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Growth enhancement and Phytophthora blight (*Phytophthora capsici* Leonian) control by arbuscular mycorrhizal fungal inoculation in pepper

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Abstract

The effects of selected arbuscular mycorrhizal (AM) fungi, *Glomus mosseae*, *Glomus etunicatum*, *Glomus fasciculatum* and *Gigaspora margarita*, on growth of pepper seedlings and Phytophthora blight caused by *Phytophthora capsici* and the role of the phytoalexin, capsidiol were investigated. Root colonization by AM fungi reached between 61.3% and 68.1% in roots of pepper 4 weeks after transplanting. All tested AM fungi increased the shoot height between 23.4% and 31.7% and fresh and dry weights of shoots and roots of plants were enhanced by *G. etunicatum*, *G. fasciculatum* and *Gigaspora margarita* compared to uninoculated plants in pot experiments. *G. fasciculatum* increased yield significantly by 22% under greenhouse conditions. *G. mosseae* reduced the disease severity of *P. capsici* by 91.7%, 43.0% and 57.2% under pot, greenhouse and field conditions, respectively. Compared to the control, the capsidiol level was increased by preinoculation with *G. mosseae* and in the necrotic stems of *P. capsici*-inoculated pepper plants. In conclusion, AM fungi, especially *G. mosseae* enhanced the development of plants and reduced Phytophthora blight of pepper.
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Keywords: Pepper; *Phytophthora capsici*; Growth enhancement; Arbuscular mycorrhizal fungi; Capsidiol

1. Introduction

Phytophthora blight of pepper caused by *Phytophthora capsici* Leonian is the most important fungal disease of pepper growing areas worldwide (Ristaino and Johnston, 1999). The pathogen is soilborne and causes blight on single or groups of plants in the field, especially in soil saturated with water after irrigation or rainfall. In the early stages, the first signs of disease are brown necrotic areas on the root and crown of plants, after which the disease develops rapidly, causing plants to wilt and die (Black et al., 1991).

The roots of most plants are generally infected by arbuscular mycorrhizal (AM) fungi which are beneficial to their host plants (Agrios, 1997). AM fungi have the effect of promoting host plant growth mainly by enhancing mineral uptake through symbiosis in plant roots (Marschner and Dell, 1994). In addition, there are many reports on their role in controlling plant disease, especially soilborne fungal pathogens. The disease severity reducing effects by AM fungi are known in some plant–pathogen systems as reported in peanut—*Sclerotium rolfsii* (Krishna and Bagyaraj, 1983), eggplant—Verticillium wilt (Matsubara et al., 1995), tomato—*Phytophthora nicotianae* var. *parasitica* (Trotta et al., 1996), pea—*Rhizoctonia solani* (Karagiannidis et al., 2002) and tomato–Fusarium wilt (Caron et al., 1986; Akkopru and Demir, 2006).

Phytoalexins are low molecular mass antimicrobial compounds that are synthesized and accumulated in response to some abiotic factors or after pathogen infection in plants (Paxton and Groth, 1994). In some Solanaceous plants, the phytoalexin, capsidiol was isolated from pepper (Ward, 1976) and tobacco (Chappell et al., 1997). Phytoalexin accumulation has an important role as part

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of the multicomponent disease resistance mechanisms in plants (Mansfield, 1984; Kuc and Rush, 1985; Hammerschmidt, 1999).

The aim of the present work is to study the effects of the AM fungi, *Glomus mosseae*, *Glomus etuniatum*, *Glomus fasciculatum* and *Gigaspora margarita* on development of pepper plants and on *P. capsici* under pot, greenhouse and field conditions and to analyse the effect of capsidiol in disease resistance.

