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NEMATODE-DESTROYING FUNGI: INFECTION STRUCTURES, INTERACTION MECHANISMS AND BIOCONTROL

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ABSTRACT. Fungi are pathogenic for different nematode groups, but their relationship with soil nematodes goes a grade beyond parasitism and into predation. Approximately, 200 species of taxonomically various fungi can attack active nematodes, which are effective animals nearly 0.1 to 1.0 mm long. Among these nematode-destroying fungi, only a few species are obligate parasites of nematodes; the majority are facultative saprotrophs. Nematode-destroying fungi have four general groups: (a) fungi with specialized structures (b) fungi with toxins; (c) fungi with spore germination; (d) fungi with colony-forming. Nematode-destroying fungi are natural enemies of nematodes in soil ecosystems and have potential as biocontrol agents against plant- and animal-parasitic nematodes. These predator fungi catches free-living nematodes in the soil ecosystem using traps produced by the fungal mycelium that cling to the worm, then, penetrate, kill, and digest the tissue of the nematode. Five kinds of trapping apparatus belonging to fungi are defined. These are adhesive or sticky column, adhesive or sticky knob, adhesive or sticky system, constricting and non-constricting rings.

1. INTRODUCTION

Nematode-destroying or hunting fungi are inherent enemies of nematodes called as roundworms. Nematode-destroying fungi can infect the eggs, larvae, or adult stages of the nematode. They reduce the population density by stopping the feeding activity of the nematode. These fungi contain more than 200 taxonomically distinct group types that can be classified as nematode-destroying or nematophagous fungi and endophytic fungi. The fungi that destroy the nematode are also divided into egg- and female-parasitic fungi invading nematode eggs or females with their hyphal ends, endo-parasitic fungi using their spores and toxin-producing fungi immobilizing nematodes before the invasion [1-4]. The taxonomy of nematophagous fungi, as well as their mode of action, is briefly shown in Table 1.

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Nematode oppositional fungi have so far received a lot of attention, partly because of their high negative activity against both plant- and animal-parasitic nematodes, and their remarkable morphological adaptations in hunting and parasitizing nematodes [5, 6].

Studies on fungi that trap and hunt nematodes are considerably higher than studies with other organisms. Fungi forming traps are capable of catching nematodes by creating traps in various ways [7-10].

According to another classification, nematode-destroying fungi contain three main groups of fungi: nematode capture and endo-parasitic fungi that attack vermiform viable nematodes using special structures, and egg- and cyst-parasitic fungi that attack these stages with their hyphal ends [11-14]. The continuing interest in these fungi is partly due to their potential as biocontrol agents against plant- and animal-parasitic nematodes. Egg- and cyst-parasitic fungi have been thoroughly researched for their promise as biocontrol agents. Another reason for continued shooting in nematode-destroying fungi is remarkable morphological conformations and theatrical capture of nematodes by both nematode capture and endo-parasitic fungi [15-17]. In addition, both fungi and nematodes can be grown quite easily in the laboratory and provide a perfect model system for interaction studies [18-20].

In general, fungi that hunter fungi can be divided into two groups. They are good saprophytes, fast growing, sticky or adhesive hyphae network and more predators, catching nematodes by forming sticky knobs, constricting arms or sticky rings [21-22].

Nematode capture and endo-parasitic fungi are found in all major taxonomic fungal groups and are found mainly in any soil environment in which they survive as saprophytes [23, 24]. The ability to use nematodes as an additional source of nutrients gives them a dietary advantage. When fungi change their morphology, they enter parasitic stages and traps or mature spores are formed. The development of infectious structures is a pre-requisite for capturing nematodes. The mechanisms behind this development and the mechanisms behind the capture process, including the attraction, adhesion, penetration and digestion of nematodes, are the main themes of this article [25-27].

TABLE 1. Species of some nematode-destroying fungi and their trapping appatarus.

