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# Effect of phosphate and the arbuscular mycorrhizal fungus *Glomus intraradices* on disease severity of root rot of peas (*Pisum sativum*) caused by *Aphanomyces euteiches*

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**Abstract** The effects of inorganic phosphate levels and the presence of arbuscular mycorrhiza on disease severity of *Aphanomyces euteiches* in pea roots were studied. Disease severity on roots and epicotyl as well as the oospore number within infected root tissue were correlated with the phosphorus (P) level in the growth medium. The arbuscular mycorrhizal fungus *Glomus intraradices* increased P uptake and the P concentration in the plant but reduced disease development in peas. Polyacrylamide gel electrophoresis followed by densitometry of glucose-6-phosphate dehydrogenase specific to *A.euteiches* was used to measure the activity of the pathogen in roots. The enzyme activity increased with disease severity and disease incidence, except in plants supplemented with P at the highest level, where a peak in activity was seen 12 days after inoculation with the pathogen, followed by a decrease in activity. The epicotyl of mycorrhizal plants showed a reduction in disease severity although this part of the plants was not mycorrhizal. Thus, an induced systemic factor may be responsible for increased resistance in mycorrhizal plants.

**Key words** Peas · *Aphanomyces euteiches* · Phosphorus · PAGE · Isozymes

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## Introduction

Arbuscular mycorrhizas have been reported to have a suppressive effect on diseases caused by a number of root-infecting fungi (Dehne 1982; Garbaye 1991; Sharma et al. 1992). Several mechanisms are likely to be involved in the interactions between arbuscular mycorrhizal (AM) fungi and soil pathogens, but the background for the disease suppression is not fully understood (Linderman 1994; Azcon-Aguilar and Barea 1996; Cordier et al 1996; Dumas-Gaudot et al. 1996; Trotta et al. 1996). Arbuscular mycorrhizas are known to enhance plant uptake of phosphate (P) and other mineral nutrients (Abbott and Robson 1984). The nutritional superiority of more vigorous AM plants has been proposed to be a mechanism in reduction of root diseases (Linderman 1994). This enhanced plant development may lead to disease escape or to higher tolerance against soil-borne pathogens (Dehne 1982). However, the reports on the role of an enhanced P nutrition due to arbuscular mycorrhizas in host resistance are conflicting. The effect of P on the interaction between *Phytophthora parasitica* and arbuscular mycorrhiza fungi in tomato showed that the protecting effect of mycorrhiza was not related to enhanced nutritional status of the host (Trotta et al. 1996). In other studies, improved P nutrition was correlated to both a disease increase (Davis et al. 1979) and a decrease in disease (Graham and Menge 1982).

The conflicting results from studies on mycorrhiza – pathogen interactions may be explained by the different methods used for recording the disease and the pathogen. Some studies recorded indirect effects of the pathogen by scoring the symptoms of the host plant (Graham and Menge 1982), or the loss in dry weight of diseased plants (Hwang et al. 1993). Others used a direct measurement of the pathogen in the host tissue (Rosendahl 1985; Cordier et al. 1996). In a recent study, the effect on a pathogen was measured by recording the enzymatic activity of the pathogen under influence of the AM fungus (Kjøller and Rosendahl

1996). The results showed that AM fungi may influence the activity pattern of the pathogen without reducing the biomass of the pathogen in the root. This altered activity pattern resulted in a reduced expression of the disease in mycorrhizal plants.

Common root rot of peas (*Pisum sativum* L.) caused by *Aphanomyces euteiches* (Drechsl.) is one of the major limiting soil-borne pathogens world-wide in pea production (Papavizas and Ayers 1974; Kraft et al. 1994). Chemical control of the pathogen is insufficient, but the presence of arbuscular mycorrhiza in pea roots is known to reduce the disease (Rosendahl 1985; Kjøller and Rosendahl 1996). The aim of the present study was to determine the effect of inorganic P fertiliser levels on disease severity of *A. euteiches* in pea to see whether the enhanced disease tolerance of arbuscular mycorrhizae is due to improved P supply to the plant.

