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A Review on Nematophagus Fungi: A Potential Nematicide for the Biocontrol of Nematodes

Ibrahim Lawal¹, Aminu Yusuf Fardami^{2*}, Fatima Isma'il Ahmad¹, Sani Yahaya⁴, Abdullahi Sani Abubakar³, Muhammad Abdullahi Sa'id¹, Musa Marwana³ and Kamilu Adamu Maiyadi⁴

¹Department of Biological Sciences, Al-Qalam University Katsina, Dutsinma Road, 820102, Katsina, Nigeria.

²Department of Microbiology, Faculty Chemical and Life Sciences, Usmanu Danfodiyo University, P.M.B. 2346 Sokoto, Nigeria.

³Department of Sciences Laboratory Technology, Al-Qalam University Katsina, Katsina State, Dutsinma Road, 820102, Katsina, Nigeria.

⁴Department of Microbiology, Faculty of Life Sciences, College of Natural and Pharmaceutical Sciences, Bayero University Kano, PMB 3011, Gwarzo Road, Kano State, Nigeria.

*Corresponding author:

Aminu Yusuf Fardami,

Department of Microbiology, Faculty of Chemical and Life Sciences,
Usmanu Danfodiyo University,
Sokoto,
Nigeria.

Email: aminufy@gmail.com

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ABSTRACT

Filamentous fungi offer an interesting biocontrol alternative. Trichoderma, mycorrhizal, and endophytic fungi are the main filamentous fungi used to induce nematode resistance. They can reduce plant-parasitic nematode damage by producing lytic enzymes, antibiosis, paralysis, and parasitism. They minimize space and resource competition by increasing nutrient and water uptake, or by modifying root morphology and/or rhizosphere interactions, which benefits plant growth. Filamentous fungi can induce nematode resistance by activating hormone-mediated plant-defense mechanisms (salicylic and jasmonic acid, strigolactones). Altering the transport of chemical defense components or the synthesis of secondary metabolites and enzymes can also boost plant defenses. Using filamentous fungi as BCAs against plant-parasitic nematodes is a promising biocontrol strategy in agriculture. By increasing a plant's ability to absorb nutrients and water, or by changing root shape and/or rhizosphere interactions, they reduce competition for space and resources. Filamentous fungi can activate hormone-mediated plant defenses (e.g., strigolactones, salicylic and jasmonic acids). Changing how chemical defense components are transported or synthesizing secondary metabolites and enzymes can improve a plant's defenses. Using filamentous fungi as BCAs in agriculture is a promising, long-lasting biocontrol method against plant-parasitic nematodes.

INTRODUCTION

Nematodes, often known as roundworms, are non-segmented, cylindrical organisms that can infect both humans and animals and live in the wild. Nematodes are the most prevalent kind of human parasite infestation, affecting over 25% of the world's population; susceptible hosts frequently harbor several distinct harmful nematodes [1]. There are at least 60 species that have been proven to infect people and ten times that number that are known to afflict other animals, yet only a small number of pathogens—particularly *Ascaris*, hookworm, and whipworm—account for the majority of human infections. This highlights the fact that repeated interaction with fecally contaminated soil or food and drink is required to perpetuate the cycle of infestation. All three of these organisms require a time of maturity outside the human body, usually in warm, wet soil.

Because they may both complete their life cycles on or inside of human hosts, *Strongyloides* and *Enterobius* are unique in that they can both cause chronic infection and be transmitted via direct close-person contact when there is a chance of fecal-oral contamination [1].

The kingdom of fungi (plural: fungus) includes heterotrophic (unable to produce their own food) eukaryotic creatures that are typically multicellular and play significant roles in the cycling of nutrients in ecosystems. Additionally, to having asexual and sexual reproduction, fungi also collaborate with bacteria and plants in symbiotic relationships [2]. However, they are also to blame for a few ailments that affect both plants and animals. The term "mycology" refers to the study of fungi. While some fungi have single cells, others have several cells. Yeast is the name for single-celled fungi.