Nematode-destroying fungi	Classification	Trapping apparatus
Arthrobotrys brochopaga	Orbiliomycetes	Constricting rings
A.conoides	Orbiliomycetes	Adhesive networks
A.dactyloides	Orbiliomycetes	Constricting rings
A.haptotyla	Orbiliomycetes	Adhesive knobs
A.irregularis	Orbiliomycetes	Adhesive networks
A.microscaphoides	Orbiliomycetes	Adhesive networks
A.musiformis	Orbiliomycetes	Adhesive networks
A.oligospora	Orbiliomycetes	Adhesive networks
A.robusta	Orbiliomycetes	Adhesive networks
A.shizishanna	Orbiliomycetes	Adhesine networks
A.superba	Orbiliomycetes	Adhesive networks
A.thaumasia	Orbiliomycetes	Adhesive networks
Cystopage cladospora	Zygomycetes	Adhesive hyphae
Dactylaria candida	Orbiliomycetes	Adhesive knobs, non-constricting rings
D. eutermata	Orbiliomycetes	Adhesive networks
Dactylella bembicodes	Orbiliomycetes	Constricting rings
D. ellipsospora	Orbiliomycetes	Adhesive knobs
D. lobata	Orbiliomycetes	Adhesive hyphae
D. zhongdianensis	Orbiliomycetes	Adhesive networks
Dactylellina haptotyla	Orbiliomycetes	Adhesive knobs
D. sichuanensis	Orbiliomycetes	Adhesive knobs, non-constricting rings
D. varietas	Orbiliomycetes	Adhesive knobs, non-constricting rings
Drechslerella anchonia	Orbiliomycetes	Constricting rings
D. brochopaga	Orbiliomycetes	Constricting rings
D. dactyloides	Orbiliomycetes	Constricting rings
Duddingtonia flagrans	Orbiliomycetes	Adhesive networks
Geniculifera perpasta	Orbiliomycetes	Adhesive networks
Helicocephalum oligosporum	Zygomycetes	Adhesive hyphae
Monacrosporium bembicodes	Orbiliomycetes	Constricting rings
M. cionopagum	Orbiliomycetes	Adhesive networks
M. elegans	Orbiliomycetes	Adhesive networks
M. ellipsosporum	Orbiliomycetes	Adhesive knobs
M. eudermatum	Orbiliomycetes	Adhesive networks
M. gephyropagum	Orbiliomycetes	Adhesive branches
M. haptotylum	Orbiliomycetes	Adhesive knobs
M. megalosporum	Orbiliomycetes	Adhesive networks
M. psychrophilum	Orbiliomycetes	Adhesive networks
Peniophorella praetermissum	Basidiomycetes	Adhesive hyphae
Stropharia rugosoannulata	Basidiomycetes	Adhesive hyphae
Stylopage hadra	Zygomycetes	Adhesive hyphae
S. leiohypha	Zygomycetes	Adhesive hyphae

2. Characteristics of Nematode-Destroying Fungi

Nematode-destroying fungi infect the nematodes' eggs, juveniles, and adults and use them as foods. The fungi differ in their saprophytic-parasitic ability. While many of the trap-forming and egg-parasitic fungi can alive in soil ecosystem, the endo-parasites are mostly more dependent on nematodes as a nutrient that is called obligate parasites [28-32].

The ability to capture nematodes is linked to a certain developmental stage of the fungal mycelium. The trapping (predatory) fungi have developed advanced hyphal structures such as hyphal nets, rings, branches, or knobs, in which nematodes adhere or are mechanically captured (Figure 1). The different methods used by this type of nematode-destroying fungi to catch prey are also photographed in laboratory studies and presented in a guidebook [33]. Endo-parasites attack nematodes by their spores that adhere or assimilate to the surface of the nematodes. Regardless of the method of infection, the results are always the same: the death of the nematode. Examples of the first group are *Arthrobotrys* species, such as *A. oligospora, A. connoides, A. musiformis,* and *A. superba,* all of which form three-dimensional adhesive networks, and mechanical expansion of ring cells with nematodes, *A. dactyloides* [34, 35]. Sticky branches or arms and sticky buttons or knobs appear in the genus *Monacrosporium*. *M. haptotylum* (*Dactylaria candida*) produces both sticky knobs and non-shrinkable or constricting rings.

Among the endo-parasites, *Drechmeria coniospora, Hirsutella rhossoliensis, Haptoglossa dickii* and *Catenaria anguillulae* infect nematodes with their spores and engage their herbal lives in infected nematodes [36-37]. The *Nematoctonus* genus captures nematodes with both sticky traps and sticky spores, thereby forming a link between the two groups. Another mechanism for capturing nematodes is evident in wood-decomposed oyster mushroom *Pleurotus ostreatus*. Oyster mushrooms immobilize the nematode host with a toxin produced in special hyphal stems, and the hyphal ends grow chemo-tropically through the mouth of their victims and digest the content [38-39]. Egg parasite fungi, *Pochonia chlamydosporia* (*Verticillium chlamydosporium*) use appressoria to penetrate the nematode eggshells. Several stages of all these fungi have been described in a movie showing different strategies used by fungi [40-43].

