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Effects of arbuscular mycorrhizal fungi and a non-pathogenic *Fusarium oxysporum* on *Meloidogyne incognita* infestation of tomato

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Abstract Arbuscular mycorrhizal (AM) fungi and non-pathogenic strains of soil-borne pathogens have been shown to control plant parasitic nematodes. As AM fungi and non-pathogenic fungi improve plant health by different mechanisms, combination of two such partners with complementary mechanisms might increase overall control efficacy and, therefore, provide an environmentally safe alternative to nematicide application. Experiments were conducted to study possible interactions between the AM fungus *Glomus coronatum* and the non-pathogenic *Fusarium oxysporum* strain Fo162 in the control of *Meloidogyne incognita* on tomato. Pre-inoculation of tomato plants with *G. coronatum* or Fo162 stimulated plant growth and reduced *M. incognita* infestation. Combined application of the AM fungus and Fo162 enhanced mycorrhization of tomato roots but did not increase overall nematode control or plant growth. A higher number of nematodes per gall was found for mycorrhizal than non-mycorrhizal plants. In synergisms between biocontrol agents, differences in their antagonistic mechanisms seem to be less important than their effects on different growth stages of the pathogen.

Keywords Arbuscular mycorrhiza · Non-pathogenic · *Fusarium oxysporum* · *Meloidogyne incognita* · Tomato

Introduction

The rhizosphere harbors a large number and diversity of soil micro-organisms, some of which are also able to colonize roots endogenously. With the exception of damaging pathogens, plants may benefit from rhizosphere micro-organisms either directly, as in the case of symbionts such as mycorrhizal fungi, or indirectly by the antagonistic activity of beneficial micro-organisms toward plant pathogens. The protective effect of arbuscular mycorrhizal (AM) fungi against plant parasitic nematodes is well documented (Hussey and Roncadori 1982; Saleh and Sikora 1984; Cooper and Grandison 1986). Similarly, non-pathogenic strains of *Fusarium oxysporum* are known to reduce plant infestation by plant parasitic nematodes (Hallmann and Sikora 1994). Whereas the main effects of AM fungi are seen in competition for nutrient sources and space, as well as the prevention of juvenile penetration, non-pathogenic fungi produce nematicidal substances and/or directly parasitize different stages of the nematode (Hallmann and Sikora 1996). The combination of two fungi with different antagonistic mechanisms could, therefore, improve efficacy and consistency of biological control. However, the effective interaction of two antagonists requires that they do not interfere with each other. Experiments were conducted to study interactions between the AM fungus *Glomus coronatum*, a non-pathogenic *F. oxysporum* and *Meloidogyne incognita*, and their effects on the growth and health of tomato.

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Materials and methods

The AM fungus *G. coronatum* isolated from the rhizosphere of wheat in a field near Kerpen-Buir, Germany was used for inoculum production on maize plants. After 12 weeks, the upper plant parts were removed and the roots colonized by *G. coronatum* were mixed with soil containing spores of *G. coronatum* to give a fresh inoculum.

Fo162, a non-pathogenic strain of *F. oxysporum,* was originally isolated from surface-sterilized tomato roots and selected for its antagonism toward *M. incognita* on tomato (Hallmann and Sikora 1994). Inoculum of Fo162 was produced by cultivating the fungus on potato dextrose agar (PDA) for 14 days under low-energy UV-light. The mycelium and conidia formed were scraped from the PDA and suspended in 100 ml sterile water. Spores were separated from the mycelium by passage through four layers of cheese cloth and resuspended at a concentration of 10^7 spores/ml.

The AM fungus was applied as a fine layer by filling plastic pots (Ø 16 cm, volume 3 l) with 800 g of heat-sterilized sand (twice at 180°C for 1 h), sprinkling 20 g of *G. coronatum* inoculum on the surface and covering the inoculum with 200 g sand. Three surface-sterilized (10 min in 1% NaOCl) seeds of tomato cv. Rheinlands Ruhm susceptible to *M. incognita* were placed at 1 cm depth into the soil. The first emerging seedling was used for the experiment

and the others were removed. Fo162 was applied 10 days after sowing by pipetting 1-ml aliquots of fungal spore suspension at three spots around the stem base.