Depending on the stage of their life cycle, several fungi can transform between single-celled yeast and multicellular forms. Like plant and animal cells, fungi cells have a nucleus and organelles. Chitin, a hard material also present in the exoskeletons of insects and other arthropods like crustaceans, is a component of the cell walls of fungi. They lack cellulose, which is typically found in plant cell walls [2]. Nematophagous fungus, which naturally opposes nematodes that feed on various phases of these animals, are global microorganisms, according to Larriba et al. [2] numerous nematophagous fungi are facultative parasites that can transform from saprophytes to parasites in the presence of their hosts and create infection structures, which are used to categorize them according to their predation features. Numerous methods, including the use of chemical nematicides, have been developed for nematode management in agriculture due to the substantial economic damage caused by parasitic worms. However, the loss of pesticides as a result of EU legislation, as they are damaging to human health and a contaminant for the environment, has increased the need to implement effective nematode resistance [3].

The use of biocontrol strategies is recommended as a considerably safer and more workable approach for managing plant-parasitic nematodes. The use of live creatures to reduce a specific pest organism's population density or impact, making it less numerous or harmful than it otherwise would be, is known as biological control (or biocontrol). The regulation of nematode populations and/or a decrease in nematode damage through the activity of creatures' antagonist to them, which occur naturally or through the manipulation of the environment or the introduction of antagonists, are specifically characterized as biological control of nematodes. The biological control agent is the organism that prevents the infection from spreading (BCA). These organisms can compete for nutrients or space, engage in antagonism with the pathogen directly, or interact with the pathogen indirectly through the host plant by, for example, producing plant resistance (systemic acquired resistance, or SAR, and induced systemic resistance, or ISR) [4].

Although the use of plant-parasitic nematodes for biocontrol dates back to the early 20th century, research on their potential has only recently started. In addition to serving as BCAs against plant-parasitic nematodes, these nematodes are essential in promoting the cycling of plant nutrients, which enables plants to fight diseases more successfully. There are numerous instances given in the literature, including *M. gaugleri*, which is effective against *Heteroderaoryzae* and *Meloidogyne incognit*, and *Odontopharynxlongicaudata*, which is effective against *M. incognita* and *M. javanica* (among others) [2].

Nematodes that parasitize plants and have dense populations reduce yields in most agricultural crops by economically significant amounts. Plant-parasitic nematodes cause about 12% of the world's food output to fail [4]. Plant-parasitic nematodes may cause a US\$121 billion global economic loss. In India, the annual loss in 24 crops from economically significant nematodes is estimated to be over Rs. 21068 million. The preventable yield loss owing to *M. incognita* in vegetable crops is as high as 40.5 percent [5].

The creation of cutting-edge methods to control these nematodes is essential because chemical nematicides have been related to dangers to the environment and human health. One solution to control is to use nematodes that parasitize both

plants and their natural enemies. Nematode-destroying fungi, which are among them and are a group of soil-dwelling fungi, are crucial natural enemies of plant-parasitic nematodes [6]. An approach that is environmentally sustainable uses nematode-destroying fungus as a biocontrol agent, either on its own or in conjunction with other worm management techniques.

Mode of Action of Nematophagous Fungi

Nematode-eliminating fungus, also known as nematophagous fungi, includes a broad and diverse spectrum of fungi, according to Walia et al. [5]. They are predatory, pathogenic, or parasitic, and some of them infect and consume nematodes. The majority of nematode-eating fungi are saprophytic in soil, but when a host is present, they transition into a parasitic phase that is primarily found in soil with high organic matter content. There are over 700 kinds of fungi known to eliminate nematodes. Larriba et al. [2] divided nematode-destroying fungus into two categories: (a) nematode-trapping or predacious fungi, and (b) endozoic or endoparasitic fungi. Endozoic or endoparasitic fungi are further broken down into (i) egg parasites, (ii) cyst and female parasites, (iii) vermiform nematode parasites, and (iv) parasites of all worm stages. In their study, Zheng and Yang [3] divided nematode-destroying fungus into toxin-producing fungi, endoparasitic fungi, opportunistic fungi, or egg and cyst parasitic fungi.

Nematodes and Nematicides

Invertebrates of the phylum Nematoda include nematodes. They have a body made of unsegmented thread. Many of them live inside their host as parasites. The nematodes are helminths, along with other parasitic worms such as flatworms, cestodes, and trematodes. The nematodes differ from other helminths by having an undifferentiated body that resembles a thread, a strong outer cuticle, and a tubular digestive tract with openings on both ends [7].