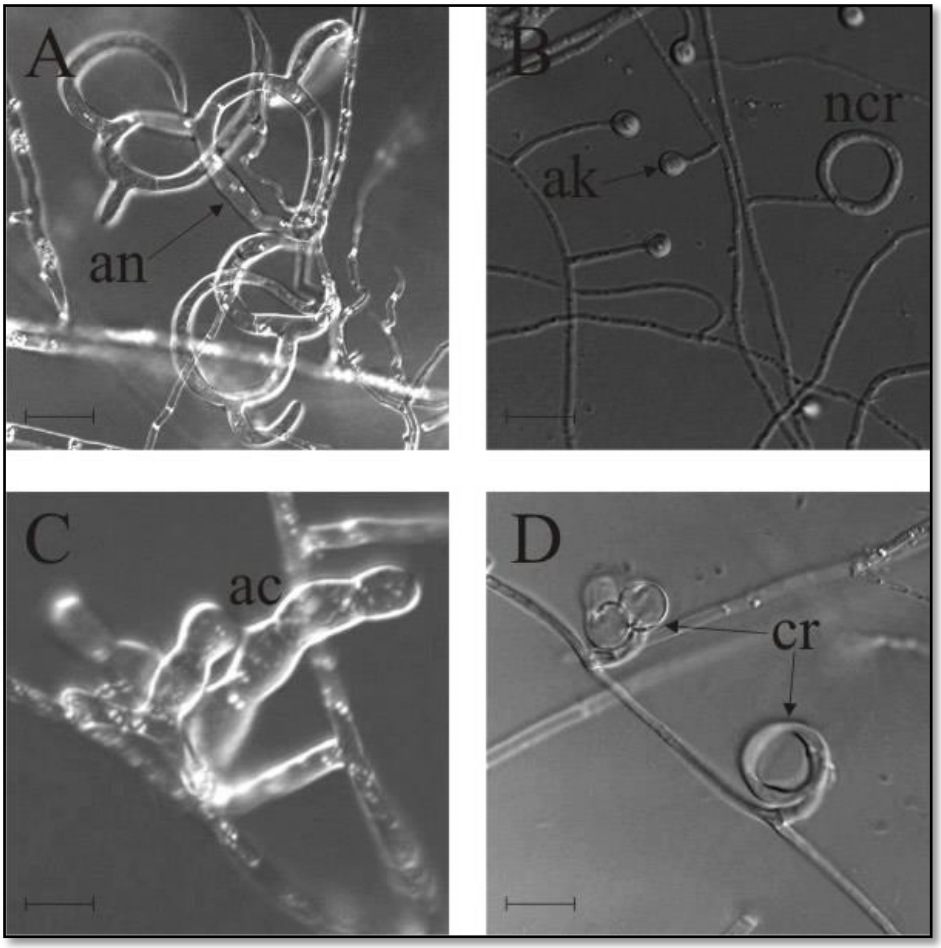

FIGURE 1. Natural nematode-trapping or capture apparatus. **A.** Adhesive network (**an**), **B**. Adhesive knob (**ak**) with non-constricting or non-compression rings (**ncr**), **C.** Adhesive column (**ac**), **D.** Constricting or compression ring (**cr**). Scale bars = 10 μm.

3. INFECTION STRUCTURES OF FUNGI

Nematode-destroying fungi show a large variety not only in terms of taxonomic distribution but also in the thrust structures formed (Table 2). The type of nematode capture structures formed depends on the species and even the strain of the species

as well as both biotic and abiotic environmental conditions. The most crucial biotic factor is living nematodes that not only stimulate the creation of trap structures by touching mycelium, but also act as a food source for the fungi after being invaded by fungi [44]. Thus, the relationship with the nematodes is two-fold: first, the nematodes can then induce the creation of the structures from which they were captured; and secondly, they serve as an extra nutrient source after the nematodes are invaded by the fungus [45-47].

For example, *Arthrobotrys* spp. it is generally more saprophytic than endo-parasites [48]. *Arthrobotrys* spp. They do not automatically create traps, but the fungi depend on environmental conditions, especially the presence of nematodes for the induction of traps. Trap structures of other fungi, such as branches, knobs, and collapsing rings, can be created automatically, indicating that these fungi need more nematodes as a food source [49].

