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Interactions between indigenous arbuscular mycorrhizal fungi and *Aphanomyces euteiches* in field-grown pea

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Abstract This is the first reported study of the interactions between indigenous arbuscular mycorrhizal fungi (AMF) and *Aphanomyces euteiches* in pea under field conditions. *A. euteiches* was applied to the soil by adding oospores produced in vitro. Attempts were made to create a non-mycorrhizal control by incorporating carbendazim (Derosal Fl) in the topsoil before sowing. However, all carbendazim-treated plants showed approximately 20% root colonisation with AMF. Pea plants not treated with carbendazim showed a wide variation in AMF colonisation of 35–70% at the full flowering stage. In these control plots, root length infected with oospores of *A. euteiches* and colonisation by AMF were negatively correlated. Application of carbendazim increased the percent root length infected with oospores by 50–70%, depending on inoculum density of *A. euteiches*. Despite the lower levels of AMF colonisation in these treated plots, a negative correlation with oospore-containing root length was still observed. No correlation was found between AMF colonisation and disease severity, disease incidence or pathogen enzymatic activity (glucose-6-phosphate dehydrogenase). Thus, AMF do not seem to influence the vegetative stage of pathogen development during which cortical root rotting takes place, but rather the reproductive stage when oospores are produced. The results of this study underline the importance of field experiments for validating the significance of mycorrhizal fungi for plant health.

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Introduction

Common root rot of pea (*Pisum sativum* L.) caused by *Aphanomyces euteiches* Drechsl. is one of the major soil-borne pathogens in pea production world wide (Oloffson 1967; Papavizas and Ayers 1974; Kraft et al. 1994; Persson et al. 1997). Some reports suggest potential control of the pathogen by fungicides (Oyarzun et al. 1990), breeding lines (Kraft et al. 1994) and biocontrol agents (Parke et al. 1991; King and Parke 1993). However, avoiding the build-up of soil-borne inoculum by exploitation and stimulation of microbial regulatory mechanisms in the field is probably one of the key strategies in sustainable pea production.

Arbuscular mycorrhizal fungi (AMF) constitute an important component of the microbial soil community and several studies have shown that the presence of these fungi has considerable impact on plant health (Dehne 1982; Perrin 1990; Hooker et al. 1994; Linderman 1994; Azcon-Aguilar and Barea 1996). Interactions between AMF and *A. euteiches* also studied in experiments under controlled conditions resulted in a reduction in disease severity (Kjøller and Rosendahl 1996; Bødker et al. 1998) and oospore production by the pathogen (Rosendahl 1985; Bødker et al. 1998; Larsen and Bødker 2001).

The interaction between AMF and pathogens is examined often under greenhouse conditions where roots are pre-colonised by AMF in disinfested soil before challenge with a pathogen. Only a few reports under field conditions are available. Newsham et al. (1995) reported a beneficial effect against *Fusarium oxysporum* of inoculating the annual grass *Vulpia ciliata* var. *ambigua* with a *Glomus* sp. and transplanting inoculated plants into a natural population of grass species from where both fungi had been isolated. In field-grown onion, the presence of mycorrhiza provided significant protection against

white rot caused by *Sclerotium cepivorum* (Torres-Barragán et al. 1996).

Field-grown pea roots are heavily colonised by AMF, but the percentage of colonised root length may vary between pea plants as well as between fields. Thus, from a practical point of view, it is more relevant to study differences in disease development in plants with high and low levels of mycorrhizal colonisation than differences between mycorrhizal and non-mycorrhizal plants.

The aim of the present study was to examine the impact of different levels of indigenous mycorrhizal fungi on disease incidence, disease severity, infection and activity of the root rot pathogen *A. euteiches* in field-grown pea. Different levels of mycorrhizal colonisation were obtained by the application of a soil drench with carbendazim, a fungicide previously reported to reduce AMF development under field conditions (West et al. 1993; Kahiluoto and Vestberg 2000).

