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Rhizosphere Colonization and Control of *Meloidogyne* spp. by Nematode-trapping Fungi

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Abstract: The ability of nematode-trapping fungi to colonize the rhizosphere of crop plants has been suggested to be an important factor in biological control of root-infecting nematodes. In this study, rhizosphere colonization was evaluated for 38 isolates of nematode-trapping fungi representing 11 species. In an initial screen, *Arthrobotrys dactyloides, A. superba,* and *Monacrosporium ellipsosporum* were most frequently detected in the tomato rhizosphere. In subsequent pot experiments these fungi and the non-root colonizing *M. geophyropagum* were introduced to soil in a sodium alginate matrix, and further tested both for establishment in the tomato rhizosphere and suppression of root-knot nematodes. The knob-forming *M. ellipsosporum* showed a high capacity to colonize the rhizosphere both in the initial screen and the pot experiments, with more than twice as many fungal propagules in the rhizosphere as in the root-free soil. However, neither this fungus nor the other nematode-trapping fungi tested reduced nematode damage to tomato plants.

Key words: Arthrobotrys dactyloides, Arthrobotrys superba, biological control, *Meloidogyne incognita, Meloidogyne javanica, Monacrosporium ellipsosporum, Monacrosporium geophyropagum,* nematode, nematode-trapping fungi, rhizosphere, root-knot nematodes, tomato.

Root-knot nematodes (*Meloidogyne* spp.) are an important group of plant parasites that cause severe damage to many crop plants, especially in subtropical and tropical agriculture (Netscher and Sikora, 1990). Due to the ban of many nematicides, e.g., ethylene dibromide (EDB), and the ongoing phaseout of methyl bromide usage worldwide, the development of new and nonhazardous control methods is of vital importance. Biological control using antagonistic microorganisms, alone or in combination with other control methods in integrated pest management programs, may be a possible solution. Outlines of such control strategies have been suggested by several authors (Kerry, 1987; Stirling, 1988, 1991). The most studied group among the nematode-antagonistic organisms is the nematophagous fungi. This group includes more than 150 species (Barron, 1977) and may be divided into nematode-trapping, endoparasitic, egg- and female-parasitic, and toxin-producing fungi (Jansson et al., 1997).

Root-knot nematodes feed in or on plant roots, and therefore we hypothesize that the activity of the biological control agent in the rhizosphere of the crop plants should enhance control. Nematode-trapping fungi have been shown to colonize the rhizosphere of various plant species (Gaspard and Mankau, 1986; Peterson and Katznelson, 1965), and leguminous plants seem to be especially important in supporting both number of propagules and species diversity of nematode-trapping fungi (Persmark and Jansson, 1997). One can expect that rhizosphere colonization by nematode-trapping fungi will differ not only according to target plant species but also to fungal species and isolates.

This paper presents a technique for screening nematode-trapping fungi for their rhizosphere-colonizing ability on tomato roots. In a pot experiment we examined the colonization of soil and rhizosphere by four nematode-trapping fungi and their ability to reduce damage to tomato roots with the aim of finding a correlation between root colonization and nematode suppression.

Materials and Methods

Organisms: The fungi used (Table 1) were isolated from soils in Central America and

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Europe. They were cultivated on corn meal agar (Difco, Detroit, MI) diluted 10-fold (CMA 1:10) and stored at 4 °C under paraffin oil.

A mixed population of *Meloidogyne incognita* (Kofoid and White) Chitwood and *M. javanica* (Treub) Chitwood, collected from coffee roots and soil from Nicaragua, was used in the biological control experiment. The population was maintained on tomato plants, *Lycopersicon esculentum* Mill. cv. Money Maker, in a greenhouse at 25 °C,

TABLE 1. Isolates of nematode-trapping fungi screened for their rhizosphere-colonizing capability, expressed as percent colonized root segments out of 20 segments total, in a first and a second test, and average percentage of colonized root systems from the two tests.

