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Interactions between Saprotrophic *Fusarium* Strains and Arbuscular Mycorrhizas of Soybean Plants

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Abstract

We studied the effect of inoculation with the saprotrophic fungi *Fusarium concolor*-2183, *F. equiseti*-91, *F. graminearum*-122, *F. lateritium*-2317, *F. moniliforme*-379, *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126, *F. solani*-51, *F. solani*-339, *F. solani*-2584 and *F. stilboide*-2169 on soybean (*Glycine max*) in unsterile and sterilized soils and in soils with or without arbuscular mycorrhizal (AM) inoculation with *Glomus mosseae*, in a greenhouse trial. Plant dry weight of non AM soybean was unaffected by the presence of any *Fusarium*. In contrast, AM colonization increased under all experimental conditions when *F. oxysporum*-738, *F. oxysporum*-126 or *F. stilboide*-2169 was used, and AM plant shoot dry weight increased in the presence of *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126 or *F. solani*-51. Synergistic effect of some *Fusarium* strains on *G. mosseae* but not effect of the AM fungus on the saprotrophic fungi were found.

Keywords: Arbuscular mycorrhizas, *Fusarium*, *Glomus mosseae*, *Glycine max*, saprotrophic fungi

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1. Introduction

Saprotrophic fungi live in the rhizoplane and mycorrhizosphere of plants, where they obtain nutritional benefit from organic matter, inorganic compounds, exudates, mucilages and sloughed cells from living roots, as well as from dead fungi (Finlay and Söderström, 1992). The activity and metabolism of these fungi may result in the production of substances that promote or inhibit the growth of other rhizosphere microorganisms (Dix and Webster, 1995). Saprotrophic fungi of the genus *Fusarium* are common and cosmopolitan species that occur in association with many plants and soils (Booth, 1971). They are highly competitive against pathogenic fungi, and some of them produce plant growth-promoting substances (Domsch et al., 1980).

The beneficial effects of arbuscular mycorrhizal (AM) fungi on plant growth depend in part on the members of the symbiosis and their interactions with other organisms in the rhizosphere (Ocampo, 1993). In spite of increasing interest in the interactions between AM and saprotrophic fungi, information about these interactions is scarce (Camprubi et al., 1995; McAllister et al., 1996; Tarafdar and Marschner, 1995). Synergistic and antagonistic interactions between *Glomus mosseae* and saprotrophic fungi have been observed (McAllister et al., 1994; 1996). Some experimental results confirm the existence of synergistic effects between AM and saprotrophic fungi (Calvet et al., 1992), and combined inoculation can therefore have beneficial effects for the host plant (Calvet et al., 1993). Previous studies show that *F. solani* did not inhibit germination of *G. mosseae* spores, and markedly stimulated endophyte hyphal development (McAllister et al., 1994). *F. equiseti* inhibited spore germination but increased hyphal growth of *G. mosseae* spores (McAllister et al., 1996). The saprotrophic fungi *F. solani* and *F. equiseti* did not affect AM colonization of maize roots (McAllister et al., 1994; 1996).

The aim of this work was to study the effect of inoculation with the AM fungus *G. mosseae* and saprotrophic strains of *Fusarium* sp. on AM colonization of roots and growth of the host plant.

2. Materials and Methods

Plants were grown in 300 ml open pots of soil collected from the Province of Granada, Spain. The soils were a calcexerollic Xerochrept type, pH 8.4 (soil No. 1) and an aquic Xerofluvent pH 8.1 (soil No. 2) (for full details see García-Romera and Ocampo, 1988). The soils were used either unsterilized or steam-sterilized and mixed with sterilized quartz sand (1:1, V:V). Soybean (*Glycine max* L.) was used as the test plant. Seeds were sown in moistened sand, and after 2 weeks seedlings were transplanted to the pots and grown under greenhouse

conditions. Natural light was supplemented by Sylvania incandescent and cool-white lamps, 400 nmol m^{-2} s^{-1}, 400–700 nm. A 16–8 h light-dark cycle at 25 to 19°C was used and relative humidity was 50%. Plants were watered from below by capillarity, and fed with a nutrient solution (Hewitt, 1952) lacking phosphate.

The AM inoculum consisted of 5 g of rhizosphere soil from alfalfa-plant pot cultures of an isolate of *G. mosseae* (Nicol. & Gerd.) Gerd. and Trappe, which contained spores (15 sporocarps per g with 1 to 5 spores per sporocarp), mycelium and colonized root fragments. Uninoculated plants were given filtered leachings from the inoculum soil. Soil filtrate (Whatman No. 1 filter paper) from the rhizosphere of mycorrhizal plants was added to the AM uninoculated treatment. The filtrate contained common soil microorganisms, but no propagules of *G. mosseae*.