Endo-parasites and spontaneous trap builders exhibit a large parasitic ability, while more saprophytic trap builders such as *Arthrobotrys* spp. has a unique ability to change their morphology to increase their parasitic abilities [23, 24]. As noted above, outer stimuli, such as nematodes, cause the formation of sticky traps in all trap-forming fungi. In *A. oligospora*, small peptides with highly non-polar and aromatic amino acids, or their low nutritional value, and amino acid components stimulate trap creation in both solid and liquid media. Based on this information, a growth technique has been developed in which the fungus can be studied both in its saprophytic and parasitic stages [9, 10, 38].

Most *Arthrobotrys* spp. are defined by an adhesive net trap. This trap can consist of a single ring or a fully developed three-dimensional network. Under some conditions, for example, *A. superba* may not develop full networks, but it can capture nematodes by sticky branches [7, 8]. Sticky branches form automatically in *Monacrosporium gephyropagum* regularly. Sometimes, such branches can merge to form simple rings. Sticky knobs are formed on the sensitive handle in the *M. haptotylum* mycelium. This species also procreates rings that do not contract on the sensitive stem. Both knobs and rings can be separated from the underlying mycelium and carried by nematodes [39].

TABLE 2. Species of some endoparasitic fungi and their mode of infection.

Endoparasitic fungi	Classification	Mode of infection
Catenaria anguillulae	Chytridiomycetes	Zoospores
C. vermiformis	Chytridiomycetes	Zoospores
Chlamydomyzium anomalum	Oomycetes	Zoospores
C. sphaericum	Oomycetes	Zoospores
Drechmeria coniospora	Deuteromycetes	Adhesive conidia
Haptocillium bactrosporum	Sordariomycetes	Adhesive conidia
H. balanoides	Sordariomycetes	Adhesive conidia
H. obovatum	Sordariomycetes	Adhesive conidia
Haptoglossa dickii	Oomycetes	'Gun cells', injection
H. erumpens	Oomycetes	'Gun cells', injection
H. heteromorpha	Oomycetes	'Gun cells', injection
H. mirabilis	Oomycetes	'Gun cells', injection
H. zoospora	Oomycetes	'Gun cells', injection
Harposporium anguillulae	Deuteromycetes	Ingested spores
H. bysmatosporum	Deuteromycetes	Ingested spores
H. leptospira	Deuteromycetes	Ingested spores
Hirsutella rhossiliensis	Deuteromycetes	Adhesive spores
Gonimochaete horridula	Oomycetes	Adhesive spores
G. latitubus	Oomycetes	Adhesive spores
G. lignicola	Oomycetes	Adhesive spores
G. pyriforme	Oomycetes	Adhesive spores
Meria coniospora	Deuteromycetes	Adhesive conidia
Meristacrum asterospermum	Zygomycetes	Adhesive conidia
Myzocytiopsis glutinospora	Oomycetes	Zoospores
M. humicola	Oomycetes	Zoospores
M. intermedia	Oomycetes	Zoospores
M. lenticularis	Oomycetes	Zoospores
M. papillata	Oomycetes	Zoospores
M. zoophthora	Oomycetes	Zoospores
Nematoctonus concurrens	Basidiomycetes	Adhesive hour-glass knobs, Adhesive spores
N. leiosporus	Basidiomycetes	Adhesive hour-glass knobs, Adhesive spores
Olpidium vermicola	Chytridiomycetes	Zoospores
Pythium (Lagenidium) caudatum	Oomycetes	Zoospores
Spirogyromyces vermicola	Unknown	Ingested spores
Verticillium balanoides	Deuteromycetes	Adhesive spores

Some groups of fungi form an adhesive network. These crotch-shaped loops are wound around the nematode body. The hyphae loops formed by the fungus hold the host and wrap the entire body of the nematode with a sticky substance. The body of the nematode is pierced through the parts where the hyphae loop is contacted (eg. *Arthrobotrys dactyloides* and *A. digospoa*). In addition, this group of fungi has the ability to enter the plant tissue. It is also known that they penetrate and kill *Ditylenchus dipsaci*, which develops in plant tissue.