Species and trap type	Isolate	Colonized root segments		Colonized root systems[a]
		Test 1	Test 2	
Arthrobotrys conoides Drechsler (network)	A 5	—	—	–
	A 14	10	5	++
	A 30	5	—	+
	P 22	—	—	–
	P 47	—	—	–
Arthrobotrys dactyloides Drechsler (constricting-rings)	CBS 335.94	—	5	+
	CBS 334.94	20	10	+++
	CBS 264.83	5	—	+
Arthrobotrys musiformis Drechsler (network)	A 9	—		–
	A 19	5	10	++
	A 23	—	—	–
	A 24	—	—	–
	P 17	—	—	–
	P 29	5	—	+
Arthrobotrys oligospora Fresenius (network)	A 2	—	—	–
	A 20	10	—	+
	P 35	5	—	+
	P 41	—	—	–
	P 46	—	10	++
	P 53	—	5	+
	ATCC 24927	—	15	++
	CT	—	—	–
	Transf. C	—	—	–
Arthrobotrys oviformis Soprunov (network)	P 27	—	—	–
Arthrobotrys superba Corda (network)	CBS 341.94	10	15	+++
	L 9012	—	5	+
	LU 11	—	5	+
Monacrosporium ellipsopsporum (Grove) Cooke & Dickinsson (knobs)	CBS 225.54	—	—	–
	P 39	55	15	+++++
	P 44	—	5	+
Monacrosporium eudermatum (Drechsler) Subramanian (network)	A 21	5	5	++
	A 22	—	—	–
	P 42	—	5	+
Monacrosporium gephyropagum (Drechsler) Subramanian (branches)	CBS 228.52	—	—	–
Monacrosporium haptotylum Drechsler Xing-Z. Liu & K.-Q. Zhang (knobs)	CBS 325.94	10	—	+
	CBS 326.94	10	10	++
	P 48	—	—	–
Monacrosporium megalosporum (Drechsler) Subramanian (network)	A 1	5	—	+

[a] Percentage of root systems from both experiments as follows: – = no colonization, + = 0–19%, ++ = 20–39%, +++ = 40–59%, ++++ = 60–79%, +++++ = 80–100%.

with 16 hours light and 8 hours darkness. Eggs and juveniles were extracted from the infected roots using a technique modified after Myers (1990). The roots were cut in 1-cm pieces, macerated with tap water for 15 seconds at speed 6 in a Sorval Omni-mixer (Model 17106, du Pont Instruments, Stockholm, Sweden), and thereafter shaken with 0.5% NaOCl for 2 minutes. The eggs and larvae were separated from the root pieces by pouring the water-root mixture through a 5- and 40-μm-pore sieve combination.

Panagrellus redivivus Goodey, which had been axenically cultured and harvested (Jansson and Nordbring-Hertz, 1979) were used as bait (see below).

Screening for root colonization: Thirty-eight isolates (Table 1), representing 11 different species of nematode-trapping fungi, were tested for their rhizosphere-colonizing capability. Three tomato seeds were planted in 125-ml rectangular pots filled with nonsterile fertilized peat containing 15% sand, pH 5.5–6.5 (Kronmull, Hammenhög AB, Sweden), and the fungi were added in the four corners about 2 cm from the seeds at a depth of 2 cm. The fungi were introduced to the soil as agar (CMA 1:10) plugs cut with a sterile cork borer (1-cm diam.) from the edge of 3-week-old fungal colonies. The pots were kept in the greenhouse at 25 °C, with 16 hours light and 8 hours darkness. The seedlings were thinned after 2 weeks, leaving one plant per pot. The plants were harvested after 4 weeks, and the roots were shaken to detach loosely adhering soil. Two of the lateral roots, randomly selected, were cut from the tip into four 1-cm segments, and two segments were placed in each well (16-mm diam.) in microtiter plates containing 1% water agar. Approximately 100 nematodes (*P. redivivus*) were added to each well as bait, and the plates were incubated at room temperature (20–22 °C). The root pieces were examined for the presence of the introduced fungi under a stereo microscope at ×50 after 7 and 14 days of incubation. Five replicates were used for each fungal isolate, and the entire test was performed twice. The results are given as percentage of root segments colonized by fungus and as the average percentage of root systems colonized by fungus of both trials.

