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REVIEW

Xingzhong Liu · Meichun Xiang · Yongsheng Che

The living strategy of nematophagous fungi

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Abstract The infection structures, trophism, and ecological character of nematophagous fungi are reviewed in this article on the basis of data extracted from the literature and the most recent experiments conducted in this area. Traditionally, nematophagous fungi are classified into four groups according to their modes of attacking nematodes: nematode-trapping fungi using adhesive or mechanical hyphal traps, endoparasitic fungi using their spores, egg-parasitic fungi invading nematode eggs or females with their hyphal tips, and toxin-producing fungi immobilizing nematodes before invasion. In the present review, we focus on the first two groups. The living strategies of these nematophagous fungi depend on the diversity of their infection structures, such as different traps and spore types, which determine the modes of infecting nematodes. The diversity of trophic modes of nematophagous fungi is an important prerequisite for fungal survival and activity in soil. The abundance and activity of *Hirsutella rhossiliensis* and *H. minnesotensis*, representatives of endoparasites and potential biocontrol agents against nematodes, are highly dependent on environmental factors. Comprehensive understanding of the survival and activity of nematophagous fungi in soil is fundamental for the exploitation of these fungi as successful biocontrol agents.

Key words Diversity · *Hirsutella* spp. · Infection structures · Nematophagous fungi · Trophism

Introduction

Nematophagous fungi are carnivorous fungal species that use their spores or mycelial structures to capture vermiform nematodes, or use their hyphal tips to parasitize the eggs and cysts of nematodes (Nordbring-Hertz 2004), or produce toxins to attack nematodes (Li et al. 2000). They are the natural enemies of nematodes and have developed very sophisticated strategies to either infect or capture these small animals. Nematophagous fungi are a diverse group of microorganisms, and their nematophagous habit is generally considered to have evolved independently in different fungal classes. Traditionally, they are classified into two groups, the nematode-trapping fungi (or predatory) and the endoparasites, based on their parasitic modes on nematodes (Barron 1977; Gray 1987). Species belonging to the predatory group produce an extensive hyphal system, and the trapping devices are formed along the hyphae to catch and hold live nematodes. The captured victim is then penetrated, with its entire body contents being consumed rapidly (Barron 1977). The endoparasites do not produce extensive mycelia but exist as conidia in the environment and infect nematodes by either adhering to the surface of the prey or direct ingesting. The conidia germinate rapidly and invade the entire nematode with assimilative hyphae absorbing all the body contents (Gray 1987). As the third group, egg- or female parasites are facultative fungi that are common soil saprophytes and are opportunistic isolates obtained from the sedentary stages (female and egg stages) of sedentary nematodes, such as *Heterodera*, *Globodera*, and *Meloidogyne* (Kerry and Jaffee 1997). Some fungi that produce nematode toxins by special structures are proposed to be classified into a fourth group (Jansson et al. 1997; Li et al. 2000). Recently, the fungus *Stropharia rugosoannulata* was found to kill nematodes by damaging their cuticles mechanically with a special spiny ball structure, an acanthocyte, and it could be a representative of a fifth group (Luo et al. 2006).

A wide range of fungi have been isolated from the sedentary stages of nematodes or found to produce toxins to kill nematodes. These fungi do not produce specialized infection structures other than appressoria or toxins and may survive and proliferate in soil in the absence of nematodes. Thus, these fungi are not examined in this review. The living strategies of nematophagous fungi are discussed

X.-Z. Liu (✉) · M.-C. Xiang · Y.-S. Che
Key Laboratory of Systematic Mycology & Lichenology, Institute of Microbiology, Chinese Academy of Sciences, 3 Datun Road, Chaoyang District, Beijing 100101, P. R. China
Tel. +86-10-8261-8785
e-mail: liuxz@im.ac.cn

in several aspects, i.e., the diversity of infection structures and trophism, and the effects of soil environmental factors on survival and activities of *Hirsutella rhossiliensis* and *H. minnesotensis*.