Sticky knobs formed by fungi are small spheres or lobes and consist of 1-2 cells. *Stylopage harda*, *Doctylella lobata* and *D. cionopaga* are examples of fungi forming sticky knobs.

It may be less effective than fully developed traps in capturing nematodes. Some species (e.g. *A. superba*) may capture nematodes on initials or branches of adhesive nets, or even on adhesive hyphae, as in *Stylopage* and *Cystopage* spp. This growth pattern occurs in almost all trap-forming species when conidia are allowed to germinate in natural substrates such as cow manure or rhizosphere soil [50]. A mutant of *A. oligospora* does not only form conidial traps on the conidia when it is in upright conidiophores; it also produces large amounts of normal traps in mycelium. These examples may show an increased efficiency of these fungi to reduce the number of nematodes in the environment. Another morphological adaptation of the *A. oligospora* mycelium is the response to the presence of other fungi. *A. oligospora* can roam around hyphae and consume the contents of these cells called as mycoparasitism [27, 48, 49].

In addition, *A. oligospora* can create appressoria in response to plant roots. The winding of both the rhizosphere and the hyphae and appressoria are examples of the diversity of the ways nematode-catching fungi cope with changing environmental conditions. All these adaptations show the plasticity of the infection structures in nematode trapping fungi [27].

Endo-parasitic fungi are obligate parasites of nematodes that spend their entire vegetative life in the nematode they infect. Nematodes may encounter spores such as conidia or zoospores as they pass through soil pores. Spores infect the nematode in two ways: (a) orally, that is, when the spores are swallowed with food by the nematodes; or (b) percutaneous, i.e. spores adhere to the cuticle of the nematodes. In this case, zoospores float toward the nematode and are thrown around natural holes such as the mouth, anus, or vulva. There is a similar variety among endo-parasites.

D. coniospora creates a large number of conidia compared to hyphal material production. In a single contaminated nematode, *D. coniospora* can procreates as much as 10,000 conidia, while the single endo-parasite *H. rhossoliensis*, which does sports alone, procreates 100-1000 conidia per contaminated nematode. Both fungi develop a sticky bud in their conidia where they infect the nematode [51-53]. The genus *Harposporium* contains fungi that procreates spores of unusual forms that are ingested by nematodes. Due to their shape, spores get stuck in the oesophagus and from there they start a contamination of the nematodes. *C. anguillulae* contaminates nematodes with mobile zoospores that are thrown and moved over the nematode. Finally, spores in the genus *Haptoglossa* form a contamination "gun cell" that forcefully injects the infective principle into the nematode host [54, 55].

The fungi that parasitize the non-motile stages of nematodes, i.e. eggs use a different tactic. Hyphae of *P. chlamydospora* and other fungi grow towards the eggs, and appressoria occurs on hyphae ends that penetrate the eggshell. Fungi then digest the egg content of both immature and mature (containing juveniles) eggs [56]. Egg-parasitic fungi are those that use appressoria or zoospores to infect the eggs of plant-parasitic nematodes [57-60]. This group of fungi can survive saprotrophically in the rhizosphere and is relatively easy for mass culture [4].

An additional advantage of their potential is that their hosts are often stalk-free in the form of eggs, developing juveniles, and sedentary females (Table 3).

TABLE 3. Species of some nematode egg-and female-parasitic fungi and their infection mechanisms.

Nematode-destroying Fungi	**Classification**	**Mode of infection**
Dactylella ovaparasitica	Orbiliomycetes	Appressoria
Helicocephalum oligosporum	Zygomycetes	Adhesive hyphae
Lecanicillium psalliotae	Deuteromycetes	Appressoria
Nematophthora gynophila	Oomycetes	Zoospores
Olpidium vermicola	Chytridiomycetes	Zoospores
Paecilomyces lilacinus	Deuteromycetes	Appressoria
Pochonia chlamydosporia	Deuteromycetes	Appressoria
P. rubescens	Deuteromycetes	Appressoria
Rhopalomyces elegans	Zygomycetes	Appressoria

4. Interaction mechanisms

Nematodes are attracted by mycelium compounds and nematode trapping fungal traps and spores of endo-parasites. Both morphology and consequently saprophytic parasitic ability strongly affects the fascination of fungi [70, 71]. More parasitic fungi appear to have a stronger charm than more saprophytic ones; that is, endo-parasitic species infecting conidia and nematodes are more effective in fascinating nematodes than more saprophytic species with different trapping apparatus [72, 73].