Materials and methods

Pot experiment with carbendazim and *Aphanomyces euteiches*

A preliminary pot experiment was performed to test for any direct effect of carbendazim on *A. euteiches* (ATCC 201684). Soil from a field at Højbakkegård in Tåstrup was partial sterilised (γ-radiation, 11 kGy, Risø) to kill AMF and mixed with sand (1:3 v/v). Seeds of *Pisum sativum* L. (c.v. Solara) were surface-disinfested 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 soil). Before sowing, the growth media were supplemented with 4.5 ml of a dense *Rhizobium* culture (Risø strain 18a) and other nutrients (K_2SO_4 71 mg kg^{-1}, $CaCl_2$ 71 mg kg^{-1}, $CuSO_4.5H_2O$ 2 mg kg^{-1}, $ZnSO_4.H_2O$ 5 mg kg^{-1}, $MnSO_4.H_2O$ 10 mg kg^{-1}, $CoSO_4.7H_2O$ 0.35 mg kg^{-1}, $NaMoO_4.2H_2O$ 0.18 mg kg^{-1}, $MgSO_4.H_2O$ 45 mg kg^{-1}). A combination of carbendazim (0, 1, 10 and 100 l Derosal Fl ha^{-1}) and oospores of *A. euteiches* (500 oospores ml^{-1} soil) was added and thoroughly mixed into the growth medium. All treatments were arranged in a randomised block design with four replications for each treatment.

The plants were placed under greenhouse conditions (22°C). Light supplementation was not necessary due to the high light intensity in the spring. The pots were watered every second day to field capacity (same weight) to maintain a saturated soil moisture condition. Plants were harvested 7, 13 and 21 days after germination. The root system was washed by gently rubbing under running tap water and the roots were cleared and stained as described below.

Experimental design of field trial

The trial was conducted on the experimental farm Højbakkegaard (55°42′N 12°17′E) at Taastrup 20 km west of Copenhagen, Denmark in a field which had been managed organically since 1987. The soil was a clay loam with pH 6.8 and 27 mg P kg^{-1} soil (0.5 M $NaHCO_3$ extractable P). Carbendazim (0, 70 l Derosal Fl) and *A. euteiches* (0, 100 and 1,000 oospores ml^{-1} soil to 10–12 cm depth) were applied to the soil in a randomised complete block design with four replicate plots for each of the six treatments. The two infestation levels of *A. euteiches* were chosen on the basis of a pot experiment giving low and high disease severity at 100 and 1,000 oospores ml^{-1}, respectively (L. Bødker, unpublished results). The plot size was 1.5×6 m with 90 plants per square metre.

Application of carbendazim and *Aphanomyces euteiches* in a field trial

Oospores of *A. euteiches* were produced in sterile oat meal broth (20 g oat meal in 1 l distilled water), homogenised in a Waring blender, mixed into vermiculite and dried in a sterile-flow hood before storage at 5°C until use (Papavizas and Ayers 1974). In April, after seedbed preparation, a fungicide drench (0 or 70 l Derosal Fl ha^{-1} (100 times normal dose) was applied to the soil surface with a Hardy 4110–12 flat nozzle sprayer (300 l water ha^{-1}). Oospores and fungicide were mixed into the topsoil (0–12 cm) with a rotary cultivator. Pea seeds (c.v. Birthe) were sown at a depth of 7–8 cm.

Harvest and root colonisation

Samples were collected 22, 40, 54, 62 (flowering) and 69 days (pod setting) after sowing. Each sample consisted of 10 plants taken at random from each plot. Plants were gently dug up and excess soil removed. Plants were cut at the cotyledon level and fresh and dry weights of shoots were measured. The remaining root system was washed by gently rubbing under running tap water and kept on ice until scoring for disease severity (Persson et al. 1997) and disease incidence (proportion of plants with visible symptoms of *A. euteiches* infection).

Roots were dried between sheets of paper towels, cut into 1- to 1.5-cm segments and divided in two fractions. One fraction was cleared and stained according to Kormanick and McGraw (1992), except that trypan blue was substituted for acid fuchsin. The percent root length infection by *A. euteiches* (oospores) and the colonisation by indigenous AMF (arbuscules) were estimated by the grid-line intersect method (Giovannetti and Mosse 1980; Rosendahl 1985). The second fraction was freeze-dried and used for measuring the activity of *A. euteiches* glucose-6-phosphate dehydrogenase (G6PD) in the roots (Kjøller and Rosendahl 1997).