Second-stage juveniles (J2) of *M. incognita* were used as nematode inoculum. Eggs were extracted from galled tomato roots using 1.5% NaOCl as described by Hussey and Barker (1973). Nematode eggs collected on a 25-µm mesh sieve were transferred to tap water and agitated for 7 days to induce juvenile hatching. Freshly hatched second-stage juveniles were separated from eggs using a modified Baerman technique (Oostenbrink 1960). The juvenile concentration was adjusted to deliver 1500 J2 per ml per pot. Aliquots of 1 ml J2 suspension were inoculated with a syringe at three spots 2 cm deep into the root zone of 3-week-old tomato seedlings.

Plants were grown under greenhouse conditions and fertilized weekly with 0.1% Flory 2 (NPK 16–9-22, Euflor, Munich. The experiment consisted of 8 treatments: 1. control, 2. AM fungus *G. coronatum* (AM), 3. *F. oxysporum* Fo162 (Fo), 4. *M. incognita* (Mi), 5. AM + Mi, 6. Fo + Mi, 7. AM + Fo, and 8. AM + Fo + Mi. Each treatment consisted of 10 replicates resulting in 240 pots (= 8×10 × 3). The experiment was carried out in a completely randomized design and was repeated once in a time-independent experiment. Data were taken at 3 sampling times 9, 12 and 15 weeks after sowing.

At each sampling time, the following parameters were recorded: shoot fresh weight, root length, gall index, number of egg masses, number of nematodes per gall and root colonization by *G. coronatum* and *F. oxysporum* Fo162. For root length, roots were cut into 1-cm sections and measured with a Comair root length scanner (Hawker de Havilland). The nematode gall index was rated on a scale of 0–10 with 0 = no gall formation and 10 = completely galled (Zeck 1971). Thereafter, 10 root sections 1 cm in length were cut from different parts of the root system and imprinted on PDA for re-isolation of Fo162 from the root surface. For evaluation of internal growth, the root sections were surface sterilized with 1% NaOCl for 3 min, rinsed 3 times in sterile water and slightly pressed onto PDA containing 100 ppm chloramphenicol and 100 ppm ampicillin to suppress bacterial growth. The root sections were incubated at 22°C in a growth chamber illuminated with low-energy UV-light. Mycelium growing out of the root sections was transferred to fresh PDA and incubated for 14 days. Re-isolation of Fo162 from the root surface and interior was confirmed by microscopic comparison of fungal conidia with those of the original isolate. In addition, 20 1-cm root sections were used to assess root colonization by the AM fungus. These roots were cleared in 10% KOH at 60°C for 1 h and stained in a solution of 10% blue ink (Pelikan Co., Hanover) in 5% acetic acid, as described by Vierheilig et al. (1998). The intensity of root mycorrhization was expressed as percentage of total length of 20 root sections colonized by *G. coronatum*.

For the assessment of egg masses, plant roots were immersed for 15 min in 0.015% Phloxine B, which specifically stains the gelatinous matrix of nematode egg masses bright red and simplifies counting. Samples of 20 galls were randomly collected from all plants of each treatment and bleached in 10% KOH (w/v) at 75°C overnight. Galls were rinsed with tap water, acidified with 1% HCl for 5 min and stained in a solution of 10% blue ink in 5% acetic acid for 2 h. The galls were squeezed between two microscope slides and the number of nematodes per gall counted.

The experiment was replicated once and data were analyzed according to standard analysis of variance procedures with the software SigmaStat for Windows 2.0 (SPSS Science Software, Erkrath). The Tukey test was used for mean comparison. Statistical differences referred to in the text are significant at P=0.05.

Results

Plant growth

At 9 weeks after sowing, all treatments apparently stimulated shoot fresh weight over the control, but the differences were only significant for *F. oxysporum* Fo162 (Fo) (Table 1). No differences in shoot weight were observed 12 weeks after treatment. At 15 weeks after treatment, the highest shoot weight (7 g) was recorded for AM + Fo, followed by AM (6.9 g) and the control (6.6 g). At this time, treatments with *M. incognita* showed the lowest shoot fresh weights and differences were significant for Mi with 4.7 g.