2. Materials and methods

2.1. Plant, pathogen and AM fungi

Pepper (*Capsicum annuum* L.) cv. Charliston Bagci was used in pot, greenhouse and field experiments. *P. capsici* Leonian was isolated from diseased tissue of naturally infected pepper plants on corn meal agar with pimaricin ($10\,mg\,l^{-1}$), vancomycin ($200\,mg\ l^{-1}$) and PCNB ($100\,mg\,l^{-1}$). AM inoculum was obtained from the Soil Department, Agricultural Faculty, University of Cukurova and inoculum of four AM fungi *G. mosseae* (Nicol.&Gerd.) Gerdemann&Trappe, *G. etunicatum* Becker&Gerdemann, *G. fasciculatum* (Thaxter) Gerd.&Trappe and *Gigaspora margarita* Becker&Hall was bulked up on maize (*Zea mays* L.) and used in the experiments.

2.2. AM fungus inoculation, seedling production and plant growth conditions

Pepper seeds were surface disinfested in 2% NaOCl solutions for 5 min and thoroughly washed twice with sterile distilled water. Pepper seedlings were produced in plastic containers (30 × 40 cm). The mixture of soil, sand, and pumice (1/1/1, v/v/v) was autoclaved at 121 °C and 100 kPa twice for 1 h each time and used as growth medium. For the AM seedling production, AM inocula, soil infected with spores mixed with root fragments, was incorporated 2–3 cm below the seeds for each AM fungus (Menge and Timmer, 1982). The inoculum amount used was determined after quantifying the spore numbers for each AM fungus (Gerdemann and Nicholson, 1963) and the inoculum was added as a band in plastic containers with spore inocula of *G. mosseae* (188 spores $10\,g^{-1}$ soil, 2.1 kg), *G. etunicatum* (268 spores $10\,g^{-1}$ soil, 1.3 kg), *G. fasciculatum* (229 spores $10\,g^{-1}$ soil, 1.7 kg) and *Gigaspora margarita* (235 spores $10\,g^{-1}$ soil, 1.6 kg). Pepper seeds were sown in containers without AM fungus inoculation using same growth medium. The plastic containers were placed in a growth room at 25 ± 2 °C temperatures. During seedling production until 3–4 leaf stage, seedlings were watered with deionized water.

When seedlings were transplanted into pots, greenhouse and field, AM fungal spore inoculum for each fungus was added to seedling beds (*G. mosseae* (50 g), *G. etunicatum* (35 g), *G. fasciculatum* (45 g) and *Gigaspora margarita* (40 g)).

2.3. Plant growth and yield

For the determination of the effect of mycorrhizal fungi on development of the plant, important plant growth parameters such as plant height, shoot and root fresh and dry weights in pot conditions and yield under greenhouse conditions were examined.

Plants with 2–3 leaves infected with or without AM fungi were transplanted to 15 cm-diameter pots containing an autoclaved mixture of soil, sand and pumice (1/1/1, v/v/v). The following treatments with four replications and five plants in each treatment were included: *G. mosseae* (GM), *G. etunicatum* (GE), *G. fasciculatum* (GF), *Gigaspora margarita* (GiM) and uninoculated control. All pots were maintained in a growth room at 25 ± 2 °C temperatures with 8.000 lux illumination for 12 h a day in a completely randomized block experimental design.

Four weeks after transplanting, the colonization percentage of pepper roots by the four AM fungi was determined. The roots were cleared and stained as described by Koske and Gemma (1989) and the percentage of root colonization was estimated by a gridline intersect method (Giovannetti and Mosse, 1980). Plant height was measured weekly for 8 weeks. For determining the fresh and dry weights of shoots and roots, plants were harvested at the end of 8 weeks and shoots were separated from roots. The roots were washed with tap water and then with distilled water, and washed roots were left on two layers of filter paper to remove excess water. The shoots and roots in each treatment were weighed to determine fresh weight and then dried at 70 °C for 2 days to determine dry weight.

For determining the effect of AM fungi on pepper yield, another experiment was conducted in greenhouse conditions. In the experimental area ($250\,m^2$), plots were prepared and uniform seedlings with 2–3 leaves with and without mycorrhizal fungus were transplanted into plots. Treatments were: GM, GE, GF, GiM and an uninoculated control. In the experimental area, a drip irrigation system was used. The experiment was designed as a completely randomized design with four replications and each plot contained 70 plants. At the time of harvesting from 10 weeks, ripened fruits were harvested in each plot and total yield was determined at the end of experiment.