Fungi present in the rhizosphere soil and roots of maize cultivated in the Province of Buenos Aires (Argentina) were isolated by the particle washing method (Widden and Bisset, 1972) using a multichamber washing apparatus. Thirty washings were necessary to remove sclerotia, spores, and other fungal structures from soil particles and the roots of maize. Twenty soil particles (2 mm) were dried on sterilized filter paper and plated on 2% malt extract agar containing antibiotics (5 μg ml^{-1} streptomycin and 10 μg ml^{-1} tetracyclin). From the resulting colonies *Fusarium concolor* Reinking, BAFC Cult. No. 2183; *F. equiseti* (Corda) Sacc., BAFC Cult. No. 91; *F. graminearum* Schwave, BAFC Cult. No. 122; *F. lateritium* Nees, BAFC Cult. No. 2317; *F. moniliforme* Sheldon, BAFC Cult. No. 379; *F. oxysporum* Schlecht., BAFC Cult. No. 93; *F. oxysporum* Schlecht., BAFC Cult. No. 738; *F. oxysporum* Schlecht,. BAFC Cult. No. 126; *F. solani* (Mart.) Sacc., BAFC Cult. No. 51, *F. solani* (Mart.) Sacc., BAFC Cult. No. 339; *F. solani* (Mart.) Sacc., BAFC Cult. No. 2584; and *F. stilboide* Wollenw., No. 2169 (Booth, 1977) were selected and transferred to tubes of potato dextrose agar and 2% malt extract at 4°C as stock cultures. Strains are kept at the fungal culture collection of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires in Buenos Aires, Argentina.

An aqueous suspension of *Fusarium* strains in sterile distilled water containing approximately 2×10^5 spores ml^{-1} was prepared from cultures grown in potato dextrose agar (1 week, 27°C). Four treatments were used in experiments with sterilized soils: (1) uninoculated controls, (2) soil inoculated with *Fusarium*, (3) soil inoculated with *G. mosseae*, and (4) soil inoculated with both *G. mosseae* and *Fusarium*. Two treatments were used in experiments with unsterilized soils: (1) uninoculated controls and (2) soil inoculated with *Fusarium*. Plants were inoculated at the time of transplanting (after 2 weeks of growth). The saprotrophic fungus was inoculated 2 weeks after *G. mosseae*.

To evaluate the population of *Fusarium* strains inoculated to sterilized soils No. 1 and 2, rhizosphere soils were sampled as described by García-Garrido and Ocampo (1988). About 1.5 g of rhizosphere soil was taken from each of the experimental pots and 10-fold aqueous dilution series (from 10^{-1} to 10^{-4}) were prepared for each sample. The number of saprotrophic colony forming units (CFUs) in suitable dilutions of such samples, taken from the five replicate pots of each treatment, were counted on potato dextrose agar medium. Rhizosphere soil was quantified as follows: soil from dilutions of 10^{-1} and 10^{-2} was recovered, dried at 105°C and weighed. The number of CFUs was expressed per g of dry soil.

Plants were harvested after 8 weeks and dry matter weight was determined. Part of the root system was cleared and stained (Phillips and Hayman 1970), and the percentage of root colonization was measured (Giovannetti and Mosse, 1980).

The results were evaluated statistically with Duncan's new multiple range test.

3. Results

The *Fusarium* isolates were not pathogenic to soybean plants even when plants were inoculated with high concentration of fungal conidia. Plant dry weight of soybean was not affected by the presence of *Fusarium* strains (data not shown).

Shoot dry weight of soybean grown in unsterilized soil No. 1 was not affected by the presence of *F. lateritium*-2317, *F. moniliforme*-379 and *F. stilboide*-2169, but increased in response to the other saprotrophic fungi tested (Table 1). However, root dry weight was lower in plants inoculated with *F. lateritium*-2317, *F. moniliforme*-379, *F. oxysporum*-126, *F. solani*-339, and *F. stilboide*-2169 than in controls. The rest of the *Fusarium* strains did not affect root dry weight. Root colonization by indigenous AM endophytes in soil No. 1 was significantly increased by inoculation with *F. equiseti*-91, *F. graminearum*-122, *F. moniliforme*-379, *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126, *F. solani*-51, *F. solani*-339, *F. solani*-2584 and *F. stilboide*-2169, but was not affected by *F. concolor*-2183 or *F. lateritium*-2317.