Root length was not affected by separate applications of AM and Fo, but was significantly reduced by Mi 12 and 15 weeks after sowing (Table 2). Differences in root length between treatments increased over time and were highest 15 weeks after sowing, when root length of the control was 44.3 m, compared with 19.9 m for Mi. Pre-inoculation with the AM fungus did not improve root length, but significantly reduced losses in root length due to *M. incognita*. Compared with AM, Fo was less effective in root length compensation. Root length was also reduced by the combined application of AM + Fo,

Table 1 Effect of *Glomus coronatum* (*AM*), *Fusarium oxysporum* Fo162 (*Fo*) and/or *Meloidogyne incognita* (*Mi*) on shoot dry weight of tomato cv. Rheinlands Ruhm with time after sowing. Means followed by different letters within each column are significantly different based on the Tukey test (P=0.05, n=10)

Treatment	Shoot dry weight (g per plant)		
	9 weeks	12 weeks	15 weeks
Not inoculated	2.2 b	5.3 a	6.6 ab
AM	3.5 ab	5.3 a	6.9 a
Fo	4.6 a	5.8 a	6.2 ab
Mi	4.4 ab	4.9 a	4.7 b
AM + Mi	4.0 ab	4.7 a	5.1 ab
Fo + Mi	3.4 ab	4.5 a	5.3 ab
AM + Fo	3.2 ab	4.4 a	7.0 a
AM + Fo + Mi	2.6 b	3.6 a	5.0 ab

Table 2 Effect of separate and combined application of *G. coronatum* (*AM*), *F. oxysporum* Fo162 (*Fo*) and *M. incognita* (*Mi*) on tomato root length with time after sowing. Means followed by different letters within each column are significantly different based on the Tukey test (P=0.05, n=10)

Treatment	Root length (m per plant)		
	9 weeks	12 weeks	15 weeks
Not inoculated	32.6 a	41.0 a	44.3 a
AM	37.9 a	38.0 a	44.4 a
Fo	39.3 a	38.3 a	43.4 a
Mi	33.0 a	29.6 b	19.9 c
AM + Mi	34.5 a	32.8 ab	32.9 b
Fo + Mi	32.0 a	27.3 b	28.0 bc
AM + Fo	39.5 a	33.9 ab	35.2 b
AM + Fo + Mi	33.2 a	27.0 b	26.5 bc

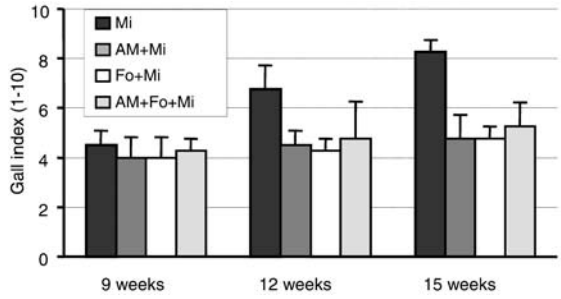

Fig. 1 Effect of *Glomus coronatum* (*AM*) and/or *Fusarium oxysporum* Fo162 (*Fo*) on the gall index of *Meloidogyne incognita* (*Mi*) on tomato cv. Rheinlands Ruhm, presented as means and standard deviations (P=0.05, n=10)

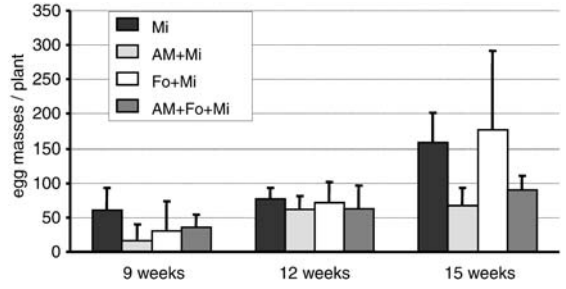

Fig. 2 Effect of *G. coronatum* (*AM*) and/or *F. oxysporum* Fo162 (*Fo*) on the egg masses formed by *M. incognita* (*Mi*) on tomato cv. Rheinlands Ruhm, presented as means and standard deviations (P=0.05, n=10)

although this treatment resulted in the highest shoot weight.