Diversity of infection structures

Diversity and evolution of trapping structures

Predation plays a major role in energy and nutrient flow in the biological food chain and is one of the basic life strategies for fungi, except for saprophytism and parasitism. Predatory devices are important structures for the life and behavior of nematode-trapping fungi. Adhesive traps survive over a long period of time, compared to normal hyphae, based on survival studies conducted in the laboratory (Veenhuis et al. 1985). More than 200 species of fungi (distributed in Ascomycota, Basidiomycota, and Zygomycota) use these special structures (traps) to capture free-living nematodes in soil (Li et al. 2000). Within a few hours of close contact with nematodes, the sparse mycelia of these fungi will be induced to spontaneously differentiate into functional devices (traps), and the mycelial traps will then capture, penetrate, kill, and digest the nematode contents. Five types of trapping devices, i.e., adhesive networks, knobs, and columns, and nonconstricting and constricting rings, have been recognized and studied in predatory fungi (Barron 1977). An adhesive network, the most widely distributed trap, is formed by an erect lateral branch growing from a vegetative hypha, curving around to meet and fuse with a branch formed on the parent hypha some 20–25 μm from the initial hypha (Nordbring-Hertz et al. 1989), and developing more loops either exterior to the original loop or on the parent hypha. The adhesive knob is a morphologically distinct globose or subglobose adhesive cell that is either sessile on the hypha or at the apex of a slender, erect, and nonadhesive stalk composed of one to three cells. Nonconstricting rings (NCR), which are always accompanied with adhesive knobs, are produced when the erect lateral branches from a vegetative hypha thicken and curve to form a generally three-celled ring that then fuses to the supporting stalk. The detachable knob and the ring provide a distinct advantage for the fungus because of their ability to travel with the swimming nematode and to spread extensively (Barron 1977). The adhesive column is a short erect column consisting of a few swollen cells produced on a hypha. These trapping devices all capture nematodes by means of an adhesive layer covering part or all of the surfaces of the device. The constricting ring, the fifth type of trapping device, is the most sophisticated one that captures prey with a different mechanism. When a nematode enters a constricting ring, the three cells of the ring are triggered to rapidly swell inward and firmly lasso the victim within 1–2 s (Gray 1987; Yang et al. 2007).

Generally, a species of the nematode-trapping fungi produces only one type of trapping device, except for the NCR-forming fungi. However, some species, such as *Arthrobotrys oligospora*, can develop several different mycelial structures involved in infection and parasitism. The capture of nematodes by *Arthrobotrys* spp. does not require a fully developed loop because nematodes can be trapped even on the first-forming branch (Nordbring-Hertz 2004). In an isolate of *Arthrobotrys superba*, nematodes were trapped on a basal cell, which subsequently developed into either a fully developed network or a conidiophore, depending on environmental conditions (Jansson and Nordbring-Hertz 1981).

The most common predatory fungi are in the family of Orbiliaceae, Ascomycota. To understand the origin and evolution of these fascinating trapping devices, it is essential to gain insights on how those novel devices are differentiated, and how the nematode-trapping fungi are related to other organisms, as well as their reactions to the environment. A recent study based on comprehensive phylogenetic analysis of the nucleotide sequences of three protein-coding genes and rDNA in the internal transcribed spacer (ITS) region demonstrated that the initial trapping structure evolved along two lineages, yielding two distinct trapping mechanisms: one developed into the constricting rings and the other developed into the adhesive traps. Among adhesive trapping devices, the adhesive network separated itself from others at an early stage and evolved steadily and gently. The adhesive knob evolved through stalk elongation and finally developed into nonconstricting rings. Our data suggest that the derived adhesive traps are at a highly differentiated stage. The development of trapping devices is a felicitous proof of adaptive evolution (Yang et al. 2007).