The shoot dry weight of soybean plants grown in unsterilized diluted soil No. 1 (Table 2) increased in the presence of *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126 and *F. solani*-51, but was not significantly affected by *F. equiseti*-91, *F. graminearum*-122 or *F. stilboide*-2169. Root dry weight increased only in the presence of *F. equiseti*-91 and *F. oxysporum*-738. The percentage of root length colonized by AM fungi (Table 2) in soybean plants grown in diluted

Table 1. Plant dry weight (shoot and root) and percentage of AM colonized root length in soybean (*Glycine max*) grown in unsterile soil No. 1 inoculated or uninoculated with *Fusarium* strains.

Fusarium strains	Dry weight (mg)		Root length colonization (%)
	Shoot	Root	
Control	1,080 a	1,183 efgh	50 ab
F. concolor-2183	2,020 e	1,365 gh	36 a
F. equiseti-91	1,540 bcd	961 bcde	77 def
F. graminearum-122	1,762 cde	1,150 defg	72 cd
F. lateritium-2137	1,250 ab	886 bc	45 a
F. moniliforme-379	1,416 abc	442 a	69 cd
F. oxysporum-93	1,840 de	1,303 fgh	72 cd
F. oxysporum-738	1,816 de	1,401 h	74 cde
F. oxysporum-126	1,810 de	902 bc	88 ef
F. solani-51	1,651 bcd	1,119 cdef	90 f
F. solani-339	1,671 bcde	762 b	69 cd
F. solani-2584	1,781 de	1,388 h	63 bcd
F. stilboide-2169	1,336 ab	943 bcd	91 f

Each figure is the mean for five pots. Column values followed by the same letter are not significantly different according to Duncan's multiple range test (P = 0.05).

Table 2. Plant dry weight (shoot and root) and percentage of AM colonized root length in soybean (*Glycine max*) grown in unsterile diluted soil No. 1 inoculated or uninoculated with *Fusarium* strains.

Fusarium strains	Dry weight (mg)		Root length colonization (%)
	Shoot	Root	
Control	1,102 a	1,475 a	25 a
F. equiseti-91	1,820 ab	2,503 bc	32 ab
F. graminearum-122	1,621 ab	1,960 ab	29 ab
F. oxysporum-93	2,000 b	1,560 ab	44 c
F. oxysporum-738	2,111 b	3,025 c	46 c
F. oxysporum-126	2,102 b	2,375 abc	48 c
F. solani-51	1,958 b	1,870 ab	44 c
F. stilboide-2169	1,521 ab	1,420 a	51 c

Each figure is the mean for five pots. Column values followed by the same letter are not significantly different according to Duncan's multiple range test (P = 0.05).

Table 3. Plant dry weight (shoot and root) and percentage of AM colonized root length in soybean (*Glycine max*) grown in sterilized diluted No. 1 soil in the presence or in the absence of *G. mosseae* and inoculated or uninoculated with *Fusarium* strains.

Fusarium strains	Dry weight (mg)		CFU × 10 g^{-1} soil	Root length colonization (%)
	Shoot	Root		
Without AM inoculum				
Control	1,202 a	2,117 b	0	
F. equiseti-91	1,213 a	2,160 b	126 a	
F. graminearum-122	1,252 a	1,875 a	70 a	
F. oxysporum-93	1,291 a	1,797 a	31 a	
F. oxysporum-738	1,084 a	1,761 a	170 a	
F. oxysporum-126	1,009 a	1,412 a	99 a	
F. solani-51	1,302 ab	1,867 a	82 a	
F. stilboide-2169	1,191 a	2,219 b	34 a	
With AM inoculum				
Control	1,422 b	2,960 e	0	71 b
F. equiseti-91	1,741 c	1,710 a	230 a	80 c
F. graminearum-122	2,178 d	2,625 d	45 a	70 b
F. oxysporum-93	1,846 cd	2,160 b	31 a	67 b
F. oxysporum-738	1,906 cd	2,460 c	180 a	83 c
F. oxysporum-126	1,847 cd	1,455 a	87 a	89 c
F. solani-51	1,726 c	2,405 b	58 a	68 b
F. stilboide-2169	1,811 c	2,605 d	40 a	78 c

Each figure is the mean for five pots. Column values followed by the same letter are not significantly different according to Duncan's multiple range test (P = 0.05).

unsterilized soil No. 1 was increased by *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126, *F. solani*-51 and *F. stilboide*-2169; none of the other fusaria affected root colonization.