2.4. Determination of the effects of AM fungi on *P. capsici* under pot conditions

Mycorrhizal and non-mycorrhizal plants with 3–4 leaves were transplanted into 15 cm-diameter pots containing autoclaved soil. The following treatments, with four replications and five plants in each treatment were included: GM+PC, GE+PC, GF+PC, GiM+PC and PC.

Four weeks later, plants were inoculated with the pathogen, *P. capsici*. The fungus was grown on oatmeal agar plates at 28 °C for 7 days and placed under fluorescent light for sporulation. Culture plates were incubated in sterile distilled water for 40 min at 4 °C and then for 30 min

at room temperature. Zoospores released from sporangia of *P. capsici* were collected by filtering through two-layers of cheesecloth and zoospore concentration was adjusted to 2×10^6 zoospore ml^{-1} using haemocytometer. A 10 ml suspension was applied to soil around the root and crown of plants in each pot. One week after inoculation, symptoms were evaluated based on a 0–5 scale: where 0 = no visible disease symptoms; 1 = leaves slightly wilted with brownish lesions beginning to appear on stems; 2 = 30–50% of entire plant diseased; 3 = 50–70% of entire plant diseased; 4 = 70–90% of entire plant diseased and 5 = plant dead according to Sunwoo et al. (1996). Also, lesion length formed by *P. capsici* on stems was measured for each treatment.

2.5. Determination of the effect of AM fungi on disease severity of P. capsici under greenhouse and field conditions

Experiments were conducted under greenhouse and field conditions. For each treatment, 2 m^2 plots were prepared and 70 cm safety zone was provided between plots for both experiments. In each plot, 20 seedlings with 3–4 leaves with or without mycorrhizal fungi were transplanted into the greenhouse and field. Experiments were designed as a completely randomized design in the greenhouse and a randomized complete block design in the field with four replications.

The treatments were as follows: GM+PC, GE+PC, GF+PC, GiM+PC and PC.

Four weeks after transplanting, plants were inoculated artificially with *P. capsici* (2×10^6 zoospores ml^{-1}) and evaluated 2 weeks after inoculation according to Sunwoo et al. (1996).

2.6. Capsidiol analysis

A capsidiol standard was obtained according to Egea et al. (1996a) and Ustun (1995). To obtain capsidiol in sufficient quantities, 100 ml of 1% $CuSO_4$ suspension was used as the elicitor in fruits. Fifty semi-ripe pepper fruits were injected with elicitor and incubated in sterilized, covered glass tray at 15 °C for 3 days. The seeds were then removed and the liquid within the fruits was collected and poured into a container. Chloroform-soluble substances were isolated from the diffusate by three extractions and separated by thin-layer chromatography at RF 0.2.

For the determination of the quantity of capsidiol in treatments, at the 2–3 leaved-stage, mycorrhizal fungi-inoculated and uninoculated plants were transferred to 15 cm-diameter pots which were placed in growth room at 25 ± 2 °C and illuminated by 8.000 lux for 12 h a day. Treatments were as follows: GM, GE, GF, GiM, PC and uninoculated control. Treatments were repeated three times. Plants were maintained for 1 week in a growth room and then inoculated with *P. capsici* at a concentration of 2×10^6 zoospores ml^{-1}. Six days after inoculation, capsidiol was extracted from 1 g of the stem of plants with $CHCl_3$:MeOH (2:1, v/v), separated by thin-layer chromatography, and identified and quantified by gas chromatography (Egea et al., 1996a).

Quantification was made by a ATI UNICAM 610 Series GC equipped with flame ionization detector and Schimadzu CPBS-S25-050 30 m capillary column. Column, injector and detector were kept at 150, 240 and 300 °C, respectively. Capsidiol quantity was determined with a ATI UNICAM integrator system attached to the gas chromatograph.

2.7. Statistical analysis

The data were subjected to analysis of variance (*F*-test). Means were compared using Fisher's least significant difference (LSD) test at $P = 0.05$ (Gomez and Gomez, 1983).