The contact and adhesion of nematodes to the traps and spores of fungi that destroyed the nematode can be seen in the electron microscope. In *A. oligospora*, three-dimensional networks are surrounded by an extracellular fibril sheet. After contact, these fibrils are directed perpendicular to the surface of the host, possibly to simplify anchorage of the nematode and further fungal infestation [74, 75]. Endo-parasite *D. coniospora* shows a completely different type of adhesive, as if it consisted of spreading fibrils, regardless of whether contact with the nematode was established. In addition, *D. coniospora* spores adhere properly to the sensory organs at the tip of the nematode head, thereby preventing nematode charm. The chemical combination of surface fibrils of nematode-destroying fungi is not known in detail, but they contain both proteins and carbohydrate-containing polymers [76-78].

The adhesion of the traps in the nematode causes the fungi to differentiate. In *A. oligospora*, a penetration tube forms and pierces the nematode cuticle. This step probably includes both the activity of the hydrolytic enzymes that dissolve the macromolecules of the cuticle, and the activity of a mechanical pressure produced by the penetrating growing fungus. The nematode cuticle mainly consists of proteins, including collagen, and several proteases are isolated from nematode-destroying fungi that can hydrolyse the proteins of the cuticle. In any case, these proteases belong to the serine protease family and have been shown to have high homology to subtilisin-type serine proteins after obtaining data from sequencing [79, 80]. In endo-parasite *D. coniospora*, it appears that a chymoptrypsin-like protease is involved in the penetration process.

More detailed studies of subtilisin PII produced by *A. oligospora* have shown that such proteases may have a number of different functions [81]. Therefore, PII appears to have a nematotoxic activity, as well as being involved in the penetration and digestion of the cuticle and tissues of infected nematodes.

After penetration, the nematode is digested by the infected fungus. After entering the nematode, the penetration tube of *A. oligospora* is disintegrated to form a large bulb of infection. The development of bulbs and trophic hyphae occurs in parallel with dramatic changes in the infrastructure and physiology of the fungus. Dense objects are reduced in trap cells and ampoules. The bulb and trophic hyphae typically contain typical cell organelles, the endoplasmatic reticulum is mainly well developed. In the later stages, lipid droplets accumulate in trophic hyphae, possibly involved in the assimilation and storage of nutrients from the infected nematode [58, 64, 65].

Unlike trap-forming fungi, endo-parasite *D. coniospora* does not form an infection bulb upon penetration and does not have dense stems typical for trap-forming fungi. With the formation of lipid droplets, another way for *A. oligospora* to store host-derived nutrients is to produce a large amount of lectin in the cytoplasm [82]. This protein is *Arthrobotrys oligospora* lectin, AOL. Until recently, it is a member of the low molecular weight lectin family that shares similar primary sequences and binding properties that have been identified in only a few filamentous fungi [83, 84]. During infection of nematodes, AOL is rapidly synthesized in *A. oligospora* after the nematodes penetrate and digestion begins. Large amounts of AOL accumulate in trophic hyphae growing in the nematode. Lectin is then transported from the infected nematode to other parts of the mycelium, where it can break down and promote the growth of the fungus. It has been suggested that AOL, like other lectins, is involved in a recognition event during interaction with nematodes. Binding of the AOL lectin family to sugar structures specific to animal glycoproteins, including nematodes, but not found in fungi, supports this hypothesis.

Although the nematode infection patterns of other predatory fungi that use adhesive layers to capture nematodes (nets, hyphae or knobs) have been less studied, they often seem to be similar to those described for *A. oligospora*. In contrast, the catch mechanism of contraction rings is completely different. When a nematode moves into the ring, the three cells that form the ring trigger a response so that it swells inward quickly and closes around the nematode. Other stimuli can also trigger trap closure, such as touching a needle or heat. The reaction is rapid (0.1 s), irreversible, and is consorted by a large increase in cell volume, leading to the almost complete closure of the trap's opening [85]. Following capture, the fungus produces a diffusion tube that pierces the nematode cuticle. A small bulb of infection is formed inside the nematode, in which trophic hyphae develop.

The traps created by these fungi can be either sticky traps or sticky arms, sticky network, sticky knobs. Sticky arms are short lateral arms that are several cells long. They form a loop and attack the nematode. But they are never in the form of a mixed network. During the random movement of the nematode, these sticky arms come into contact with the nematode and catch it.