Statistical analysis

The variables disease severity index and relative G6PD activity were found to follow a normal distribution when the appropriate transformation was applied. Logit transformation was used for disease severity index and square root transformation was used for relative G6PD activity. These variables were analysed using a split-plot type including the effects of blocks and treatments in the whole-plot stratum and harvest days and interactions with harvest days as sub-plot treatments.

The variables percent diseased plants, percent infected roots were analysed using a generalised linear model (McCullagh and Nelder 1989), assuming a binomial distribution, using the logit function as link function and taking a possible correlation between recordings from the same plot into account. For the variable percent diseased plants, an over dispersion parameter was included in the model. For both types of model, the unknown parameters were estimated by the method of restricted maximum likelihood (REML) (Patterson and Thompson 1971; Searle et al. 1992). All analyses in the figures were performed using the procedures Mixed and Genmod of the SAS system (SAS 1996a, b).

Results

In the pot experiment, high doses of carbendazim initially reduced oospore production in pea roots, but this effect was no longer significant after 23 days (Table 1).

In the field experiment, both carbendazim and *A. euteiches* caused a significant reduction in AMF colonisation (Fig. 1). However, no interaction between these two factors was detected. At full flowering stage (60–62 days

Table 1 Percent infected root length (colonisation) of pea with oospores of *Aphanomyces euteiches* at four dosages of carbendazim (0, 1, 10, 100 l Derosal Fl ha^{-1}) mixed into the soil in a pot experiment 13 and 23 days after germination. Figures in the same column followed by different letters are significantly different (P<0.05)

Dosage	Percent infected root length	
	Day 13	Day 23
0	20.0 a	44.8 a
1	13.5 ab	34.5 a
10	2.3 b	20.3 a
100	3.0 b	21.5 a

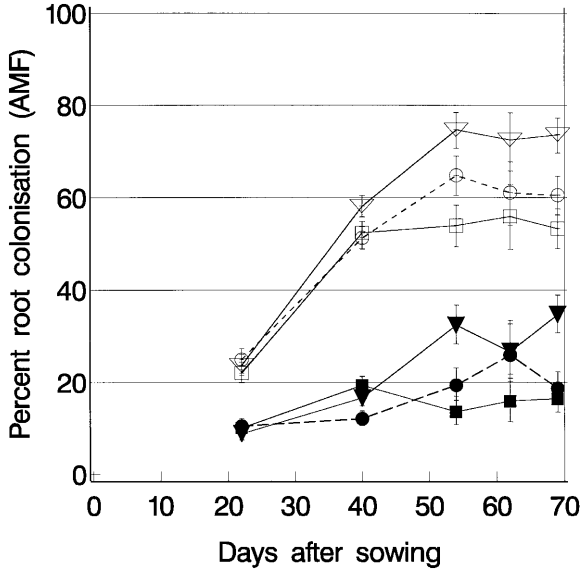

Fig. 1 Percent root colonisation of pea with arbuscular mycorrhizal fungi (*AMF*) at three levels of *Aphanomyces euteiches* infestation (0, 100 and 1,000 oospores ml^{-1}) and two levels of carbendazim (0 and 70 l Derosal Fl ha^{-1}) applied to the soil before sowing (▽ 0–0, ▼ 0–70, ○ 100–0, ● 100–70, □ 1,000–0, ■ 1,000–70)

after sowing), application of carbendazim had reduced root colonisation of AMF by almost 50%.

Disease incidence (number of symptomatic plants with *A. euteiches*) at days 54, 62 and 69 was significantly higher when 1,000 oospores ml^{-1} were applied that at an infestation level of 100 oospores ml^{-1} (Fig. 2). No symptomatic plants were seen in non-infested plots, with or without carbendazim treatment. No symptomatic plants were seen in the infested plots before day 54, when disease incidence was 27–87%. There were no differences between carbendazim-treated and non-treated plants nor did carbendazim interact with the infestation level of the pathogen.

A similar development was seen when disease severity was recorded as a root rot index (Fig. 3). A statistically significant difference in disease severity between levels of inoculum was detected but no difference between fungicide and non-fungicide treated plots was observed.