3. Results

3.1. The effects of AM fungi on development and yield of pepper

Root colonization by AM and their effects on plant growth are summarized in Table 1. Colonization of root of pepper plants by AM fungi varied between 61.3% and 68.1%, 4 weeks after transplanting. In GF- and GM-inoculated plants, the percentage of colonization was 68.1% and 65.7%, respectively, and this was higher than other two species.

Eight weeks after transplanting, plant height, fresh and dry weights of shoots and roots were higher in AM fungi-infected plants than those of uninoculated plants. All

Table 1
Root colonization and growth response of pepper plants inoculated with AM fungi

Treatments	Root colonization (%)	Plant height (cm)	Fresh weight of shoot (g)	Fresh weight of root (g)	Dry weight of shoot (g)	Dry weight of root (g)
Control		42.1 b[a]	30.9 c	4.9 c	4.6 d	0.593 d
GE	65.7	54.0 a	38.6 a	7.7 a	5.6 bc	0.802 b
GM	63.0	51.9 a	35.2 b	6.4 b	5.3 c	0.691 c
GF	68.1	55.4 a	39.9 a	8.1 a	5.8 ab	0.756 bc
GiM	61.3	52.7 a	39.1 a	8.1 a	6.1 a	0.941 a

[a]Means within column followed by different letters are significantly different ($P = 0.05$) according to Fisher's LSD test.

Table 2
The effect of inoculation with AM fungi on yield of pepper

Treatments	Yield (kg)	% Increase
Control	34.4 c[a]	0.0
GE	36.8 bc	7.0
GM	35.6 bc	3.5
GF	41.9 a	22.0
GiM	38.8 ab	12.7

[a]Means within column followed by different letters are significantly different ($P = 0.05$) according to Fisher's LSD test.

Table 3
The effect of inoculation with AM fungi on disease severity of *P. capsici* at pot conditions

Treatments	Disease index	Disease severity (%)	% Effect	Lesion length (cm)
PC	3.10	64.0 d[a]		5.3 d
GM+PC	0.25	5.3 a	91.7	0.6 a
GE+PC	1.15	24.0 b	62.5	2.0 bc
GF+PC	1.65	30.7 c	52.1	2.5 c
GiM+PC	0.85	16.0 b	75.0	1.2 ab

AM fungi treatments were inoculated with *P. capsici*.
[a]Means within column followed by different letters are significantly different ($P = 0.05$) according to Fisher's LSD test.

mycorrhizal fungi tested increased plant height compared to the control. Plant height was increased by preinoculation with GF by 31.7%. GE, GiM and GM treatments increased the plant height by 28.3%, 25.1% and 23.4%, respectively. The results presented in Table 1 also revealed that fresh weights of shoots and roots were increased by AM fungi. Fresh weight of shoots was increased by GF, GiM and GE with the highest effect by 29.0%, 26.6% and 24.8%, respectively. The results of the fresh weight of roots were parallel to the fresh weight of shoots. The fresh weight of roots was 4.9 g in control plants, whereas in GiM, GF and GE treatments, it was 8.1 g (66.3%), 8.1 g (66.3%) and 7.7 g (58.0%), respectively. In GM treatments, it increased by 30.1%.

Mycorrhizal plants exhibited significantly higher dry weight of shoots and roots compared to the control. GiM application showed the highest effect on shoot and root dry weights, increasing them by 34.1% and 58.6%, respectively.

The data presented in Table 2 show that GF had the highest effect on yield compared to the control. The mean yield in the control plot was 34.4 kg, while in the GF treatment it reached 41.9 kg, a 22% increase. This was followed by GiM with a 38.8 kg mean yield, a 12.7% increase. GM and GE had the least effect on yield.

3.2. *The effect of AM on P. capsici in pot conditions*

The data presented in Table 3 show that AM fungi reduced disease severity by *P. capsici* between 52.1% and 91.7%. The disease severity of *P. capsici* was 64.0%, whereas in the GM application treatment it decreased to 5.3% (91.7% decrease). GiM and GE reduced the disease severity by 75.0% and 62.5%, respectively. GF had the lowest effect with a 52.1% decrease.