Dactylella ellipsospora's sticky hyphae loops adhere to the nematode, making the nematode completely immobile within two hours. Then the fungus hyphae penetrates into the nematode cuticle and develops and spreads inside the nematode body. After all, it absorbs the body fluid of the nematode, killing the nematode.

Non-suffocating rings formed by some group of fungi are only responsible for capturing the nematode. After the nematode is caught, the fungal hyphae grow rapidly, penetrating the nematode cuticle and absorb body fluid. *Dactylella doedyeoides* can be given as an example to this group of fungi.

The cells of the *Nematoctonus haptocladus* first secrete, the nematode that enters this secretion is caught by the fungus with short and sticky hyphae arms, and then the nematode is penetrated and killed.

The mechanism by which the compression rings are closed is not known in elaboration. Electron microscopy showed that during the ring cell enlargement, the outer cell wall of the ring cells was torn along a defined line on the inner surface of the ring. It has been suggested that this release of wall compression will lead to rapid water uptake and subsequently the enlargement of the flexible inner wall of the ring cells. The signal transduction track involved in bloating ring cells has been studied in *A. dactyloides*. In this fungus, the pressure exerted by a nematode on the ring appears to activate the G-proteins in the ring cells. Activation leads to increased calmodulin in cytoplasmic Ca^{2+} activation and finally opening of water canals. Ring cells tighten to narrow the ring, thereby fixing the nematode [86].

5. BIOCONTROL

Biocontrol or biological control is considered an alternative to chemicals, as it is not only an environmentally friendly measure but can also support sustainability in agricultural production [87-89]. Demonstrating that selected biocontrol agents can provide adequate control levels for political non-chemical disease management programs, along with political pressures, contributed to a change in attitudes towards biological control research [90-92]. Many organisms have shown antagonistic effect

against phytonematodes [93-95], and fungi among them are considered the most important group [4, 96-98]. These organisms often did not provide consistent or adequate control. However, the best results for biocontrol of soil microorganisms can be achieved when short-term conservation will result in significant yield benefits and where natural application of target areas is possible [99].

Many fungal plants from different taxonomic categories can adversely affect plant-parasitic nematodes [4], but having aggressiveness is not the only feature required to become a qualified biocontrol agent.

An important feature of nematophagous fungi is the possibility of using them for biological or biological control of plant- and animal-parasitic nematodes. Plant-parasitic nematodes, e.g. root-knot (*Meloidogyne* spp.) and cyst (*Heterodera* spp., *Globodera* spp.) nematodes are global pests that cause serious yield losses in agriculture and horticulture [100-104]. Many nematicides, such as methyl bromide, are prohibited due to health and environmental concerns. Therefore, new alternates are needed for nematode control. Biocontrol can be such an alternating [105-108].
There are two general ways to implement the biocontrol of nematodes using fungi that destroy nematodes: adding large amounts of fungus to the soil; or stimulating the activity of existing fungi using various changes. Initial experiments for plant-parasitic nematodes include nematode-trapping fungi, e.g. *Arthrobotrys* or *Monacrosporium* species and later endo-parasitic fungi, e.g. *H. rhossoliensis* and *D. coniospora* and egg-parasitic fungi, e.g. *P. chlamydosporia*. The performances of these biocontrol agents have been varied and so far no commercial products are available [60, 67].

The hyphae arms of the fungi forming stifling rings form a ring by bending backwards on it. These rings are 3-4 cells and the middle of the ring is empty. When the nematode enters the ring, it stimulates the ring cells as a result of the contact effect. The cell wall permeability of the stimulated cells increases and the cells reach 3 times the size by taking a lot of water from the environment. As a result, the ring space is narrowed and the nematode in the space is choked and their bodies are divided into two. *Monacrosporium lysipagum* is a good example of this group of fungi [67].

The use of nematode trapping fungi is of particular interest due to the increased knowledge of the biology of these fungi and partly because of the better formulation and application of fungal biocontrol agents to the soil. One way to improve the

control potential of nematode-destroying fungi would be to use genetic engineering to increase the pathogenicity and survival of the introduced fungus. Using genetic transmutation, it was possible to produce nematode-trapping fungi *A. oligospora* mutants that overexpress a protease gene (P II). Mutants containing additional copies of the P II gene developed a higher number of infectious structures and increased rates of catching and killing nematodes [81]. Also, it has recently been reported that the formulation of fungal *A. dactyloides* capturing nematodes can reduce tomato infection with knot-root nematodes in field experiments. In the same experiment, a similar decrease was not shown with egg parasite *P. chlamydosporia*. An important problem of adding nematode destructors and other biocontrol fungi to the soil is their low ability to form in a complex soil environment. Bourne et al. [109] it is of great importance that rhizosphere colonization is necessary for an accomplished enterprise, and therefore scanning the rhizosphere-authorized strains of nematode-destructive fungi [110, 111].