Nematode infestation

At 9 weeks after sowing, inoculation with *M. incognita* had no effect on gall index between treatments (Fig. 1). However, the gall index of the control continuously increased with time to a final score of 8.25 at 15 weeks after sowing. In all treatments receiving fungal inoculum, the gall index was around 5 and significantly lower than in the control. At 15 weeks after treatment, reductions in gall index were 42% for AM and Fo and 36% for AM + Fo.

The number of egg masses was significantly reduced by AM at 9 and 15 weeks after sowing (Fig. 2). In comparison, pre-inoculation with Fo alone had no effect on the number of egg masses, whereas the combination of AM + Fo significantly reduced their number 15 weeks after sowing. In general, one nematode per gall was observed for plants inoculated with Mi or Mi + Fo (Fig. 3). The number of nematodes per gall was similar at all three sampling times. In contrast, plants pre-inoculated with AM harbored an average of 1.7–2.3 nematodes per gall, and individual galls contained up to 4 nematodes (Fig. 4).

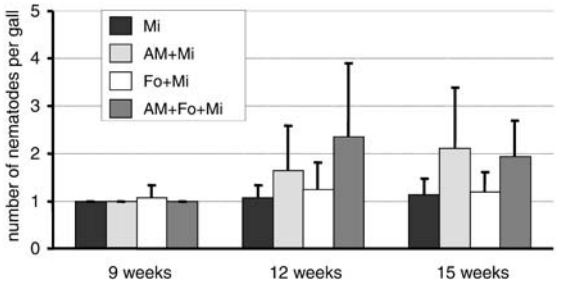

Fig. 3 Effect of *G. coronatum* (*AM*) and *F. oxysporum* Fo162 (*Fo*) on the number of *M. incognita* (*Mi*) per gall of tomato roots, presented as means and standard deviations (P=0.05, n=10)

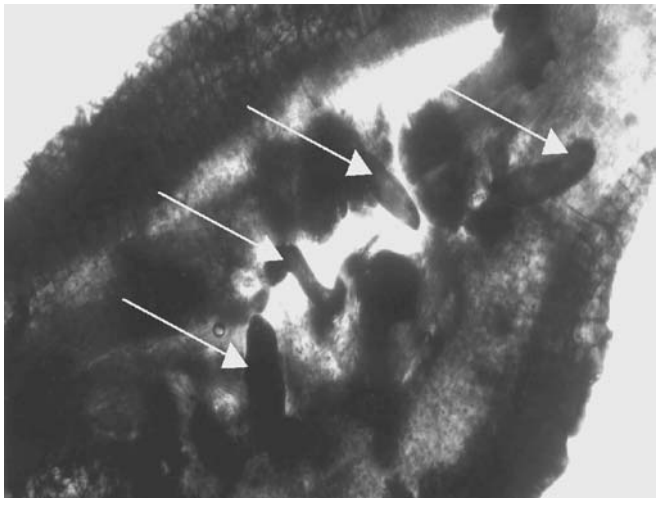

Fig. 4 Longitudinal section of a root gall of a 15-week-old mycorrhizal tomato plant harboring four larvae (*arrows*) of *M. incognita*

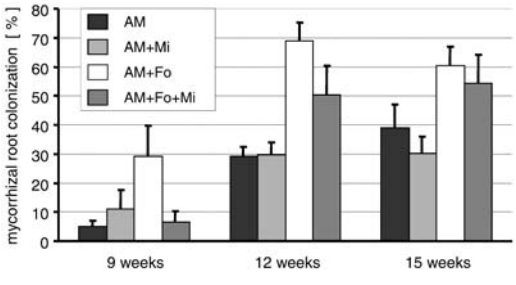

Fig. 5 Effect of *F. oxysporum* Fo162 (*Fo*) and *M. incognita* (*Mi*) on the intensity of *G. coronatum* (*AM*) colonization of tomato roots cv. Rheinlands Ruhm, presented as means and standard deviations (P=0.05, n=10)

Root colonization by antagonistic fungi

Root colonization by AM increased from below 5% root length at 9 weeks after sowing to 29% and 39% at 12 and 15 weeks after sowing, respectively. In the presence of Fo, root colonization by AM was significantly enhanced (Fig. 5). This positive effect of Fo on AM root colonization was also evident in the presence of *M. incognita*.