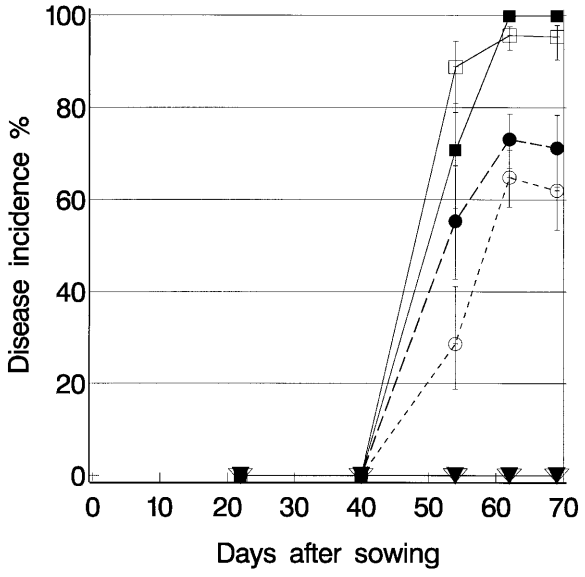

Fig. 2 Disease incidence of plants with root rot at three levels of *A. euteiches* infestation (0, 100 and 1,000 oospores ml^{-1}) and two levels of carbendazim (0 and 70 l Derosal Fl ha^{-1}) applied to the soil before sowing (▽ 0–0, ▼ 0–70, ○ 100–0, ● 100–70, □ 1,000–0, ■ 1,000–70)

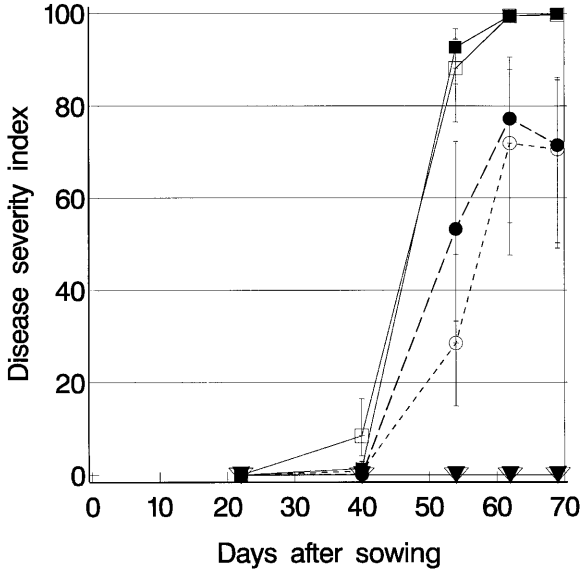

Fig. 3 Disease severity index of pea roots at three levels of *A. euteiches* infestation (0, 100 and 1,000 oospores ml^{-1}) and two levels of carbendazim (0 and 70 l Derosal Fl ha^{-1}) applied to the soil before sowing (▽ 0–0, ▼ 0–70, ○ 100–0, ● 100–70, □ 1,000–0, ■ 1,000–70)

The percent root length with oospores at days 54, 62 and 69 was significantly higher in plots infested with the highest inoculum level of *A. euteiches* and when carbendazim was applied than in other treatments (Fig. 4). Application of carbendazim significantly increased the root length containing oospores for both inoculum densities of *A. euteiches*.

The G6PD activity of *A. euteiches* in the pea roots during development of the infection showed a sharp in-

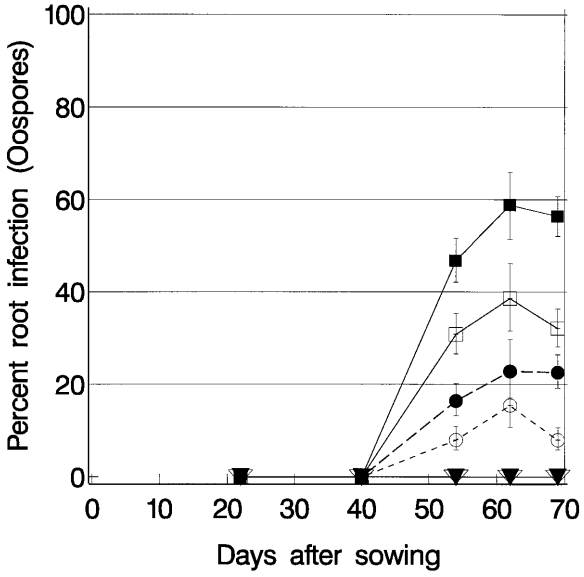

Fig. 4 Percent root infection of pea with oospores at three levels of *A. euteiches* infestation (0, 100 and 1,000 oospores ml^{-1}) and two levels of carbendazim (0 and 70 l Derosal Fl ha^{-1}) applied to the soil before sowing (▽ 0–0, ▼ 0–70, ○ 100–0, ● 100–70, □ 1,000–0, ■ 1,000–70)