There are numerous disease-causing species. An early pulmonary phase associated with larval migration and a later, protracted intestinal phase defines the nematode *Ascaris lumbricoides* infection. Adult worms live in the small intestine lumen and range in length from 15 to 40 cm. Infection occurs after eating contaminated food that contains eggs, or more frequently, after touching contaminated dirt with your hands and then transferring the infection to your mouth. Mebendazole or pyrantel pamoate are used as treatments. Along with filariasis, hookworms, pinworms, and whipworms, other parasitic nematodes exist [8].

Any worm belonging to the phylum Nematoda is a nematode, usually known as a roundworm. The majority of animals on Earth is nematodes. They can be found as free-living organisms in soil, fresh water, marine settings, and even strange locations like vinegar, beer malts, and water-filled crevices deep below the Earth's crust. They can also exist as parasites on plants and animals. There are roughly 20,000 recognized species, although only a small part of the free-living forms has likely been identified. Because the majority of the parasitic forms have some sort of medicinal, veterinary, or economic relevance, extensive research has been done on them [7].

Nematodes often have a long, slender, threadlike body ('nema' is Greek for thread), but not segmented like that of earthworms, according to Li et al. [9]. The gut and gonad are encircled by the body wall, which is made up of dorsal and ventral longitudinal muscles, an epidermis, and a cuticle. A chamber that is pressured and filled with fluid sits between the inner and outer tubes and serves as a hydrostatic skeleton.

Because of their structure, nematodes can lie on one side and move gracefully in sinusoidal waves. It probably also imposes a strong restriction on the evolution of this basic body plan. Nematodes never developed any appendages, such as legs or wings, probably because they rely on their strong body wall and pressurized body cavity as an antagonist for muscle activation. Because of this, this group's morphological variety is constrained and far lower than that of other successful groups like arthropods or vertebrates. An artificial insecticide called a nematicide is used to eradicate nematodes that attack plants. Nematicides typically have a wide range of harmful effects and high volatility or other characteristics that facilitate soil mobility [9].

Nematophagous Fungi as Biocontrol Agents

Recent years have seen a significant increase in the use of chemical nematicides, crop rotation, and resistance cultivars, whenever they are available, to control plant parasitic nematodes [10]. The public's growing awareness of environmental risks, the high price of chemical nematicides, the restricted number of crop rotation alternatives, and the scarcity of resistant cultivars, however, necessitates the creation of novel management approaches. In these conditions, biological control, in which the employment of advantageous or antagonistic microorganisms can decrease soil-borne pathogens in soil, appears to be an alternate technique in the management of plant parasitic nematodes [11].

Given that it is environmentally safe, commercially viable, and provides a sustainable and cost-effective alternative to chemical nematicides, biological management is regarded as the most pertinent and least harmful technique [12]. It can either be natural or induced. In the former scenario, an organism's natural population prevents nematodes from growing and developing, but in the latter scenario, biocontrol agents (BCAs) are forcibly introduced (Brand et al., 2010). The term "biological control" refers to the naturally occurring process of nematode population decrease caused by living species other than the nematode-resistant host plant, or through manipulation of the environment or the introduction of antagonists [13].

Instead of eradicating the nematode population as pesticides do, the goal is to keep it below the economic threshold level. Therefore, biological control is formally defined as a decrease in nematode population achieved through the introduction of antagonists or modification of the environment to make it conducive to the activity of naturally occurring antagonists. Numerous natural enemies hunt out nematodes and diminish their population, but nematophagous fungi are the most promising and practical BCA for controlling soil concentrations of plant parasitic nematodes. Nematode antagonists that infect, kill, and consume their hosts are a diverse variety [14]. Uniquely, nematophagous fungi stop the nematode by using specific structures designed to combat nematodes. These carnivorous mushrooms play a significant role in regulating nematode concentrations in soil due to their predatory and parasitic behaviors [12].