G. mosseae increased shoot dry weight of soybean plants grown in sterilized soil No. 1 (Table 3), but none of the *Fusarium* fungi when inoculated alone affected the shoot dry weight of the plants. *F. equiseti*-91, *F. graminearum*-122, *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126, *F. solani*-51 and *F. stilboide*-2169 increased shoot dry weight of soybean plants when they were inoculated together with *G. mosseae*. Root dry weight was greater in AM

plants. Root dry weights of plants inoculated with *Fusarium* were lower than those of plants inoculated only with *G. mosseae*. The presence of *F. equiseti*-91 or *F. oxysporum*-126 decreased root dry weight in comparison with uninoculated control. *F. graminearum*-122, *F. oxysporum*-738 and *F. stilboide*-2169 increased root dry weight; *F. oxysporum*-93 and *F. solani*-51 had no effect on this parameter. The population of the different *Fusarium* strains in the rhizosphere of soybean was not affected by the presence of *G. mosseae*. When plants were inoculated with *G. mosseae*, the presence of *F. equiseti*-91, *F. oxysporum*-738, *F. oxysporum*-126 and *F. stilboide*-2169 significantly increased the percentage of AM colonized root length, whereas the other *Fusarium* strains had no effect.

Some *Fusarium* strains, *F. equiseti*-91, *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126 and *F. solani*-51 increased shoot dry weights of soybean plants grown in unsterilized soil No. 2 (Table 4). In contrast, *F. graminearum*-122 and *F. stilboide*-2169 had no effect. However, root dry weight increased only in the presence of *F. oxysporum*-738 and *F. oxysporum*-126. All saprotrophic fungi increased root colonization of soybean plants grown in unsterilized soil No. 2.

Neither *G. mosseae* nor the *Fusarium* strains significantly increased the shoot dry weight of soybean plants grown in sterilized soil No. 2 when these microorganisms were inoculated individually (Table 5). *F. oxysporum*-93, *F. oxysporum*-738, *F. oxysporum*-126, *F. solani*-51 and *F. stilboide*-2169 increased

Table 4. Plant dry weight (shoot and root) and percentage of AM colonized root length in soybean (*Glycine max*) grown in unsterile soil No. 2 inoculated or uninoculated with *Fusarium* strains.

Fusarium strains	Dry weight (mg)		Root length colonization (%)
	Shoot	Root	
Control	831 a	905 a	52 a
F. equiseti-91	1,036 bc	1,415 a	71 c
F. graminearum-122	1,022 abc	970 a	69 c
F. oxysporum-93	1,365 cd	1,305 a	66 bc
F. oxysporum-738	1,775 e	2,522 b	60 b
F. oxysporum-126	1,234 bcd	2,631 b	64 bc
F. solani-51	1,445 de	1,364 a	70 c
F. stilboide-2169	962 ab	1,003 a	65 bc

Each figure is the mean for five pots. Column values followed by the same letter are not significantly different according to Duncan's multiple range test (P = 0.05).

Table 5. Plant dry weight (shoot and root) and percentage of AM colonized root length in soybean (*Glycine max*) grown in sterilized No. 2 soil in the presence or in the absence of *G. mosseae* and inoculated or uninoculated with *Fusarium* strains.

Fusarium strains	Dry weight (mg)		CFU × 10 g^{-1} soil	Root length colonization (%)
	Shoot	Root		
Without AM inoculum				
Control	1,221 abc	1,502 ab	0	
F. equiseti-91	1,233 abcd	1,533 ab	9.7 a	
F. graminearum-122	1,475 bcde	1311 ab	3.6 a	
F. oxysporum-93	1,312 abcd	1,275 ab	2.5 a	
F. oxysporum-738	1,102 ab	1,250 ab	21.8 a	
F. oxysporum-126	1,025 a	1,002 a	8.2 a	
F. solani-51	1,321 abcd	1,325 ab	20.3 a	
F. stilboide-2169	1,210 abc	1,575 ab	5.6 a	
With AM inoculum				
Control	1,325 abcd	1,551 ab	0	18 a
F. equiseti-91	1,450 abcde	1,616 ab	18.1 a	31 a
F. graminearum-122	1,650 de	1,525 ab	22.2 a	39 ab
F. oxysporum-93	1,875 ef	1,850 ab	1.6 a	36 ab
F. oxysporum-738	1,850 ef	1,375 ab	12.3 a	59 bc
F. oxysporum-126	2,250 f	2,075 b	2.4 a	67 c
F. solani-51	2,252 f	1,325 ab	8.3 a	63 bc
F. stilboide-2169	2,675 g	1,875 ab	1.8 a	60 bc