## Materials and method

Soil from an organic fertilised field at Højbakkegård in Tåstrup was partially sterilised by g-radiation (11 kGy) and mixed with sand (1:3). Seeds of*P. sativum* L. (c.v. Solara) were surface disinfected in 1.5% NaOCl for 8 min, washed three times in water and planted at a depth of 3 cm with two seeds per pot (600 ml, 760 g of the soil-sand mix). Before sowing, the growth media [pH 7.5, 0.5% organic matter, 5.3 mg P (Olsen) and 3.0 mg K per kg soil] were supplemented with 4.5 ml dense *Rhizobium leguminosarum* culture (Risø strain 18a) and other minerals ($K_2SO_4$ 71.0 mg/kg, $CaCl_2$ 71.0 mg/kg, $CuSO_4 \cdot 5H_2O$ 2.0 mg/kg, $ZnSO_4 \cdot 7H_2O$ 5.0 mg/kg, $MnSO_4 \cdot H_2O$ 10.0 mg/kg, $CoSO_4 \cdot 7H_2O$ 0.35 mg/kg, $NaMoO_4 \cdot 2H_2O$ 0.18 mg/kg, $MgSO_4 \cdot 7H_2O$ 45.0 mg/kg). Phosphorus was supplemented at concentrations of 0, 30 and 90 mg $KH_2PO_4$/kg growth medium.

### Fungal material

Inoculum of the AM fungus *Glomus intraradices* Schenck & Smith, isolate 28A, BEG 87 was produced on maize (*Zea mays* L.) cv F1 Spirit in a soil/sand mixture. The soil and root system were homogenised and 25 g of this mixture, containing colonised roots, spores and external mycelium, was added to the pots of mycorrhizal treatments. An equal amount of disinfected soil/sand mixture was added to pots of the non-mycorrhizal treatments. Two weeks after sowing, pots with emerged seedlings (two seedlings/pot) were inoculated with 30 000 zoospores per pot at the base of each plant. Zoospores of *A. euteiches* (strain 63, Dept. of Mycology, Copenhagen) were produced according to Papavizas and Ayers (1974).

### Experimental design

The experiment consisted of inoculation with *A. euteiches* as one factor, application of P at 0, 30 and 90 ppm as the other, and two additional treatments where plants were preinoculated with the mycorrhizal fungus *G. intraradices* and inoculated with *A. euteiches* or left uninoculated. All treatments were arranged in a randomised block design with five replications for each treatment. The plants were grown under greenhouse conditions in June with no light supplement. The pots were watered every second day to field capacity (same weight).

### Harvest

Plants were harvested 4, 8, 12, 16 and 21 days after inoculation with *A. euteiches*. At time of harvest, the shoots were cut off at the cotyledons and the dry weight of shoots was measured after drying at 80 °C for 24 h. The P concentration in the shoots was measured by the vanado-molybdate method after combining all replicates from the same treatment. The root system was washed by gently rubbing under running tap water and then kept on ice (0 °C) for further processing. The roots and epicotyl of each individual plant were scored for disease severity as percent softened, discoloured tissue due to infection by *A. euteiches*. The roots were blotted on paper towels, cut into 1.5-cm segments and divided in two fractions. One fraction was cleared and stained (Phillips and Hayman 1970). The percentage root length infected with *A. euteiches* and root length with arbuscular mycorrhiza was measured by the grid-line intersect method (Giovannetti and Mosse 1980; Rosendahl 1985). The other fraction was freeze dried and ground to a fine powder in a mortar. The ground root material (100 mg) was mixed in a 1.5-ml Eppendorf tube with 1 ml extraction buffer (20 mM Tris-HCl, 10 mM $NaHCO_3$, 10 mM $MgCl_2$, 0.1 mM $Na_2EDTA$, 10 mM b-mercaptoethanol, 10% sucrose, 0.1% Triton X-100, pH 8.0; Rosendahl and Sen 1992) and the suspension was mixed for 30 s on a vortex mixer at maximal speed. The samples were centrifuged twice for 20 min at 20 000 *g* and the supernatant recovered and frozen in aliquots at –80 °C until use.

### Electrophoresis

Electrophoresis was carried out in a discontinuous, vertical electrophoresis system (Hoefer SE 250-Mighty Small II) with $80 \times 70 \times 0.7$ mm polyacrylamide gels. The separation gel was 7.5% acrylamide, 375 mM Tris-HCl, pH 8.8; the stacking gel was 3.75% acrylamide, 124 mM Tris-HCl, pH 6.8 and the electrode buffer was 25 mM Tris and 192 mM glycine at pH 8.3. The gels were run at 200 V and 15 mA per gel for 75 min with cooling to 4 °C and 10 µl extract was loaded in each well. The gels were stained for glucose-6-phosphate dehydrogenase (Gd) (Soltis and Soltis 1989) and bands were scanned with a densitometer (Hoefer, model GS 300) in order to quantify the activity. The enzyme activity was expressed arbitrarily as the peak height of the densitometric tracings of the gels (Kjøller and Rosendahl 1996).

