion genes in nematode-trapping fungi genomes and with associated increase in trap surface adhesiveness (Ji *et al.* 2020).

Endo-parasitic fungi

Zhang *et al.* (2020) reviewed the detail mode of action of endo-parasitic fungi which are obligate parasites. The conidia are produced in aggregate clusters and later develop adhesion buds. The conidia of some species may attract nematodes. A non-specific method of attraction which depend only on the density of soil nematodes to ensure infection. The conidia of *Meria coniospora* and *Cephalosporium balanoides* attract nematodes, adhere to cuticle and infect all types of nematodes. *Harposporium anguillulae* and *H. helicoides* have very strongly attracting mycelium but non attracting conidia. The mycelium produced outside newly infected nematodes or the mycelium inside the host may attract nematodes to the vicinity of conidia. This may then be ingested randomly together with food like bacteria, yeast and organic particle by bacterial feeding nematodes. In case of *Drechmeria*

coniospora, for conidial attachment to a particular nematode species, specific recognition signals for adhesion are required. Adhesive conidia of *D. coniospora* would occasionally attach but never penetrate the infective stages except adult and pre-infective stages of *Neoaplectana* spp. of insect parasitic *Neoaplectana carpocapsae*, *N. glaseri*, *N. bibionis*, *N. intermedia* and *Heterorhabditis heliothidis* (Zhang *et al.* 2016). The fungal lectin of spores has been implicated in adhesion. A recognition mechanism involving a sialic acid specific lectin located on the conidia of *D. coniospora*. The infection starts with the adhesion of spores to the nematode cuticle. The matured conidia of *D. coniospora* have an adhesive knob at the distal end of the spore. After adhesion to the nematode cuticle (usually close to the tubes of the sensory-organs), an appressorium forms and then penetrates the cuticle. The invasive growth may also involve cuticle-degrading enzymes, such as serine proteases, chitinases, acid phosphatases (Wang *et al.* 2008). Many of these fungi show specificity in adhering to different groups of nematode species. *Hirsutella rhossiliensis* produces spores that adhere to and penetrate the nematode cuticle and assimilate the body contents prior to its emergence and sporulation. The nematode remained alive until the hyphae reached the vital organs or are ingested by them. Nematodes die within 2-4 days of conidial penetration. The conidiophores of the fungus are seen emerging out of dead nematodes. When resources are depleted *H. rhossiliensis* send a long conidiophores bearing hyphae into the soil while *D. coniospora* produces conidiophores from the cadaver.

Interaction between nematophagous fungi and entomopathogenic nematodes

The third-stage juveniles are the infective and only stage that occurs in soil environment where it must survive until a new host is found. In order to survive and persist in the soil environment, entomopathogenic nematodes are need to successfully competing with other microbes in soil. Competition can be among different nematodes, between nematophagous fungi and nematodes; and between nematodes with other soil micro-organisms. El-Borai *et al.* (2011) suggest the existence of different responses relating

entomopathogenic nematodes (susceptibility) and nematophagous fungi (aggressiveness) due to differences in habitat. Habitat parameters such as soil texture and moisture, temperature, abundance of antagonists, and type of host affect entomopathogenic nematodes and their natural enemies and other food web components. Nematophagous fungi may affect EPN different species across habitats that are more or less favorable to specific nematophagous fungi depending on the soil fungal community structure (El-Borai *et al.* 2009, Shapiro-Ilan *et al.* 2017). *Hirsutella rhossiliensis* causes higher mortality of *S. glaseri* compared with *H. bacteriophora*. Density-dependent parasitism has been reported, demonstrating that an increase in nematode-trapping fungi density would lead to a decrease in nematode prey density. Higher nematophagous fungi are found in response to EPN augmentation but a lower prevalence in animal manure mulches. Moreover, trapping fungi can also alternate their lifestyle from predatory to saprophytic behavior depending upon competition with other saprophytic fungi. The mycelia of trapping fungi and conidia of endoparasitic nematophagous fungi produce some metabolite. The entomopathogenic nematode species differ in their responses to the metabolite (semiochemicals) produced by those fungi (Abd-Elgawad 2019). Therefore, the ability to sense prey among isolates of *Arthrobotrys oligospora* varied significantly (El-Borai *et al.* 2011). Aredesa *et al.* (2017) observed that *Arthrobotrys musiformis* isolate AM4 and *Arthrobotrys* sp. isolate CO₇ were the most aggressive trapping fungi tested against *Heterorhabditis indica* LPP30.

Most of the experiment was under artificial condition (i.e., agar plates with high fungal densities). The natural enemies adversely affect the nematodes because infective juveniles (*S. feltiae* and *S. glaseri*) placed in sterilized or pasteurized soils survived longer than infective juveniles placed in untreated soil. *A. oligospora*, *M. eudermatum*, *Geniculifera paucispora* suppressed *H. hepialus* in pasteurized and in raw soil at fungal propagule densities similar to those observed in the field; nematode suppression by *G. paucispora* or *M. eudermatum* was greater in raw soil containing resident *A. oligospora* than in pasteurized soil; this suggested additive nematode suppression by these fungi.