They employ unique mycelial structures, such as traps to capture vermiform moving worms, spores to adhere to the nematode cuticle, or hyphal points to assault nematode eggs, females, and cysts [15]. Important fungi that parasitize nematodes and reduce their population include *Aspergillus niger*, *Paecilomyceslilacinus*, *Trichoderma harzianum*, *Arthrobotrysoligospora*, and *Paecilomyceslilacinus*. They are plentiful on the surface of plant roots, leaf litter, and decomposing organic debris, and are found in practically all

types of soil [16]. The types and species of nematodes affect how predatory they are. Nematophagous fungus comes in more than 200 species, each with a different level of saprophytic or parasitic activity [14]. Beginning with the initial discovery of the endoparasite *Harposporiumanguillulae*, nematophagous fungi have been studied [16]. Since then, it has been discovered that numerous fungi feed on nematodes, and the number of fungi known to have embraced this lifestyle has been continuously increasing. Biological control was rendered obsolete by the development of several chemical pesticides and their commercialization beginning in the 1940s.

Classification of Nematophagous Fungi

Nematophagous fungi are diverse microorganisms that can switch from saprophytic to carnivorous behavior, enabling them to consume nematodes in an unfavorable nutritional environment. They are nematodes' natural adversaries and have evolved incredibly complex infection methods [17,18]. Over 700 nematophagous fungus species have been identified, and they come from a variety of phyla, including the Ascomycota, Basidiomycota, Chytridiomycota, and Zygomycota. Additionally, the nematophagous activity of species from the phylum Oomycota has been described [8]. According to their methods of worm predation, these fungi are traditionally divided into three groups: (a) nematode-trapping/predatorial, (b) opportunistic or ovicidal, and (c) endoparasitic. Predators create modified hyphae known as "traps," which they use to bind and digest nematode larvae through a mechanical/enzymatic process. The literature has already provided detailed descriptions of a variety of traps, including constricting and non-constricting rings, three-dimensional adhesive networks, adhesive nodules, and non-differentiated adhesive hyphae.

In addition to using traps, the ovicidal group also engages in predation. However, nematode females, cysts, and eggs are the main target populations. Hyphae are not utilized by endoparasites for predation. According to Braga and Arajo [17], these fungi are obligate nematode parasites that utilise spores (conidia, zoospores) as infection structures that can either cling to the nematode cuticle or be consumed. Toxin-producing fungi and makers of unique attack mechanisms (structures that mechanically injure nematodes' cuticles) are two novel categories of nematophagous fungi that have recently been proposed [15]. The current study focused on these two fungal groupings as well as additional fungi groups.

Economic Importance of Nematodes

Nematodes are a wide population of invertebrate animal species, and in many habitats, they serve as the main decomposers. Nematodes' feeding habits, food digestion, and waste product excretion are crucial to plants because they enable the recycling of key nutrients and minerals from decomposing organic matter, in addition to bacteria and fungus. In the world, parasitic nematodes significantly reduce agricultural output and public health. However, parasitic nematodes can cause significant losses to agricultural production and public health worldwide. Additionally, beneficial nematodes are naturally present in the soil to control soil pest insects. The majority of free-living nematodes feed on microscopic organisms such as protozoans, bacteria, fungi, and other creatures and nematodes. As a result, they play an important role in soil ecosystem by releasing relevant nutrients for plant growth and agricultural production. Nematodes are also biological indicators of the health of the soil because they reflect changes in the microbes they feed on and the physical and chemical makeup of the soil environment [19].

Plant parasitic nematodes are a costly burden in agricultural production and have a significant economic influence on crop yield [19]. They collectively harm crop productivity by an estimated \$80-118 billion dollars annually [20], the majority, which includes 15% of all known nematode species. Nematodes' feeding habits, food digestion, and waste product excretion are crucial to plants because they enable the recycling of key nutrients and minerals from decomposing organic matter, in addition to bacteria and fungus. Economically significant species immediately attack the plant roots of the main crops produced, preventing the uptake of water and nutrients, and reducing agronomic performance, quality, and crop yields [20]. Additional plant pathogenic nematode species including fungi and invertebrates are regarded as the most significant agricultural pests. Nematodes, which establish a permanent feeding site in the plant host and collect nutrients while completing their life cycles, are the most successful species of the inactive groups.

The static species of nematodes have a natural advantage over their migratory counterparts because they have an attractive and intricate strategy of altering the host cell that leads to the creation of a long-lasting feeding structure. Only a few of the more than 4000 identified plant parasitic nematode species cause financial losses in crop production. Crop losses are mostly caused by the following major genera of phytoparasitic species of nematodes: *Xiphinema*, *Rotylenchulus*, *Pratylenchus*, *Meloidogyne*, *Hoplolaimus*, and *Heterodera* [20].