### Statistical analysis

The dry weight data for shoots and roots were analysed with a two-factor analysis of variance (ANOVA) with a Student Newman-Keuls test of the mean. The infection and disease data are presented in graphs with standard error bars, and the effect of P was tested in a two-factor ANOVA by using only the data from non-mycorrhizal plants. The effect of mycorrhiza was also tested in a two-factor ANOVA using the mycorrhizal treatment and the non-mycorrhizal treatment without P application.

## Results

Application of P increased the percentage root length with oospores of *A.euteiches* as well as the disease severity index of the root (Figs. 1, 2). In mycorrhizal plants, the pathogen developed fewer oospores than in non-mycorrhizal plants (Fig. 1). This effect was statistically significant between the mycorrhizal treatment and the non-mycorrhizal treatment without added P (Table 1). The effect of mycorrhiza on the disease index of the root was not statistically significant (Table 1), but at day 12 plants supplemented with 30 and 90 ppm P

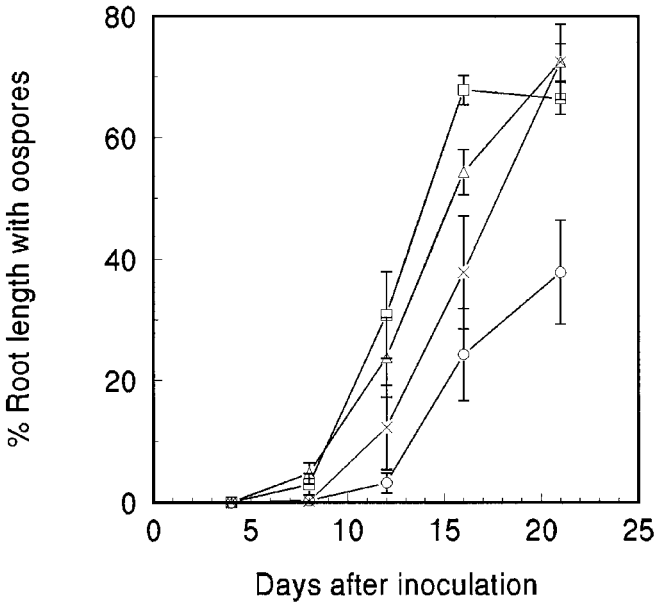


**Fig. 1** Development of percent infected root length of pea with oospores of *Aphanomyces euteiches* at three P fertiliser levels or the addition of the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* at 4, 8, 12, 16 and 21 days after inoculation. ○ + AM 0 ppm P, × AM, 0 ppm P, △ AM 30 ppm P, □ AM 90 ppm P; *bars* standard errors

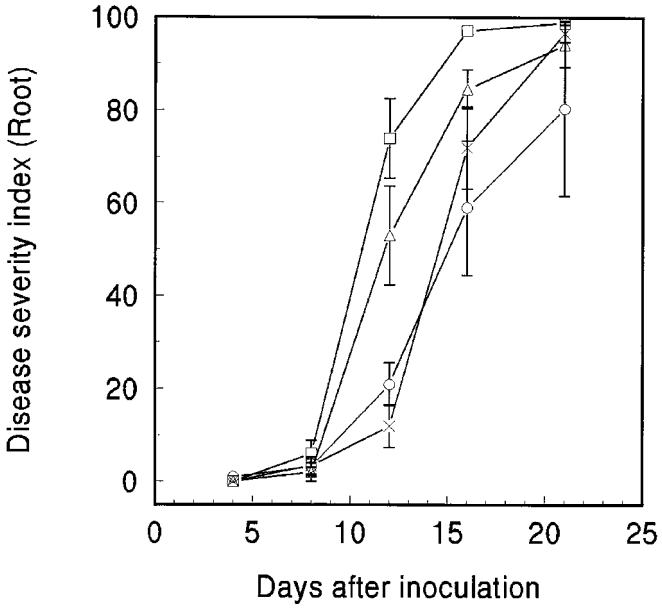


**Fig. 2** Disease severity index of the root of pea inoculated with a zoospore suspension of *A. euteiches* for three different P fertiliser levels or the addition of the AM fungus *G. intraradices* as a function of days after inoculation. ○ + AM 0 ppm P, × AM, 0 ppm P, △ AM 30 ppm P, □ AM 90 ppm P; *bars* standard errors

showed a higher disease severity index than both mycorrhizal and non-mycorrhizal plants without P addition (Fig. 2). The disease development in roots was delayed 4 days compared with disease development in the epicotyl. The disease severity of the epicotyl was not affected by P (Table 2; Fig. 3), but mycorrhizal plants had a significantly lower disease index at all harvests (Table 1; Fig. 3).