Biocontrol experiment: Four fungal isolates chosen from the screening test were examined for their growth and establishment in the tomato rhizosphere and ability to suppress nematodes. The fungi chosen were *Arthrobotrys dactyloides* (CBS 334.94), *A. superba* (CBS 341.94), and *Monacrosporium ellipsosporum* (P 39), which were most frequent in the tomato rhizosphere, and *M. gephyropagum* (CBS 228.52), which did not colonize the tomato rhizosphere. The fungal biomass was produced in 1-liter Erlenmeyer flasks containing 250 ml 2% Neutralized Soya Pepton (Oxoid, Hampshire, UK) at 25 °C on a rotary shaker (130 rpm). The flasks were inoculated with conidia and hyphal fragments. *A. superba* was grown for 4 days, and the other fungi were grown for 6 days. The mycelium was washed with distilled water and drained on a 100-μm-pore sieve for 30 minutes.

The fungi were introduced to soil as sodium alginate pellets prepared by a modification of the method of Lackey et al. (1993): 2 g alginic acid of medium viscosity (Sigma, St. Louis, MO), 1 g casamino acid (Difco) added as nutrient supply, and 5 g (f. w.) of hyphae were mixed in 100 ml distilled water for 1 minute in a Sorval Omni-mixer model 17106 at speed 6. The mixture was added to a plastic container with Pasteur pipets attached to the bottom and was allowed to drip from the pipets into 0.1 M $CaCl_2 \cdot 2H_2O$ continuously stirred to solidify the drops into pellets. The wet pellets were approximately 3 mm in diameter and contained 300 μg (f. w.) of fungal material. They were air-dried in a laminar flow cabinet on plastic trays at 20–22 °C for 24 hours. To inhibit attachment to the surface of the drying pellets, the trays were covered with a thin layer of paraffin oil. The dried pellets were stored at 4 °C for up to 4 days, which does not affect the viability of the fungi (unpublished data).

The soil used was a sandy agricultural soil from Veberöd in southern Sweden. The physical and chemical characteristics of the soil were: 83.5% sand, 9.2% silt, 5.0% clay,

with 2.3% organic matter and pH 6.9. For other soil characteristics and presence of nematophagous fungi, see Persmark et al. (1992, 1996). The soil was sieved (pore size 7 mm) and stored in darkness at 4 °C for 1 month before use.

Plastic pots (1.5 liter) were filled with soil mixed with the fungal pellets (1 pellet/g soil), and three tomato seeds were planted in the center of each pot. The seedlings were thinned after 2 weeks, leaving one plant per pot. Three weeks after beginning the experiment each pot was infested with a mixture of 4,000 freshly extracted nematode eggs and juveniles of *Meloidogyne* spp. Alginate pellets without fungus were used in the control treatment.

Fungal growth in the rhizosphere and root-free soil was followed using a modified dilution plate method, in combination with a most probable number estimation (Dackman et al., 1987). Fifty grams of root-free soil and 50 ml of 0.01% sodium hexametaphosphate (Calgon, BDH, Poole, England) were mixed in a 100-ml Erlenmayer flask with a magnetic stirrer for 15 minutes. The soil-Calgon mixture was diluted with tap water to obtain 0.2, 0.04, 0.008, 0.0016, and 0.00032 g soil/ml water. One ml of each dilution was spread in five replicates on 9-cm-diam. petri dishes containing 1% water agar, and each plate was baited with approximately 1,000 *P. redivivus* in 0.1 ml tap water. For determination of the fungal density in the rhizosphere, the root system was shaken, weighed, cut in 1-cm pieces, and mixed with 0.01% Calgon for 15 minutes with a magnetic stirrer. The root-Calgon mixture was thereafter diluted and treated in the same way as the root-free soil. The agar plates were incubated at room temperature for 1 week and thereafter examined for presence of the introduced fungi with a stereomicroscope at ×50. The proportion of positive plates in each dilution was used to calculate the most probable number from an appropriate MPN-table, constructed after Halvorson and Ziegler (1933), giving number of fungal propagules per gram of soil (f.w.). The fungal quantity was determined by destructive sampling in the tomato rhizosphere after 4, 8, and 12 weeks, and in the root-free soil after 2, 4, 8, and 12 weeks.

Fungal suppression of the nematodes was estimated after 12 weeks by assessing the percentage of galled tomato roots on 10 replicates using a gall index of 1, 2, 3, 4, and 5 corresponding to 0–20, 20–40, 40–60, 60–80, and 80–100% of roots galled. The nematode number in the soil of each pot was determined in six 10-g (fresh weighed) soil samples using a modified Baermann funnel technique (Sohlenius, 1979), and eggs were extracted from six 5-g (fresh weight) samples of randomly selected root pieces (Myers, 1990). The nematodes and eggs were counted with a stereomicroscope at ×25. The data in Table 2 were analyzed by one-way analysis of variance.