Conidial traps

Germination of conidia usually takes place with the germ tube developing into a hypha, which in turn undergoes branching to form a mycelium. However, some species in nematode-trapping fungi form trapping structures directly on the germination of conidia, without an intermediate hyphal phase. Conidial traps are fully functional in trapping nematodes. They adhere to passing nematodes and may be carried away and spread by the nematodes, which is an efficient survival strategy that has significant advantages for the life of nematode-trapping fungi (Dackman and Nordbring-Hertz 1992; Nordbring-Hertz 2004). In most of the tested nine fungi forming an adhesive network, columns and constricting rings were able to form conidial traps on water agar surfaces in the vicinity of soil, but this ability varied among different species. Generally, *Arthrobotrys dactyloides* and *Monacrosporium gephyropagum* are the fungi most capable of forming a conidial trap, followed by *Arthrobotrys superba* and *Arthrobotrys oligospora* (Persmark and Nordbring-Hertz 1997). A mechanism study for the formation of conidial traps showed that a low nutrient level was necessary, and competition for nutrients by microorganisms was one of the reasons for conidia to directly germinate into the traps, thereby overcoming soil fungistasis (Permarck and Nordbring-Hertz 1997).

Diversity of infection spores

Found in a number of taxonomic classes, nematophagous endoparasites use spores to contact, infect, and consume vermiform nematodes. After consuming the nematode contents, this class of fungi grows out and produces new spores for the next infection cycle. On the basis of spore types and infection modes, they could be categorized into four groups: adhesive spores, encysting spores, ingested conidia, and injection conidia. Some nematophagous endoparasites produce adhesive spores that attach to the cuticle of passing nematodes: the prominent parasites of cyst nematode juveniles, *H. rhossiliensis* and *H. minnesotensis*, are representatives of adhesive spores (Jaffee et al. 1991; Chen et al. 2000). Some fungi produce motile zoospores that encyst on the nematode's surface and subsequently penetrate and infect free-living nematodes. Some species of endoparasites have developed morphologically adapted conidia that, when eaten by the saprophytic nematode, become lodged in either its buccal cavity or esophagus. These species belong almost exclusively to the genus *Harposporium* (Gray 1987). Species of *Haplograssa* also produce zoospores that encyst freely and germinate to produce a specialized infection apparatus, the injection tube, to infect nematode by injecting a sporidium (Barron 1987). All the endoparasites have some advantages for their survival by having limited growth in soil outside the colonized nematode cadaver (Kerry and Jaffee 1997) and being transmitted by infected nematodes before they were killed.

Gun cell

The gun cell is a very complex and sophisticated attack cell produced by *Haptoglossa* species to infect microscopic animals, such as nematodes, rotifers, and tardigrades (Beakes and Glockling 1998). *Haptoglossa* species produce a zoospore that encysts and germinates to form a gun cell. When a nematode touches a gun cell, a harpoon-shaped projectile is shot off and blows a hole through the cuticle of the nematode. An internal tubular device in the gun cell everts through this hole and fires a missile-like projectile that penetrates the host cuticle to form a hypodermic-like structure to penetrate into the body of the animal (Barron 1987; Beakes and Glockling 1998). The osmotic power of the basal vacuole in the gun cell is very high. It takes in water rapidly and pumps the protoplasm and nucleus from the gun cell through the hypodermic and into the body of the host to form an infection sporidium (Barron 1987). Analysis of nematode infection by *Haptoglossa zoospora* and *H. heterospora* based on a videocassette record revealed a two-step injection of a sporidium by the gun cell, in which the gun cell came in contact with the cuticle of a nematode and produced a spherical adhesorium on the tip of the cell in 0.07–0.1 s in both species. The adhesorium was ~2 μm in *H. zoospora* and ~4 μm in *H. heterospora*. When the adhesorium inflated to full size, it shot the sporidium into the nematode's body in 0.5–0.65 s for *H. zoospora* and in 0.2–0.5 (or, rarely, 1.0) s for *H. heterospora*, respectively. After shooting, the empty gun cell with an empty cyst case was immediately separated from the cuticle in both species (Hakariya et al. 2002). The ultrastructure observation on *H. erumpens* revealed that the germinating cyst developed into two similar-sized but morphologically distinct infection cells, the uninucleate, convexly accurate gun cells and the binucleate, concavely accurate gun cells. These modified bi-nucleate gun cells were never observed to fire in response to contact with *Bunomema* nematodes (Glockling and Beakes 2002). The gun cell is only about 15 μm long, but it is the most complicated cell known in fungi and is arguably more sophisticated than the "nematocyst" (Beakes and Glockling 1998).