The activity of the *A. euteiches* Gd isozyme in pea roots during development of the infection paralleled disease severity and disease incidence (Fig. 4). The densitometer readings (peak values) varied considerably, but a significant difference between plants with 0 and 90 ppm P was seen at day 12 (Fig. 4). The enzyme activity increased in all treatments after inoculation with the pathogen, but after day 12 the activity decreased in

**Table 1** Two-way ANOVA testing the significance of mycorrhiza application and harvest time on the measurements of disease caused by *Aphanomyces euteiches.* The mycorrhizal treatment was tested by using the treatment with no added P as the non-mycorrhizal treatment (*Gd* Glucose-6-phosphate dehydrogenase, *NS* not significant $P>0.005$)

| Treatment | % Root length with oospores | Disease severity of the root | Disease severity of the epicotyl | Gd activity |
|---|---|---|---|---|
| Mycorrhiza (M) | ** | NS | * | NS |
| Harvest time (H) | ** | ** | ** | ** |
| Interaction M×H | ** | NS | NS | NS |

* $P<0.05$
** $P<0.001$

**Table 2** The result of two-way ANOVA testing the significance of P application and harvest time on the measurements of the disease caused by *Aphanomyces euteiches* (*NS* not significant $P>0.05$)

| Treatment | % Root length with oospores | Disease severity of the root | Disease severity of the epicotyl | G6PDH activity |
|---|---|---|---|---|
| Phosphate (P) | * | * | NS | NS |
| Harvest time (H) | * | * | * | * |
| Interaction P×H | * | * | NS | NS |

* $P<0.001$

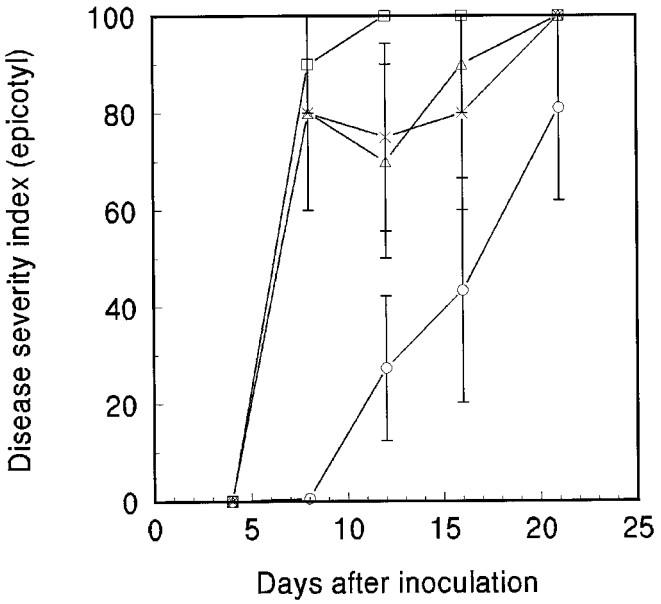


**Fig. 3** Disease severity index of the epicotyl of pea inoculated with a zoospore suspension of *A. euteiches* for three different P fertiliser levels or the addition of the AM fungus *G. intraradices* as a function of days after inoculation. ○ + AM 0 ppm P, × AM, 0 ppm P, △ AM 30 ppm P, □ AM 90 ppm P; *bars* standard errors