Results

Screening for root colonization: The results of the screening test are presented in two ways:

Table 2. Effects of treatment with nematode-trapping fungi on various parameters after 12 weeks of tomato growth in a greenhouse experiment.

	Root weight		Shoot weight		Galling		Eggs		Nematodes	
Treatment	Grams	*P*-value	Grams	*P*-value	Gall index	*P*-value	Number per gram of root	*P*-value	Number per gram of soil	*P*-value
A. dactyloides	14.2[a]	0.12[c]	44.0[a]	0.74[c]	2.1[a,d]	0.40[c]	2,010[b]	0.88[c]	7.3[b]	0.13[c]
A. superba	15.2	0.60	45.5	0.70	2.4	0.63	2,208	0.49	11.5	0.37
M. ellipsosporum	14.5	0.34	41.6	0.29	3.8	0.04	2,853	0.06	18.3	0.4
M. gephyropagum	13.9	0.70	40.8	0.25	4.0	0.02	2,853	0.15	11.8	0.44
Control	15.7		45.0		2.5		1,945		13.4	

[a] Mean value of 10 replicates.
[b] Mean value of 6 replicates.
[c] One-way analysis of variance. Treatment compared with common controls.
[d] Gall index: 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80% and 5 = 81–100% of roots galled.

(i) the percentage of root segments colonized by fungus and (ii) the percentage of root systems colonized by fungus. The percentage of root segments colonized by fungi was usually very low, and the highest value was 55% for *M. ellipsosporum* isolate P39 (Table 1). Sixteen isolates did not colonize the tomato rhizosphere and 14 were found only in one of the tests. Nine fungi were found in more than 20% of the root systems (Table 1). The best root colonizer was *M. ellipsoporum* (P 39), which colonized 80% of the root systems. Based on these results, we selected the three isolates with the highest rankings for the biological control experiments, together with *M. gephyropagum,* which did not colonize the roots.

Biological control experiment: All species colonized the root-free soil after 2 weeks, but the fungal growth followed two different courses: *A. dactyloides* and *M. ellipsosporum* increased gradually during the entire period up to 40–100 propagules/g soil, while *A. superba* and *M. gephyropagum* were found after 2 weeks and then disappeared with time. The propagule numbers of *A. dactyloides, A. superba,* and *M. ellipsosporum* increased in the rhizosphere up to week 8, which corresponded to the time of flowering. After 8 weeks, *M. ellipsosporum* had nine times as many propagules in the root zone as in root-free soil. *M. geophyropagum* failed to grow in the tomato rhizosphere in this experiment (Fig. 1).

According to the root-galling index, the number of free-living nematodes in the soil, and the number of nematode eggs in roots at week 12, none of the fungi suppressed the nematodes. *Arthrobotrys dactyloides* treatments had the lowest galling index and lowest nematode numbers in soil, but these values were not significantly different from the control. There were no differences in root and shoot weights among the various treatments (Table 2).

Discussion

The rhizosphere-colonizing capacity of the 38 tested fungi varied among isolates of the same species. Different isolates of *M. ellipsosporum,* for example, varied from 0 to 55% in tomato root segment colonization. Similar variability was observed previously for the egg-parasitic fungus *Verticillum clamydosporum* Goddard, isolates of which varied in root segment colonization between 0 and 80% (Bourne et al., 1994). Root-colonization by nematode-trapping fungi has been shown to vary among different plant species (Persmark and Jansson, 1997). These results indicate that, if fungal rhizosphere colonization is desired, a selection of isolates based on colonization of roots of the target plant should be performed. The simple and rapid screening test presented here provides a way to select rhizosphere-competent nematode-trapping fungi for use in further examinations in biological control experiments.