Diversity of trophism

Nematotrophism

Many species of nematophagous fungi are facultative parasites, and their dependence on nematodes for growth and survival differs dramatically (Kerry and Jaffee 1997). Correlation between the growth rate and the trapping device for nematode-trapping fungi was observed by Cooke (1963) and Jansson (1982), and the two ecological groups were distinguished based on such a correlation. The first group contains species with adhesive networks; they are fast-growing, good saprophytes with a weak predaceous activity. Although the second group includes species with all other types of trapping devices; they are slow-growing, weak saprophytes with higher predaceous activity (Jansson 1982; Rubner 1996). Most of the endoparasites have very limited growth in soil outside the colonized nematode cadaver. *H. rhossiliensis* is a representative of the extensively studied endoparasites that grows slowly in culture, has little competitive saprophytic ability, and produces specialized conidia for attacking nematodes. It is presumed to be an obligate parasite in nature (Jaffee and Zehr 1985; Jaffee 1992).

Mycoparasitism

Mycoparasitism, the phenomenon of hyphal coiling of one fungus around the hyphae of another, is known as one of the main mechanisms involved in the antagonism of *Trichoderma* spp., a biocontrol agent of soil-borne plant pathogenic fungi (Chet 1987). Tzean and Estey (1978) found that three well-known nematode-trapping fungi, *Arthorbotrys oligospora*, *A. robusta*, and *A. superba*, were pathogenic to *Matruchotia varians*, *Rhizoctonia solani*, and *Geotrichum* sp. by induced, specialized coil-form hyphae. The hyphal coils of *A. oligospora* were also formed in 6 of 13 fungi tested (Persson et al. 1985). Light and electron microscopic observations revealed that the coils squeezed the host hyphae and degraded the host cell walls, causing them to collapse and eventually to lyse (Tzean and Estey 1978). Other observations showed that attack of *A. oligospora* coils on host hyphae led to cell wall proliferations of the

host (*Rhizoctonia solani*) and disintegration of the host cytoplasm without penetrating the intact cells. Such interaction is interpreted as competition for nutrients (Persson et al. 1985). A double labeling experiment with ^{32}P-labeled *R. solani* and ^{33}P-labeled *A. oligospora* demonstrated that *A. oligospora*, although a nonpenetrating mycoparasite, derived a considerable proportion of nutrients from the host hyphae of *R. solani* (Olsson and Persson 1994). From a biological control point of view, *Arthrobotrys janus* was frequently isolated from the sclerotia of *Sclerotinia sclerotiorum*, which were used as the baits for mycoparasite isolation (Li et al. 2003). The colonization of *A. oligospora* was observed on plant roots, which suggested its endophytic nature (Jansson and Lopez-Llorca 2004), and this relationship might render the plants more resistant to plant parasitic nematodes and/or other fungal pathogens (Nordbring-Hertz 2004).

Natural obligate parasitism

Nematophagous fungi differ in their saprophytic and parasitic abilities. Some, such as *Myzocitium* spp., appear to be obligate parasites, whereas others, such as *A. oligospora*, compete saprophytically for certain substrates. Parasitic and saprophytic abilities of nematophagous fungi are often inversely related; i.e., efficient parasites are inefficient saprophytes and vice versa (Cooke 1963; Jansson 1982). The behavior of *H. rhossiliensis* corresponds well with this statement (Jaffee and Zehr 1985). Although *H. rhossiliensis* is able to grow on common laboratory media, the growth is very slow (Liu and Chen 2002). The nutritional requirement for this fungus is glycogen as the best carbon source and casein as the best nitrogen source (Liu and Chen 2002). However, in soil conditions, this fungus is active in parasitizing living nematodes, and the parasitized nematodes rapidly disappear from the soil under moist conditions. The fungus converts the material and energy in its assimilative hyphae within the nematode host into new fungal structure external to the host (Jaffee 1992). On the other hand, *H. rhossiliensis* is a poor parasite of the dead nematode *Criconemella xenoplax*, indicating that this fungus may be an obligate parasite in nature (Jaffee and Zehr 1985). Furthermore, spores detached from phialides by soil disturbance are no longer capable of adhering and infecting nematodes (McInnis and Jaffee 1989). The characteristics of fungi that are culturable on media but show naturally obligate parasitism have significance not only for their survival in nature but also for their advantages as biocontrol agents.