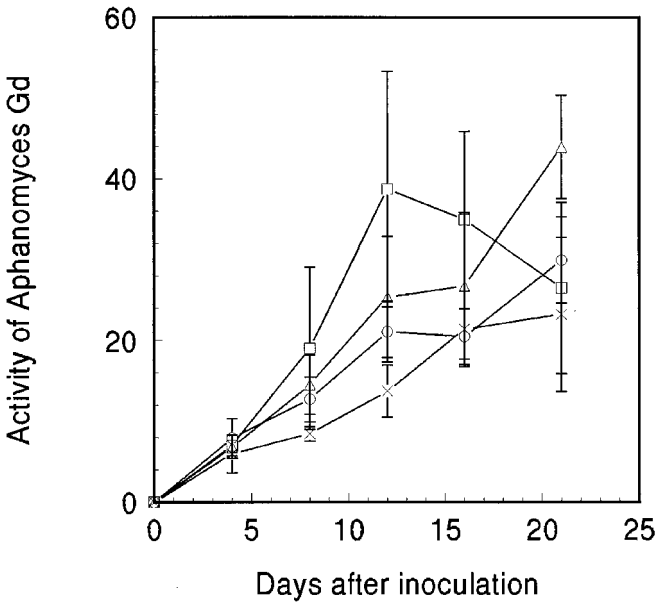


**Fig. 4** Activity of glucose-6-phosphate dehydrogenase (*Gd*) as an arbitrary densitometer reading (peak heights) in pea roots after inoculation with a zoospore suspension of *A. euteiches* at three different P fertiliser levels or the addition of the AM fungus *G. intraradices* as a function of day after inoculation. ○ + AM 0 ppm P, × AM, 0 ppm P, △ AM 30 ppm P, □ AM 90 ppm P; *bars* standard errors

plants fertilised with 90 ppm P. ANOVA did not detect significant effects of either P or mycorrhiza on the Gd activity (Tables 1, 2).

The mycorrhizal colonisation developed rapidly and reached 87% of root length 20 days after inoculation with the pathogen. Inoculation with the pathogen did not decrease the mycorrhizal colonisation significantly (data not shown). The shoot dry weights showed a response to increases in P fertiliser for non-inoculated control plants, but this effect was not seen in the *A. euteiches*-inoculated plants at the last harvest (Table 3). Inoculation with the AM fungus did not increase dry weights of shoots and even decreased them at the last harvest in plants without *A. euteiches*. The root weight was not influenced by arbuscular mycorrhiza in either *A. euteiches*–inoculated plants or in non-inoculated plants (Table 4). The P contents of the shoots were increased by application of phosphate fertiliser (Table 5), but inoculation with *G. intraradices* resulted in a higher P content than application of 90 ppm P.

## Discussion

This experiment confirms earlier findings, that the presence of mycorrhizal fungi reduces root rot of peas caused by *A. euteiches* (Rosendahl 1985; Kjøller and Rosendahl 1996). The increased uptake of P due to AM colonisation of the root systems was not responsible for the increased disease resistance, as increased P levels in non mycorrhizal plants following P fertiliser application had a negative influence on host resistance

**Table 3** Influence of soil phosphorus (0, 30, 90 ppm P) or arbuscular mycorrhizas (*AM*) (*Glomus intraradices*) on the growth of peas measured as dry weight of the shoots of control and *Aphanomyces euteiches*-inoculated pea plants. The column headings show number of days between inoculation with the pathogen and harvest. Column means followed by the same letter are not significantly different ($P<0.05$)

| Treatment | Shoot dry weight (g/plant) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Control | | | | | Inoculated | | | | |
| | 4 | 8 | 12 | 16 | 21 | 4 | 8 | 12 | 16 | 21 |
| 0P, +AM | 0.52a | 0.81b | 1.09b | 1.72b | 2.03c | 0.52c | 0.79b | 1.02c | 1.45c | 1.61b |
| 0P, −AM | 0.57a | 0.77b | 1.18b | 1.80b | 2.41b | 0.59b | 0.88ab | 1.16b | 1.60b | 1.83ab |
| 30P, −AM | 0.59a | 0.88ab | 1.35a | 1.75b | 2.37b | 0.61ab | 0.92a | 1.30a | 1.79a | 1.97a |
| 90P, −AM | 0.61a | 1.02a | 1.45a | 2.19a | 2.83a | 0.65a | 0.90a | 1.30a | 1.79a | 1.86ab |