The soil surrounding a plant's root, or the rhizosphere, has a high level of microbiological activity and is home to the majority of soil nematodes. Nematodes, which are parasites of people, animals, and insects, can be found in soil in the form of juvenile larvae and eggs. The majority of nematodes found in agricultural soil include bacterial feeders, fungal feeders, plant parasites, predators, omnivores, and others because most nematodes researched on the soil are parasitic and are categorized based on their feeding habits. When compared to omnivores, predatory nematodes predominantly consume protozoa and other small nematodes, however, they can also consume fungi and bacteria. Omnivores, on the other hand, eat a variety of foods depending on the environment and the availability of food [19]. Plant parasitic nematode species have a variety of negative effects on agricultural productivity, including the removal of cytoplasm by destroying the host cell and the establishment of feeding sites in the host tissue, which causes inactive nematodes to become immobile [19].

The migratory endoparasitic species of nematodes with economic implications, such as the nematode that causes lesions (*Pratylenchus* spp.), the worm that burrows (*Radopholus* spp.), and the nematode that attacks rice roots (*Hirschmanniella*). Consequently, nematodes play a significant role in the health of agricultural systems as described below in terms of nematode species used as biological pest control, improved soil fertility, nitrogen cycle, decomposition of organic matter, plant parasitic nematodes, used as bioindicators of soil health, and pathogenic infection of organisms [20].

Diversity and Taxonomy

The fifth kingdom of living beings is made up of fungi [21]. Nematophagous fungi (NPF) are present in all major fungal groups, including higher fungi like Ascomycetes, Basidiomycetes, and Deuteromycetes as well as lesser Oomycetes, Chytridiomycetes, and Zygomycetes.

Ecological speciation

One of the most fundamental issues in understanding biology is speciation, which is the outcome of the evolution of one species into two. The process of fungus speciation has been reviewed [22, 23, 24, 25, 26]. Ecological speciation, according to Rundle and Nosil [26], is the "process through which barriers to gene flow across populations arise as a result of environmentally grounded divergent selection." Generally speaking, fungi are regarded as effective models for studying eukaryotic speciation [23, 24], despite not being covered in general reviews.

The following factors make fungi excellent models for eukaryotic speciation, according to Giraud et al. [25]: (i) many fungi can be cultured in vitro, and their mating types and genetics have been resolved; (ii) fungi exhibit a wide range of life cycles, geographical ranges, and diverse ecological systems as a result of their habitats encouraging them to adapt to new environments, allowing speciation processes; and (iii) numerous species complexes. The morphological distinctions between fungi like *Colletotrichum* and *Cercospora* are at best arbitrary and frequently called based on the host, which is occasionally mocked as "a parrot on a mango tree." On the basis of morphological similarities, some species complexes have been grouped together once more [27]. Even when sexual stages are unquestionably recognized, the existing botanical nomenclature does not accept asexual organisms as familiar, practical names for pathologists [28]. The terms "ecological speciation" and "the ecological species concept" have been proposed as crucial elements in the evolution of living things including insects, fish, lizards, and birds between adjacent islands, sub-humid environments, and wet areas [29-31, 26, 32].

There have been reports of and/or genetic analyses of ecological speciation in fungi [33-38], as well as evidence of low genetic diversity [39]. According to Jeewon and Hyde [40], the majority of molecular approaches cannot distinguish between the active and dormant stages of fungi because mycelial propagules or dormant spores may have numerically dominant populations but be functionally inconsequential in their natural habitat.

Among the different molecular methods used in fungal diversity studies, arrayed rRNA gene clones into taxonomic groups by a series of hybridization experiments [41] and oligonucleotide fingerprinting of ribosomal RNA gene (ORFG)-based fingerprinting are promising methods [49]. Denaturing gradient gel electrophoresis (DGGE) and terminal restriction fragment length polymorphism (T-RFLP) are the two techniques most frequently employed to measure fungal diversity [8, 42, 43]. The diversity of NTF/NPF hasn't, however, been studied using molecular techniques.