The rhizosphere-colonizing capacity of the fungi chosen from the screening test was in the order: *M. ellipsosporum* > *A. dactyloides* > *A. superba,* with no root colonization by *M. gephyropagum.* The most frequent fungal isolate on the roots in the screening test, *M. ellipsosporum,* also had the largest difference in fungal density between the rhizosphere and the root-free soil in the biological control experiment. The largest difference in propagule number between the rhizosphere and the root-free soil generally coincided with the time of flowering. Leguminous plants appear to exert a stronger rhizosphere effect than cereals (Peterson and Katznelson, 1965), and this effect is greater at the time of flowering (Persmark and Jansson, 1997)—probably due to increased root exudation. Root colonization by *V. chlamydosporium* increased after infection by root-knot nematodes due to release of root exudates (Bourne et al., 1996). Peterson and Katznelson (1965) observed that *A. oligospora* was more frequent in the rhizosphere of soybean than of wheat and that root extracts from the two plants did not affect the growth and spore germination of this fungus, but that bacteria isolated from wheat roots had a stronger inhibitory effect on *A. oligospora* than did bacteria from soybean. They therefore suggested that antibiosis was an important factor in the ability to colonize the roots.

The four species examined in the biologi-

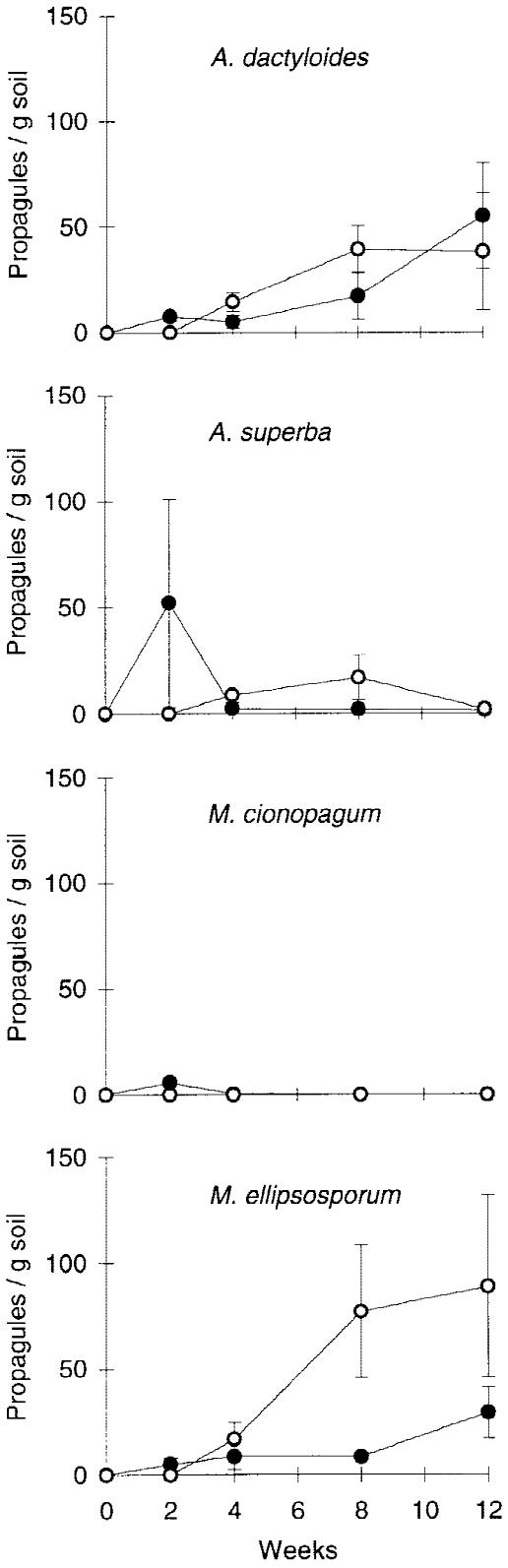

FIG. 1. Colonization of soil (●) and tomato rhizosphere (○) by nematode-trapping fungi. Vertical bars represent standard errors.

cal control experiment varied in growth and establishment in rhizosphere and soil. This may be due to the fact that the fungi have different growth requirements in the soil and, furthermore, may respond differently to the nutrient source applied with the pellets. The amino acid food base in the pellets was added to give the fungi a good nutritional start to overcome competition and fungistasis (Lockwood, 1977). Furthermore, the presence of small peptides and amino acids may also induce trap formation in some nematode-trapping fungi (Nordbring-Hertz, 1973). It is possible that this food base became a nutrient source also for indigenous soil organisms, with increasing competition as the result.