Stem lesion formation by *P. capsici* was reduced or delayed when mycorrhizal fungi were present (Table 3). In control plants, the mean lesion length on stems was 5.3 cm, whereas in the GM application it decreased to 0.6 cm, thus showing the highest effect against the pathogen. In GiM and GE applications, the mean lesion length on the stem decreased to 1.2 and 2.0 cm, respectively. In GF applications, mean lesion length on stems was 2.5 cm.

3.3. *Determination of the effects of AM on disease severity of P. capsici under greenhouse and field conditions*

GE and GM had a similar effect on disease severity of *P. capsici* in the greenhouse (Table 4) and reduced disease severity by 50.1% and 43.0%, respectively. GiM decreased disease by 27.6% and GF had the lowest effect at 9.9%, compared to the other mycorrhizal fungi.

In the field experiment, the effect of AM on *P. capsici-induced disease* varied between 14.4% and 57.2% (Table 5). GM and GE reduced disease severity by 45.7% and 57.2% respectively, a similar effect to that in the greenhouse, followed by GiM (30.7%) and GF (14.4%).

3.4. *Capsidiol accumulation*

The amount of capsidiol in control plants was 12.5 $\mu g\, g^{-1}$ fresh weight, whereas among the AM fungi GM has the highest level of capsidiol (40.3 $\mu g\, g^{-1}$ fresh weight) (Table 6). In GF, GE and GiM treatments, the amount of capsidiol was lower at 29.4, 27.6 and 24.9 $\mu g\, g^{-1}$ fresh weight, respectively. Six days after inoculation of *P. capsici,* capsidiol accumulation was induced against pathogen infection (21.8 $\mu g\, g^{-1}$ fresh weight).

4. Discussion

AM fungi colonized 61.3–68.1% of the roots of pepper 4 weeks after inoculation. AM fungi are good colonizers of roots of Solanaceous plants and contribute to their stronger development. Pozo et al. (1999) reported that *G. mosseae* and *G. intraradices* established good colonization 4 weeks after inoculation colonizing 40% and 45%, respectively, of tomato roots, and the colonization increased with time. Aguilera-Gomez et al. (1999) showed that in seedlings to which *G. intraradices* was applied 52 days after application, 98% of the roots were colonized. Matsubara et al. (1995) reported that 10 weeks after inoculation with *G. etunicatum* and 8 weeks after inoculation with *Gigaspora margarita*, 40.8% and 40.2%, respectively, of roots of eggplants were colonized. In the pot experiment, all tested mycorrhizal fungi increased shoot

Table 4
The effect of inoculation with AM fungi on disease severity of *P. capsici* under greenhouse conditions

Treatments	Disease index	Disease severity (%)	% Effect
PC	2.02	42.6 b[a]	0.0
GM+PC	1.35	24.3 a	43.0
GE+PC	1.15	21.3 a	50.1
GF+PC	1.66	38.4 ab	9.9
GiM+PC	1.51	30.8 ab	27.6

AM fungi treatments were inoculated with *P. capsici*.
[a]Means within column followed by different letters are significantly different ($P = 0.05$) according to Fisher's LSD test.

Table 5
The effect of inoculation with AM fungi on disease severity of *P. capsici* under field conditions

Treatments	Disease index	Disease severity (%)	% Effect
PC	3.31	64.0 b[a]	0.0
GM+PC	1.53	27.4 a	57.2
GE+PC	1.93	34.7 a	45.7
GF+PC	2.48	54.8 ab	14.4
GiM+PC	2.54	44.3 ab	30.7

AM fungi treatments were inoculated with *P. capsici*.
[a]Means within column followed by different letters are significantly different ($P = 0.05$) according to Fisher's LSD test.