**Table 4** Influence of soil phosphorus (0, 30, 90 ppm P) or arbuscular mycorrhizas (AM) (*Glomus intraradices*) on the growth of peas measured as dry weight of the roots of control and *A. euteiches*-inoculated pea plants. The column headings show number of days between inoculation with the pathogen and harvest. Column means followed by the same letter are not significantly different ($P<0.05$)

| Treatment | Root dry weight (g/plant) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Control | | | | | Inoculated | | | | |
| | 4 | 8 | 12 | 16 | 21 | 4 | 8 | 12 | 16 | 21 |
| 0P, +AM | 0.25a | 0.32a | 0.37a | 0.45a | 0.52a | 0.27a | 0.31a | 0.34a | 0.37a | 0.36a |
| 0P, −AM | 0.30a | 0.30a | 0.41a | 0.47a | 0.57a | 0.31a | 0.33a | 0.36a | 0.41a | 0.41a |
| 30P, −AM | 0.18b | 0.32a | 0.38a | 0.40a | 0.48a | 0.29a | 0.33a | 0.44a | 0.40a | 0.43a |
| 90P, −AM | 0.28a | 0.33a | 0.39a | 0.48a | 0.51a | 0.30a | 0.33a | 0.37a | 0.38a | 0.38a |

**Table 5** Phosphorus contents in the shoots at the final harvest (*AM* Inoculated with *Glomus intraradices*, *APH* inoculated with *A. euteiches*)

| Treatment | *P* (mg/plant) |
|---|---|
| 0 ppm P, APH | 2.42 |
| 30 ppm P, APH | 3.44 |
| 90 ppm P, APH | 3.72 |
| AM | 4.35 |
| AM, APH | 4.84 |

to *A. euteiches*. This is in agreement with Kaye et al. (1984), who concluded that the mechanisms of disease tolerance of mycorrhizal plants appear to be distinct from improved plant nutrition. Trotta et al. (1996) also found that resistance to *Phytophthora parasitica* was increased in mycorrhizal tomato plants, and that improved P nutrition had little effect on the disease.

Quantification of the activity of plant pathogens in roots previously done with *A. euteiches* in peas (Kjøller and Rosendahl 1996) showed that the Gd activity of *A. euteiches* increased with time after inoculation. However, in the present study, Gd activity decreased 12 days after inoculation in plants supplemented with 90 ppm P where disease development was greatest. This pattern was also seen for the highest zoospore concentration in the study of Kjøller and Rosendahl (1996), indicating that in severely diseased plants the fungus changes from an active to a resting stage.

The increased P uptake in mycorrhizal plants did not result in increased shoot dry weight and at the last harvest the shoot dry weight was significantly lower in mycorrhizal plants (Table 1). Although this reduction in dry weight was not seen in root biomass, the negative effect of mycorrhiza is unexpected. The roots were heavily colonised by *G. intraradices* and the symbiosis was clearly established since P uptake by plants was increased. The presence of pathogenic microorganisms in the mycorrhizal inoculum may explain the result, though we did not find other fungi in the roots.

The epicotyls, which are not colonised by the AM fungus, showed a reduction in disease severity caused by *A. euteiches* in mycorrhizal plants. This reduction could be the result of improved plant vigour, but as P fertilisation stimulated disease development this is not likely. Alternatively, an induced systemic factor may be responsible for the disease suppression in the epicotyls. This was previously suggested by Rosendahl (1985), where the AM fungus decreased oospore production in non-mycorrhizal parts of a split-root system. In another experiment, mycorrhiza protected cucumber plants against post emergence damping off by *Pythium ultimum* before mycorrhizal colonisation occurred (Rosendahl and Rosendahl 1990). In contrast, Davis and Menge (1980) showed no systemic induced resistance in a split-root experiment with citrus and *Phytophthora cinnamomi*, indicating that several factors are involved in increased resistance in mycorrhizal plants.

*Aphanomyces euteiches* was applied as zoospores to the soil surface. Zoospores give rise to infections starting at the epicotyl and extending downward in the root system. In the mycorrhizal plants and in the plants with no added P fertiliser the downward development of the disease was reduced. This resulted in a lower disease severity and incidence when the entire root system was examined. Mycorrhizal colonisation of the roots did not prevent pathogenic infection of the roots, but reduced the downward growth of the pathogen in the roots. This reduction could be caused by competition between the two fungi for physical space in the root, but may also be the result of antimicrobial compounds produced by the plant (Morandi et al. 1984), or induced host defence responses in mycorrhizal systems (Cordier et al. 1996). Zoospores are not the natural inoculum source of the pathogen. Under field conditions, the inoculum consists of oospores which infect the entire root at the same time and future experiments should use this inoculum to confirm the results of the present study.