The network-forming *A. superba* grew rapidly during the first 2 weeks after introduction to soil, while the other fungi tested had slower growth rates. Nematode-trapping fungi with different trap structures have been shown to have growth optima at different times during decomposition of organic matter in soil. The network-forming fungi reached a peak and then declined during the first half of an 11-week period, the knob-forming fungi peaked during the second half of the period, and the ring-forming fungi appeared only in the final stage of the period (Cooke, 1963a). The rapid peak in growth of *A. superba* may also be due to the rich sporulation of the species, since the soil dilution plate technique used in the current study did not distinguish between conidia and hyphae. There is a delicate balance between trap formation and conidiophore formation in *A. superba* due to environmental factors (Jansson and Nordbring-Hertz, 1981), and under the conditions in our experiments conidiation may have been the dominant morphogenic event.

Arthrobotrys superba grew out rapidly within 2 weeks in the soil and then decreased in propagule number. The fungus may therefore have been active for too short a period for controlling the *Meloidogyne* spp., which were added as a mixture of eggs and juveniles. *Arthrobotrys dactyloides* and *M. ellipsosporum* colonized the soil and rhizosphere at a much slower rate and may have been unable

to reduce early root infection by the nematodes. A combination of slow-growing and fast-growing fungi in the same preparation may result in a more effective biological control.

We were not able to show substantial control with any of the fungi tested, and this was irrespective of the capability to colonize the rhizosphere. When tomato plants were grown together with the best root-colonizing fungus, *M. ellipsosporum,* the nematode damage even increased. The reason for this is unknown. Earlier studies, however, have shown that *M. ellipsosporum, M. gephyropagum* (Jaffee and Muldoon, 1997), *A. superba* (Jacobs, 1997), and *A. dactyloides* (Galper et al., 1995; Stirling et al., 1998; Stirling and Mani, 1995) have the capacity to suppress *Meloidogyne* spp. Jaffee and Muldoon (1997) attained control of *M. javanica* with *M. gephyropagum* when the fungus increased from the inoculum to 3,000 propagules/g soil. We never found such high densities in our experiments with any fungus, even if we used twice as many fungal pellets. The reason for this is unknown but could be due to difference in the methodology used to quantify fungal propagules, different fungal isolates used, or a soil that was less supportive for growth of the fungi. Furthermore, the control observed by Jaffee and Muldoon (1997) was at an early stage and confined to the first infection cycle of the nematodes. Our disease rating was performed after only 12 weeks. In our study, treatment with *A. dactyloides* had the lowest galling index and the lowest number of free-living nematodes in soil. This is in agreement with a study by Cooke (1963b), in which he suggested that the ring-forming species may be better adapted to control nematodes than other nematode-trapping fungi.

The predacious activity of nematode-trapping hyphomycetes is dependent on the inoculum density (Cooke, 1963b), and the insufficient nematode control in our experiments may be due to insufficient fungal density in the pellets or to antagonistic activity of indigenous soil fauna. Enchytraeids were found to digest fungal alginate pellets, and the addition of fungal pellets to soil even increased the number of enchytraeids (Jaffee, et al., 1997). Stirling and Mani (1995) suggested that a pre-fermentation step of the alginate pellets when introducing them to soil was necessary for successful control using *A. dactyloides,* and this idea was further developed in the preparation of commercial formulations of this fungus (Stirling et al., 1998). We did not perform this step in our experiments, and this might have contributed to the low degree of control observed. On the other hand, the fungus grew into the soil and also colonized the rhizosphere.

The aim of this work was to find a connection between root colonization by the nematode-trapping fungi and reduction of nematode damage to roots. Even if the fungi were able to colonize tomato roots, no substantial control was achieved. Fungal proliferation and colonization in the host plant rhizosphere have been suggested to be prerequisites for suppressing root-infecting nematodes (de Leij and Kerry, 1991), at least by the nematode egg parasite *V. chlamydosporium.* It is possible that these prerequisites may not apply to nematode-trapping fungi. In further studies it is important to find ways to infest the soil with fungi in order to minimize competition by indigenous microorganisms and soil fauna and to optimize the fungal outgrowth. It would also be valuable to find ways to facilitate the trap formation of nematode-trapping biological control agents.

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