Ecological characteristics of nematophagous fungi

Density-dependent parasitism

Although density-dependent parasitism is a common phenomenon among insects, it was noticed only two decades ago between fungi and nematodes (Jaffee and McInnes 1991). Observations, experimentation, and theory all indicate that parasitism of nematodes by *H. rhossiliensis* is density dependent. In a field survey, the percentage of nematodes parasitized was well correlated with its density when many samples were collected at one time in a mature peach orchard (Jaffee and McInnes 1991). Results from a preliminary greenhouse trial showed that the parasitism of *H. rhossiliensis* OWVT-1 was strongly correlated with the density of soybean cyst nematode (Liu et al., unpublished data). In a laboratory soil experiment, the proportion of parasitism was increased to nearly 100% when a high nematode density was maintained but declined to nearly 0% at low densities (Jaffee 1992). A mathematical model based on density-dependent parasitism was described for the laboratory dynamics (Jaffee et al. 1992). Detailed studies on *H. rhossiliensis* OWVT-1 and the soybean cyst nematode demonstrated that parasitism was dependent on fungal density but independent of nematode density in instantaneous conditions, leading to the development of a new mathematical model (Yang et al., unpublished data). This model is not only useful to describe the colonization, survival, and dynamics of nematophagous fungi but also is applicable to the screening of biocontrol agents.

Effect of soil environmental factors on the survival and activity of *Hirsutella* spp.

Environmental factors greatly affect the occurrence and activity of soil microorganisms. However, little is known about how environment affects the abundance and activity of nematophagous fungi (Dackman et al. 1992). The fungi *H. minnesotensis* and *H. rhossiliensis* are important parasites of second-stage juveniles (J2) of the soybean cyst nematode (*Heterodera glycines*) and have shown great potential as biocontrol agents of this and other plant-parasitic nematodes. Parasitism of nematodes by *H. rhossiliensis* in the field is dependent on several factors such as conidia density, the distance that the host nematode moves, soil moisture, and the size of soil particles (Jaffee et al. 1990; Timper et al. 1991; Tedford et al. 1992). The distance traveled by nematodes determined their chance of encountering natural enemies, and the movement of water in soil may disseminate fungal spores (Chen and Dickson 2004). Recently, the effects of soil temperature, water content, and texture on abundance and activity of these two fungi in soil were investigated by parasitism assay and quantitative real-time polymerase chain reaction (PCR) (Xiang 2006; Zhang 2005). In our study, *Hirsutella minnesotensis* and *H. rhossiliensis* were added to soil (1 g mycelium/100 g dry soil) contained in 50-ml plastic tubes. Soil temperature ranged from 5º to 30ºC, soil water content ranged from 6% to 22%, and the soil was supplemented with clay or sand, ranging from 0% to 70%, respectively. After 24 days, the fungal abundance was quantified by real-time PCR, and their activity was inferred from the numbers of J2 parasitized. The percentage of *H. glycines* juveniles (J2) parasitized by *H. rhossiliensis* and the DNA yield of the fungus were the highest in autoclaved soil, intermediate in microwaved soil, and the

lowest in natural soil, indicating the presence of significant antagonistic effects on the microbial community by introducing inocula in natural and microwaved soils. In addition, the amount of DNA per gram of soil and the percentage of J2 parasitized by both fungi were higher under lower soil temperature, lower soil water content, and higher clay content. High percentages of *H. glycines* J2 parasitized were observed at 10º and 5ºC, 6% and 10% water content, and clay soil for *H. minnesotensis*, whereas the high percentages were seen at 15º and 20ºC and 14% water content for *H. rhossiliensis*. High content of extracted DNA was found at 10º and 5ºC, and at 4% and 6% water content, for *H. rhossiliensis*, but at 10º and 5ºC, 6% water content, and 70% clay soil for *H. minnesotensis* (Xiang 2006; Zhang 2005). These results imply that low temperature and soil moisture may favor fungal survival, while these conditions may not be suitable for fungal infection of nematodes. The results also demonstrate that these two fungal species have great potential to multiply as well as to control nematodes in cooler, drier, and heavier soils.

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