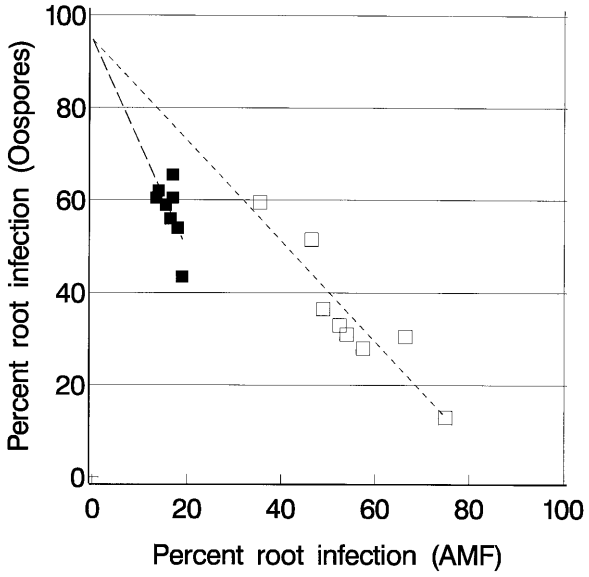

Fig. 6 Relationship between percent root colonisation of AMF and oospores of *A. euteiches* at days 62 and 69 after sowing in plots supplemented with ■ 1,000 oospores ml^{-1} and 70 l Derosal Fl ha^{-1}, □ 1,000 oospores ml^{-1} and no fungicide)

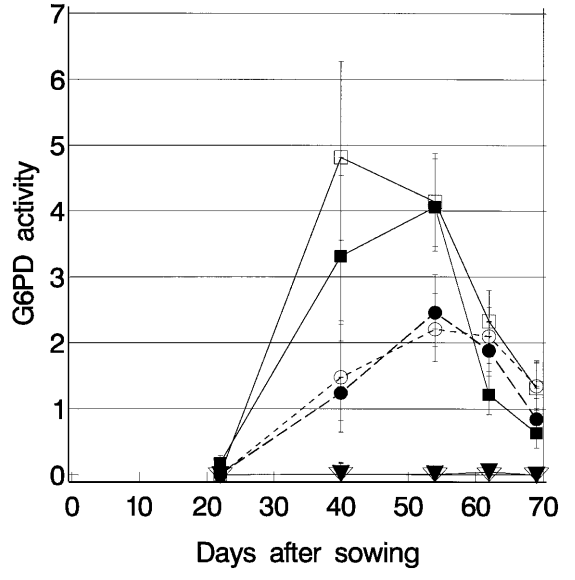

Fig. 5 Activity of glucose-6-phosphate dehydrogenase (*G6PD*) as an arbitrary densitometer reading (peak values) in pea roots at three levels of inoculum of *A. euteiches* (0, 100 and 1,000 oospores ml^{-1}) and two levels of carbendazim applied as a soil drench before sowing (0 and 70 l Derosal Fl ha^{-1}) (▽ 0–0, ▼ 0–70, ○ 100–0, ● 100–70, □ 1,000–0, ■ 1,000–70)

crease from day 22 (Fig. 5), before symptoms were observed in the roots (Fig. 3). For most treatments, the activity peaked at day 54. However, the densitometer reading varied considerably and there was only a significant difference between the two infestation levels of *A. euteiches.* No effect due to application of carbendazim was observed.

Fresh and dry shoot weights of the peas increased during the growth period but there was no difference between infested and non-infested plots or between fungicide-treated and non-treated plots (data not shown).