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## References


Abbott LK, Robson AD (1984) The effect of mycorrhizas on plant growth. In: Powell CL, Bagyaraj DJ (eds) VA mycorrhizae. CRC, Boca Raton Fla, pp 113–130

Azcon-Aguilar C, Barea JM (1996) Arbuscular mycorrhizas and biological control of soil-borne plant pathogens – an overview of the mechanisms involved. Mycorrhiza 6:457–464

Cordier C, Gianinazzi S, Gianinazzi-Pearson V (1996) Colonisation patterns of root tissues by *Phytophthora nicotianae* var. *parasitica* related to reduced disease in mycorrhizal tomato. Plant Soil 185:223–232

Davis RM, Menge JA (1980) Influence of *Glomus fasciculatus* and soil phosphorus on *Phytophtora* root rot of citrus. Phytopathology 70:447–452

Davis RM, Menge JA, Erwin DC (1979) Influence of *Glomus fasciculatus* and soil phosphorus on *Verticillium* wilt of cotton. Phytopathology 69:453–456

Dehne HW (1982) Interaction between vesicular-arbuscular mycorrhizal fungi and plant pathogens. Phytopathology 72:1115–1119

Dumas-Gaudot E, Slezack S, Dassi B, Pozo MJ, Gianinazzi-Pearson V, Gianinazzi S (1996) Plant hydrolytic enzymes (chitinases and b-1,3-glucanases) in root reactions to pathogenic and symbiotic microorganisms. Plant Soil 185:211–221

Garbaye J (1991) Biological interactions in the mycorrhizosphere. Experientia 47:370–375

Giovannetti M, Mosse B (1980) An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol 84:489–500

Graham JH, Menge JA (1982) Influence of vesicular–arbuscular mycorrhizae and soil phosphorus on take-all disease of wheat. Phytopathology 72:95–98

Hwang SF, Chakravarty P, Prevost D (1993) Effects of rhizobia, metalaxyl and VA mycorrhizal fungi on growth nitrogen fixation and development of *Pythium* root rot of sainfoin. Plant Dis 77:1093–1098

Kaye JW, Pfleger FL, Steward EL (1984) Interaction of *Glomus fasciculatum* and *Pythium ultimum* on greenhouse-grown poinsetta. Can J Bot 62:1572–1579

Kjøller R, Rosendahl S (1996) The presence of the arbuscular mycorrhizal fungus *Glomus intraradices* influences enzymatic activities of the root *pathogen Aphanomyces euteiches* in pea roots. Mycorrhiza 6:487–491

Kraft JM, Boge WL (1994) Development of an antiserum to quantify *Aphanomyces euteiches* in resistant pea lines. Plant Dis 78:179–183

Linderman RG (1994) Role of VAM fungi in biocontrol. In: Pfleger FL, Linderman RG (eds) Mycorrhizae and plant health. APS, St. Paul, Minne, pp 1–25

Morandi D, Bailey JA, Gianinazzi-Pearson (1984) Isoflavonoid accumulation in soybean roots infected by vesicular-arbuscular mycorrhizal fungi. Physiol Plant Pathol 24:357–364

Papavizas GC, Ayers WA (1974) *Aphanomyces* species and their root diseases in pea and sugarbeet. A review. USDA Technical Bulletin 1485:1–158

Phillips JM, Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi and for rapid assessment of infection. Trans Br Mycol Soc 55:158–160

Rosendahl CN, Rosendahl S (1990) The role of vesicular arbuscular mycorrhizal fungi in controlling damping-off and growth reduction in cucumber caused by *Pythium ultimum*. Sybiosis 9:363–366

Rosendahl S (1985) Interactions between the vesicular-arbuscular mycorrhizal fungus *Glomus fasciculatum* and *Aphanomyces euteiches* root rot of peas. Phytopathol Z 114:31–40

Rosendahl S, Sen R (1992) Isozyme analysis and mycorrhizal fungi and their mycorrhiza. In: Norris JR, Read DJ, Varma AK (eds) Methods in microbiology, vol 24. Academic, London, pp 169–194

Sharma AK, Johri BN, Gianinazzi S (1992) Vesicular-arbuscular mycorrhizae in relation to plant disease. World J Microbiol Biotechnol 8:559–563

Soltis DE, Soltis PS (1989) Isozymes in plant biology. Chapman & Hall, London

Trotta A, Varese G C, Gnavi E, Fusconi A, Sampo S, Berta G (1996) Interactions between the soil-borne root pathogen *Phytophthora nicotianae* var *parasitica* and the arbuscular mycorrhizal fungus *Glomus mosseae* in tomato plants. Plant Soil 185:199–209