Each figure is the mean for five pots. Column values followed by the same letter are not significantly different according to Duncan's multiple range test (P = 0.05).

shoot dry weight when they were inoculated together with *G. mosseae*. No significant differences in root dry weight of soybean plants were observed between any of the treatments tested. The population of the different *Fusarium* strains in the rhizosphere of soybean was not affected by the presence of *G. mosseae*. The presence of *F. oxysporum*-738, *F. oxysporum*-126, *F. solani*-51 and *F. stilboide*-2169 significantly increased the percentage of AM root length, whereas *F. equiseti*-91, *F. graminearum*-122 and *F. oxysporum*-93 had no effect.

4. Discussion

Dual inoculation with *G. mosseae* and some strains of *Fusarium* sp. led to additive AM colonization of roots and enhanced growth of soybean plants. Experimental results have confirmed the existence of a mutually stimulatory effect between mycorrhizal fungi and rhizosphere microorganisms (Barea and Jeffries, 1995). Synergistic and antagonistic interactions have also been reported between *G. mosseae* and saprotrophic fungi (McAllister et al., 1994). In spite of the synergistic effect of some *Fusarium* strains on the colonization of soybean root by *G. mosseae*, no influence of *G. mosseae* on the number of CFU of *Fusarium* were found in the rhizosphere of both soils. The lack of effect of other saprotrophic *Fusarium* strains on *G. mosseae* development was interpreted to depend on the time of inoculation of one microorganism with respect to the other: when *G. mosseae* was inoculated two weeks before the saprotrophic fungi, i.e. when the AM fungal mycelium was developed in the rhizosphere or when the AM fungus was established in the root, the AM fungal growth was not negatively affected by the *Fusarium* strains used (McAllister et al., 1994; 1996). Our results confirm these findings; shoot dry weight and colonization by AM fungi of the root of soybean plants cultivated in nonsterilized soils or soils inoculated with *G. mosseae* were not negatively affected by the presence of *Fusarium*. Often no apparent relationship is found between the percentage of colonization and the effect of the AM fungus on plant growth (Vierheilig and Ocampo, 1991). Plant-growth-promoting rhizobacteria could produce growth-promoting substances that could be absorbed by the AM fungal hyphae. The uptake of bacteria-produced metabolites could be enhanced by AM fungi, increasing a mycorrhizal effect (Lindermann, 1992). On the other hand, competition for metabolites between soil microorganisms and AM fungi may decrease the effectivity of AM fungi on plant growth (Bethlenfalvay et al., 1983; Ruiz-Lozano and Azcon, 1993). We found, for example, that in unsterilized soil No. 1, *F. concolor*-2183 significantly increased shoot dry weight but not the percentage of root length colonization. However, *F. stilboide*-2169 increased the percentage of root length colonization but did not increase shoot dry weight of soybean plants, whereas *F. lateritium*-2137 did not increase either parameter (Table 1). Nevertheless, the mechanisms involved in the mycorrhizal effect by soil microorganisms are unknown.

Rhizosphere microorganisms can affect root growth, and can also influence the AM symbiosis, although little is known about the mechanisms of these effects (Kothari el al., 1990). Our assays show that the effect on root dry weight of *Fusarium* alone or in combination with AM fungi varies widely. Saprotrophic fungi can affect mycorrhization in very different ways depending on the substrate where the plant was grown, or the kind of inoculum used

(McAllister et al., 1996). The ability of several of the *Fusarium* strains used in our experiments to increase AM colonization varied markedly depending on the type of inoculum and soil used. Some *Fusarium* strains increased the percentage of AM root length colonization in soybean plants grown in unsterilized soil No. 1, but were unable to increase colonization when this soil was diluted. We found that the effectiveness of different AM fungi on shoot dry weight was influenced differently by the same strain of some *Fusarium*. For example, *F. stilboide*-2169 increased the percentage of root length colonization and also increased the shoot dry weight of soybean plants grown in sterilized soils inoculated with *G. mosseae*; however, this strain failed to enhance colonization when plants were grown in unsterilized soil.

Future studies will investigate the effects of combination of *G. mosseae* and *F. oxysporum*-738 or *F. oxysporum*-126 under field conditions.

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