The interaction between nematode-hunting fungi and plant parasitic nematodes is complex. The activity of these fungi can be affected by soil pH, humidity, temperature and nutrients in the soil. On the other hand, their uncertainty in the invasion, their slow development, and their need for enormous amounts of food, sometimes very specific, hamper their success in being candidates for commercial production [42, 92].

Animal-parasitic nematodes cause disease and serious weight decrease in animal husbandry all over the world. The chemicals currently used to control these nematodes, anthelmintics have been shown to develop resistance in the parasitic nematode fauna. A promising approach has been presented in the feeding of grazing animals with fungal mycelium containing chlamydospores of nematode-trapping fungi; *Duddingtonia flagrans*. By allowing spores to be transported through the animal intestines and producing and producing traps in faeces and surrounding grass, it captures newly hatched offspring of parasites and reduces the nematode burden in the fields [112, 113]. The population structure of fungi that destroy nematodes is mostly unknown. This information is important to assess the fate and risk of undesirable spread of an applied biocontrol agent. Recently, the genetic variation in a worldwide collection of nematode-trapping fungus *D. flagrans* has been shown to be very low using various genetic markers [114]. The data show that *D. flagrans* is essentially clonal and recombination cannot be detected even within the same country. Therefore, recombination of the mass-applied *D. flagrans* strain with local isolates is unlikely.

Although not considered to be conventional biocontrol, another promising approach that nematode-destroying fungi as well as other soil fungi can be used to develop new tools to control animal- and plant-parasitic nematodes is to use the antagonist as a source for insulating new combinations with nematicidal efficiency [115-118]. According to the information I got from a nematologist, *Arthrobotrys irregularis*, one of the nematode predators, was produced commercially in France and launched as a preparation under the name of Royal 350. However, the fact that this fungus cannot grow below pH 6.5 limits the use of large areas in order to be successful, such as the necessity to use high doses and storage difficulties. Against *Ditylenchus myceliophagus*, a breed of *A. robusta* was produced and a commercial preparation named Royal 300 was obtained [18, 92].

6. Conclusions

Given the environmental safety, human health hazards and management costs, the fungal biocontrol agent is the best option, much safer and highly applicable. However, biocontrol of phytonematodes or plant-parasitic nematodes through nematode-destroying fungi provides irregular results, especially in field conditions, especially since the soil ecosystem is very complex.

Extensive research of fungi that have destroyed nematodes in the past decade has been carried out in many countries worldwide. However, most of these fungi have not yet been discovered. In addition, much research is needed on the identification of discoveries and their exploitation against economically important phytonematodes [119]. In recent years, scientists have succeeded in commercially exploiting several biocontrol agents such as *P. lilacinus*, *P. chlamydosporia, T. harzianum, A. niger* and *A. oligospora* against phytonematodes, but in all respects it was not promising [42, 92]. If one fungal biocontrol agent is successful in controlling one group of nematodes, the problem of the other group remains unresolved. It has been widely observed that if two or more species of phytonematodes are fed on a plant host, the fungal effect can only limit or control the population of one species.

Therefore, the problem of other mobile nematodes will remain unchanged. In addition, isolates of fungal biocontrol agents differ greatly in virulence and ability when installed in the soil, and therefore their results under field conditions are very uneven. On the other hand, another disadvantage is the presence of antagonists of these fungi in the soil, which, when applied in the field, often fails fungal biocontrol agents.

As a result, the use of fungal biocontrol agents is environmentally safe and the correct approach in the management of phytonematodes, but it is difficult to say that they replace nematicides. Fungi that destroy nematodes may not control the nematodes when the latter's inoculum level is too high in the soil, but the population of the nematode can be reduced to ultimately reduce crop yield loss. According to the researchers, the fungal biocontrol agent, combined with herbal and pesticides, seems to be one of the best options, as the seed treatment can prove to be economical, much safer and highly viable in field conditions.

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