Microscopic examination of root sections revealed that AM preferably colonized the root cortical parenchyma, whereas *M. incognita* was primarily located in the central cylinder. Fo162 was frequently re-isolated from the root surface of treated plants but was not isolated from or observed inside root tissue.

Discussion

Root knot nematodes of the genus *Meloidogyne* cause economic losses on several crops including tomato (Mai 1985). Nematode infestation damages the plant by disrupting the uptake and transport of water and nutrients. An early colonization of plant roots with antagonistic fungi can protect the plant against nematode invasion by parasitism, competition or physical enclosure through a mycelial mat. Lower gall indices have been observed for plants pre-inoculated with AM fungi (Hussey and Roncadori 1982; Saleh and Sikora 1984) and non-pathogenic strains of fungal pathogens (Hallmann and Sikora 1994).

AM fungi are obligate biotrophs that colonize plant roots endogenously, whereas strains of non-pathogenic *F. oxysporum* are saprophytes reported to colonize the root surface and/or the root interior of various crops (Mandeel and Baker 1991; Salerno et al. 2000; Benhamou and Garand 2001). *F. oxysporum* Fo162 also colonizes the interior of tomato roots (Hallmann and Sikora 1994); however, in the present study, Fo 162 was only re-isolated from the rhizoplane. Since both fungi reduce nematode incidence on tomato, they were applied concomitantly to study synergistic effects on nematode control and mutual interactions. The combined application of *G. coronatum* and Fo162 did not result in additive or synergistic nematode suppression or plant growth enhancement. However, the experiments indicated some interesting interactions between *G. coronatum* and *F. oxysporum*. Fo162 stimulated mycorrhization by *G. coronatum* and, furthermore, nematode galls on mycorrhizal plants contained more juveniles per gall than those on non-mycorrhizal plants.

A stimulation of mycorrhiza by saprophytic *F. oxysporum* was also reported by García-Romera et al. (1998) and Fracchia et al. (2000) for soybean, pea, and sorghum. Other saprophytic fungi as well as rhizosphere bacteria associated with AM may also increase mycorrhization and its beneficial effect on plants (Alten et al. 1993; Perotto and Bonfante 1997; Fester et al. 1998; Godeas et al. 1999). Non-pathogenic *Fusarium* strains may be able to stimulate the development of AM fungi within the roots by altering root physiology and/or to stimulate spore germination of AM fungi in the soil. They may also lead to an increase in the probability of mycorrhizal infection by protecting AM fungi outside the roots. In parallel, the mechanisms underlying disease control by non-pathogenic strains of *F. oxysporum* are not completely understood. Microbial competition for nutrients, competition for infection sites and root colonization, mycoparasitism and plant-induced resistance through the rapid stimulation of a general cascade of non-specific defense responses have been proposed (Benhamou et al. 2002). The latter effect does not depend on the colonization of root tissue as demonstrated for rhizobacteria (van Loon et al. 1998), which are also able to induce resistance against plant pathogenic nematodes (Reitz 1999).

However, it is not clear here why improved mycorrhization by Fo162 did not result in either better nematode control or plant growth. In general, nematode control appears when a certain rate of mycorrhization is reached. For cotton, Saleh and Sikora (1984) reported that 38% mycorrhization by *G. fasciculatum* was required for control of *M. incognita*. In our study, mycorrhization by *G. coronatum* was 11% after 9 weeks and around 30% after 12 and 15 weeks. While no reduction in gall index was observed after 9 weeks, reductions were significant after 12 and 15 weeks, indicating that 30% mycorrhization was the threshold level for nematode control. A further increase in mycorrhization above that level did not necessarily lead to higher nematode control. Although mycorrhization of AM + Fo was above 50% at 12 and 15weeks after sowing, compared with 30% for AM alone, differences in gall index were not observed.