Taxonomy of Nematophagous Fungi

Taxonomy is defined as "a study aimed at developing a system of classification of species, which best reflects the whole of their similarities and differences" (taxon = order or arrangement, nomos = law). It involves identification or the proper assignment to a generally recognized diagnostic, systematics (the science of diversity of species), and taxonomy in the strictest sense, or the philosophy of classification. The concept of species varies across the living world. In this case, the species concept is briefly discussed with respect to worms, specifically plant-parasitic nematodes [33]. The phenomena are significant for identification, i.e. to fix the phenomena to one or more species, from a variety of varied individuals belonging to a community of identical or non-similar populations. In nematode taxonomy, biological species and parthenogenetic, or

the lytakous species, species are important ideas. It is not well understood how fungi differ genetically. It was discovered that the inter-sterility of *Heterobasidion* species was caused by four or five genes [33].

With the identification of the sexual stages, the taxonomic placement of several NF has been clarified, since the teleomorphs of the fungi, including those of *Arthrobotrys*, *Monacrosporium*, and *Dactylella*, have been recognized as *Orbilia* spp., belonging to the Ascomycetes [44]. In addition to being both endoparasitic and nematode-trapping, *Nematoctonus* spp. vary from all other nematode-trapping Deutero-mycetes in that they also serve as nematode hosts. According to Ahrén et al. [39], teleomorphs of the majority of nematode-catching species and their forms of trapping devices can be used to assess the taxonomic position. Moosavi and Zare [45] provided a brief description of the taxonomy of nematophagous fungi (NF). Scholler et al. [46] also made an effort to categorize NF based on the genetic information of the *Arthrobotrys* (adhesive three-dimensional networks), *Dactylellina* (stalked sticky knobs and/or non-constricting rings), *Drechslerella* (constricting rings), and *Gamsylella* species (adhesive branches and unstalked knobs).

A proto-homotypic parasite/pathogen is one that has the same distribution as the host, whether it be narrow or wide, according to Durrieu [47]. Dasgupta and Mandal, [48] gave more emphasis on homotypic (a parasite with its host) parasites that have a tendency to achieve an ideal balance with their host. As a result, the likelihood of a catastrophe decreases. This is pertinent to the use of nematophagous fungi (NPF) for biological control. The coexistence of parasitic nematodes and the corresponding hyperparasitic fungus poses no challenges to natural management. However, their employment in biological control is unlikely to be very effective because the hyperparasitic fungi may not be able to completely destroy the parasitic worm. Biological control is therefore probably more successful [48].

Biocontrol of Nematodes with Nematophagous Fungi

Plant parasitic nematodes (PPNs) are thought to harm agriculture annually to the tune of >\$150 billion globally. From an ecological point of view, this particular group of nematodes is just one of many elements in the ecosystem that interact with other creatures and help to maintain and stabilize the soil food chain [1]. Our knowledge of the multitrophic interactions that occur in the rhizosphere, microbial diversity, and biological control mechanisms for nematodes have all greatly expanded over the past 30 years. In fact, a number of environmentally friendly management techniques for plant parasitic nematodes (PPNs) have been established [13].

The root-knot nematodes (RKNs; *Meloidogyne* spp.) are the PPNs that pose the greatest risks to crop productivity. Ten microfungi and three mushroom species were investigated for their capacity to inhibit RKNs as part of a summary of the biocontrol techniques assessed between 2015 and April 2020. The majority of tests were carried out in greenhouses and laboratories, thus it is unknown how effective they would be in the field [1]. The issue now is to translate the positive results from the lab into equally successful field applications.

CONCLUSION

An effective substitute for hazardous chemical nematicides for plant-parasitic nematodes is the use of biocontrol techniques. This results in the description of a wide range of efficient techniques based on the use of filamentous fungus as bio-

control agents (BCAs). There are two main categories of their mechanisms of action: those that produce secondary metabolites (antibiosis), lytic enzymes, and space competition; and those that act more directly by increasing plant nutrient and water uptake, changing root morphology and rhizosphere interactions, or competing for photosynthates or colonization/infection sites. By producing lytic enzymes, antibiosis, parasitism, paralysis, and space competition, endophytic fungi lessen the onslaught of plant-parasitic nematodes. The activation of systemic acquired resistance (SAR) and induced systemic resistance (ISR), which appear to be likewise heritable, are examples of the second category of action mechanisms. Additionally, the alteration of root exudates, synthesis of strigolactones, secondary metabolites in plants, and the development of enzymes can be done by nematophagous fungi.

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