Antagonistic interactions between trapping or endoparasitic nematophagous fungi and entomopathogenic nematodes have been detected in the soil environments (Campos-Herrera *et al.* 2016, Pathak *et al.* 2012). In a soil bioassay with *A. oligospora*, *M. eudermatum*, *G. paucispora*, *M. cionopagum* and *N. concurrens* reduced penetration of *H. marelatus* (hepialus) into wax moth larvae by up to 54%. The saprophytic fungi, *Fusarium oxysporum* may affect *H. sonorensis* in host searching ability, virulence and reproductive fitness (Navarro *et al.* 2014). There was a repellent action from *Arthrobotrys* sp. CO₇ against *S. carpocapsae* All (Aredesa *et al.* 2017). El-Borai *et al.* (2011) indicated that the tested nematodes were repelled by activated *Arthrobotrys* species but were attracted to endoparasitic fungi *Myzocyttium* sp. and *Catenaria* sp. Due to the ubiquitous distributions of these nematophagous fungi in natural environments and agricultural fields, their interactions with entomopathogenic nematodes have significant ecological and economic significance in pest management program.

Immune responses of entomopathogenic nematodes against nematophagous fungi

EPN species have different types of morphological and behavioral defense responses against nematophagous fungi. Many aspects of EPN behavior that contribute to predation rates by nematophagous fungi, such as search behavior (Jagodic *et al.* 2019), tendency to migrate from the insect cadaver, could serve to protect EPN in nature. Nematode behavior such as low motility and resistance to fungal adhesion may reduce infection of dauers from some parasitic fungi. Many nematophagous fungi rely on motile nematodes encountering their trapping structures or adhesive conidia for parasitism to occur. Highly motile nematodes will encounter more *H. rhossiliensis* and *Drechmeria coniospora* conidia. *S. carpocapsae* exhibits a sit and wait strategy for host location and may be adapted to habitats containing motile hosts or profuse nematode antagonists. In contrast, *S. glaseri* and *H. bacteriophora* actively search for hosts and may be adapted to habitats containing sedentary hosts or few antagonists. *S. feltiae* is less motile in the absence of a host than *H. spp.* or *S. glaseri*; it would be less likely to encounter nematophagous fungi.

But, these same nematode species were susceptible to infection by the trapping fungi *M. ellipsosporum* and *A. oligospora*. *H. rhossiliensis* will reduce the efficacy of entomogenous nematodes in sandy loam soil; the degree of reduction will depend on how far dauers move before locating a host that are less likely to encounter antagonists. The epidermis and the collagen-rich cuticle that surrounds the nematode provide a physical or morphological barrier to fungal pathogens. Entomopathogenic nematodes that retain their J2 cuticle, exhibit low motility and are refractory to fungal adhesion by *H. rhossiliensis*. The conidia of *Drechmeria coniospora* adhered to and infected the developing stages of *S. feltiae* and *Rhabditis* sp., but rarely adhered to and never infected dauers of *S. feltiae*, *S. bibionis*, *S. glaseri*, *S. intermedia* and *H. heliothidis*. IJs of the genus *Heterorhabditis*, which retain the cuticle of their previous stage as a sheath enable *Heterorhabditis* to defend from cuticular penetration by spores of some endoparasitic nematophagous fungi (*H. rhossiliensis*). However El-Borai *et al.* (2009) showed that *H. zealandica* was highly susceptible to these endoparasites. The J₂ cuticle may also function in reducing water loss during desiccation.

Nematode can also sense and defend against the microbial pathogens using strategies such as producing anti-microbial peptides (AMP)-coding genes regulated by the innate immunity system. Many AMPs act by disrupting microbial cell membranes (Meerupati *et al.* 2013).

CONCLUSION

Modern molecular methods (e.g., metagenomic methods, sequencing of the genomes) are able to detect nematophagous fungi in samples of nematodes or bulk soil (Campos-Herrera *et al.* 2016, Pathak *et al.* 2012) and have shown spatial associations between EPNs and nematophagous fungi under field condition (Jaffuel *et al.* 2016, Pathak *et al.* 2017). In those studies natural susceptibility of different EPN to predation by nematophagous fungi can be detected by measuring growth of nematophagous fungi on different EPN species. Meerupati *et al.* (2013) have contributed the metagenomic methods for understanding of the evolutionarily distinct strategies of fungal pathogenesis as well as habitat dynamics

of *A. oligospora*, *Monacrosporium haptotylum*, *Drechlerella stenobrocha*, *H. minnesotensis* against nematodes.

Long-term applications of composted animal manure mulches increase availability of insect prey and also decrease the prevalence of some nematophagous fungi which might be useful to increase EPN efficacy in pest management programs. Higher EPN infection of the citrus root weevil (*Diaprepes abbreviatus*) in soils treated with animal manure where prevalence of population density of nematophagous fungi was less. By understanding interactions in their habitat involving all partners in terrestrial and agricultural ecosystems, use of these nematodes in inundative or augmentative biological control programme can be enhanced (Abate *et al.* 2017, Yang *et al.* 2020). Entomopathogenic nematodes species or strains adapted to the habitat where they will be introduced for pest control should be of first preference.

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