Table 6
Accumulation of the phytoalexin, capsidiol in the stems of pepper plants in different treatments

Treatments	Capsidiol amount ($\mu g\, g^{-1}$ fresh weight)	Standard deviation	% Standard deviation
Control	12.5	1.4	10.8
PC	21.8	0.6	2.7
GM	40.3	3.4	8.5
GF	29.4	2.0	6.7
GE	27.6	0.7	2.5
GiM	24.9	1.8	7.1

The concentration of capsidiol are the means of three extractions per treatment.

height by 23.4–31.7%. *G. etunicatum*, *G. fasciculatum* and *Gigaspora margarita* increased shoot and root fresh and dry weights. Most effective was *G. fasciculatum*, which increased pepper yield by 22% under greenhouse conditions. Our results indicate that mycorrhizal inoculation significantly stimulated growth of pepper plants. Previous reports revealed similar results indicating that AM fungi had positive effects on vegetative development of plants (Aguilera-Gomez et al., 1999; Ozgonen et al., 2001; Karagiannidis et al., 2002). This beneficial effect has generally been attributed to enhanced nutrition of mycorrhizal plants (Baath and Hayman, 1983; Davies and Linderman, 1991; Smith and Read, 1997).

G. mosseae was the most effective among the AM fungi tested against *P. capsici* in the pot experiment and under greenhouse and field conditions. Inoculation with AM fungi significantly reduced the extent of necrosis caused by *P. capsici*. Mycorrhizal fungi reduced the disease severity of *P. capsici* by 43.0% and 57.2% under greenhouse and field conditions, respectively. These findings agree with others and suggest that the mycorrhizal fungi had reducing or delaying effects on disease caused by soilborne phytopathogenic fungi including Phytophthora species (Liu, 1995; Norman et al., 1996; Dar et al., 1997; Rabie, 1998; Abdel-Fattah and Shabana, 2002; Yao et al., 2002). Dehne (1982) found that reduced susceptibility and increased tolerance of plants to certain pathogens were frequently associated with an established mycorrhizal colonization. The protective effect of mycorrhizal fungi against soilborne disease was also contributed to increased plant growth (Trotta et al., 1996), phenolic compounds (Devi and Reddy, 2002) and pathogenesis-related (PR) proteins (Dumas-Gaudot et al., 1996; Dassi et al., 1998; Pozo et al., 1999), lignification-related enzymes (Zheng et al., 2005) as well as phytoalexins (Morandi and Gianninazzi-Pearson, 1986). In the present study, *G. mosseae* increased the capsidiol level significantly compared to control plants and this finding suggests that it may be an important factor in resistance against *P. capsici*. However, the other species also showed an effect on disease resistance although to a lower degree than *G. mosseae*. Therefore, it was thought that multiple factors might be operating in disease resistance. Increased capsidiol levels could account for the effect of *G. mosseae* in controlling *P. capsici* most successfully in pot greenhouse and field conditions. It has been reported that some biocontrol agents induced phytoalexin synthesis in plants against pathogens. Ahmed et al. (2000) reported that *Trichoderma harzianum* applications increased the level of capsidiol in seeds and roots of pepper plants and the combinations of *T. harzianum* and *P. capsici* increased this effect sevenfold. In *T. harzianum*-treated plants, increased capsidiol level was the main factor in delaying lesion development by *P. capsici* on stems of pepper plants.

In this study, it was determined that the capsidiol level increased in necrotic areas on stems after inoculation with the pathogen, *P. capsici*. Previous studies reported that necrosis pathogens induced increased levels of phytoalexins and soluble phenolic compounds and the PR proteins (Mauch et al., 1988; Kim and Hwang, 1994; Candela et al., 1995). Ahmed et al. (2000) reported that the capsidiol level of control and *P. capsici*-inoculated plants were, respectively, 19.9 and 32.68 $\mu g\, g^{-1}$ fresh weight 6 days after inoculation. Egea et al. (1996b) showed that in the stem necrosis of the resistant Smith-5 pepper cultivar, the capsidiol level was relatively high 6 days after inoculation with *P. capsici* and development of the pathogen was inhibited. The same study pointed to the fungistatic properties of capsidiol at a mean concentration of 3.75 mM and its fungitoxic properties at 5 mM.

In conclusion, AM fungi especially *G. mosseae* can be used against Phytophthora blight of pepper. Capsidiol, although seeming to participate in protection, more probably combines with other factors responsible for the defence. More studies are required to elucidate resistance mechanism in pepper–AM fungi and PC system based on the detailed data such as the effects of phenolic compounds.

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