AM fungi colonize parenchyma cells of plant roots and are known to alter the root physiology (Linderman 1994) and to induce local and systemic resistance to fungal pathogens (Cordier et al. 1998). Induced resistance can be associated with wall appositions reinforced by callose and the elicitation of thickenings of root cell walls. Similar mechanisms may be involved in the reduction of *M. incognita* by AM fungi. In addition, a net of extraradical hyphae influences the composition of micro-organisms and soil structure in the rhizosphere (Smith and Read 1997).

Extraradical hyphae of *G. coronatum* and Fo162 colonize a similar habitat within the rhizosphere/rhizoplane and, therefore, compete for plant-derived nutrients. Competition for nutrients and space may explain why the combination of *G. coronatum* with Fo162 did not result in additive or synergistic effects on plant growth or nematode control. Root tissue colonized by *G. coronatum* was not parasitized by *M. incognita*. Similar observations were made by Cooper and Grandison (1986) on tomato and white clover for *Meloidogyne hapla* invasion of mycorrhizal roots. Since mycorrhization was only 30–50%, galls still formed in non-mycorrhizal root sections and contained more nematodes per gall than in non-mycorrhizal plants. While mycorrhization limited potential infection sites for nematode juveniles, nematode invasion probably concentrated on the non-mycorrhizal root sections, resulting in higher numbers of nematode per gall. In contrast to *G. coronatum*, the non-pathogenic Fo162 reduced neither the number of egg masses nor the number of nematodes per gall, indicating a different mode of action.

Fo162 is reported to reduce nematode infestation by preventing juveniles from invading roots and interfering with juvenile development within the root tissue (Hallmann and Sikora 1994). Interestingly, in the present

study, Fo162 was not observed inside the tomato roots at all. This might explain why only the gall index was reduced and not the number of egg masses. The gall index refers to the number and size of galls. In small galls formed by one or few juveniles, the females lay their egg masses primarily outside the root tissue, whereas in large galls formed by several juveniles, the majority of females lay their egg masses inside the root tissue. Internal egg masses usually evade visual detection. Thus, in the presence of Fo162, it appears that fewer juveniles penetrated the root tissue. These then formed small galls and the developing females laid their egg masses outside of the root tissue. Undisturbed nematode development in the root can be expected since Fo162 did not colonize the tomato roots internally. In the absence of Fo162, more juveniles entered the root tissue, forming large galls and increasing the gall index. However, apparently only few females were able to lay their egg masses outside the root tissue because the number of egg masses was not different from the treated plants. It can only be speculated whether the lack of internal colonization by Fo162 prevented better control. Internal colonization is reported for several non-pathogenic *F. oxysporum* strains controlling fungal pathogens by mechanisms such as competition and induced resistance (Olivain and Alabouvette 1997; Larkin and Fravel 1999; Salerno et al. 2000).

Combining *G. coronatum* with *F. oxysporum* Fo162 did not result in additive or synergistic control of *M. incognita*. However, synergism was reported for combinations of the AM fungus *Glomus mosseae* with *Paecilomyces lilacinus* and *Glomus deserticola* with *Pasteuria penetrans* in the control of *Meloidogyne javanica* on tomato (Al-Raddad 1995; Rao and Gowen 1998). *P. lilacinus* is an egg pathogen and, thus, different to Fo162, which inhibits juvenile penetration and development (Hallmann and Sikora 1994). To achieve synergistic effects on nematode control, the combination of fungal partners that attack different developmental stages of the nematode might be effective. This was not the case in the present work, where *G. coronatum* and *F. oxysporum* had different modes of action, but both primarily inhibited invasion of juveniles and/or their early establishment in the root. For synergism, differences in the antagonistic mechanisms of the biocontrol agents seem to be less important than their effects on different stages of the pathogen. The induction of resistance to internal root colonization by non-pathogenic *F. oxysporum* might also contribute to limit further development of *M. incognita* within roots and to increase the efficacy of nematode control by a combination of biocontrol agents. More work has to be done to test this hypothesis and to explore the active mechanisms.

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