A significant correlation (P<0.0001) was observed between AMF colonisation levels and root length with oospores of *A. euteiches* at days 62 and 69 in plots infested with 100 or1,000 oospores ml^{-1} (Fig. 6). Roots from non-carbendazim treated plots showed variation in AMF colonisation of 35–75% for the highest inoculum level. At the same time, plants in all carbendazim-treated plots appeared to have approximately 20% AMF-colonised roots. The regression lines for the two fungicide treatments were y=94.8–1.089×(1,000 oospores ml^{-1}, 0 l Derosal Fl) and y=94.8–2.277×(1,000 oospores ml^{-1}, 70 l Derosal Fl). The correlation coefficient for the two regression lines through the same intercept (R^2) was 0.89. The lower infestation level gave identical results but at a lower level of oospore infection. However, the variation in root length with oospores between these plots was high because of the difficulty of evenly distributing low numbers of oospores in the ploughing layer. These observations were, therefore, excluded from the results depicted.

Discussion

This is the first reported investigation of interactions between indigenous AMF and *A. euteiches* in pea under field conditions. AMF had a significant effect on the formation of the resting structures (oospores) of the pathogen but no effect on disease severity, disease incidence or pathogen enzymatic activity (G6PD). This suggests

that AMF in field-grown pea do not influence the vegetative stage of pathogen development where cortical root rotting takes place but only the reproductive stage in the pathogen life cycle during which resting spores (oospores) are produced. This is in accordance with previous studies (Rosendahl 1985; Bødker et al. 1998; Larsen and Bødker 2001) showing a reduction in root length with oospores in mycorrhizal roots. However, the lack of an AMF effect on disease severity is contrary to that reported by Kjøller and Rosendahl (1996) and Bødker et al. (1998). This may be related to the fact that the pathogen inoculum source in all studies performed under controlled conditions was zoospores added to the stem base, whereas the inoculum source in field-grown peas was oospores. Under field conditions, pea roots stimulate oospore germination and release of zoospores, which can infect the entire root system and not only the stem base. Bødker et al. (1998) observed that mycorrhizal colonisation was not able to reduce pathogen infection, but only the downward growth of the pathogen in the roots. It may also be that different AMF were used in the pot experiments. *Glomus intraradices* (BEG 87) was used in the pot experiments whereas a mixture of AMF exist in the field. Five AMF isolates from the field plots were tested for their inhibitory effect against *A. euteiches* in pea under controlled conditions, i.e. two isolates of *G. mosseae* and one isolate each of *G. geosporum, G. claroideum* and *G. caledonium.* None of these isolates showed any significant effect on *A. euteiches* disease development (J. Larsen, L. Bødker; R. Kjøller, S. Rosendahl, unpublished results), contrary to the effect of *G. intraradices* in previous reports (Rosendahl 1985; Kjøller and Rosendahl 1996; Bødker et al. 1998). In another study, pre-inoculation of a natural population of AMF had a protective effect against *Phytophthora cinnamomi*. Inoculation with *G. mosseae* alone was less protective, although root colonisation was similar in both treatments (Bärtschi et al. 1981). Future studies of interactions between *A. euteiches* and AMF should be performed with oospore inoculum and with more isolates of AMF.

Investigations of indigenous AMF and bioprotection in cultivated field soils are not easy. Naturally occurring AMF need to be controlled or at least reduced by means of either fumigants or fungicides. These chemicals may have secondary effects on other non-target microorganisms which induce plant defence responses or directly interact with the pathogen. Many field studies with AMF have used fungicides such as benomyl or carbendazim, which are highly specific for true fungi (Trappe et al. 1984; West et al. 1993; Kahihuoto and Vestberg 2000). In the present study, field levels of AMF reduced by means of carbendazim were compared to indigenous AMF in untreated field plots. Mycorrhiza colonisation varied considerably in plots not treated with carbendazim within a very small area in the field and even between plants within plots. However, on average, a clear negative correlation between formation of oospore and AMF colonisation was evident. Carbendazim treatment increased *A. euteiches* oospore development in the field plots. Since application of carbendazim reduced oospore formation in the pot experiment, it is unlikely that the increase in carbendazim-treated field plots was a direct effect of the fungicide. Three pieces of circumstantial evidence indicate that the presence of AMF was the major contributor to the reduction in oospore formation. Firstly, *A. euteiches* produced fewer oospores in roots highly colonised with AMF in the field, as found in studies under controlled conditions without carbendazim (Rosendahl 1985; Kjøller and Rosendahl 1996; Bødker et al. 1998; Larsen and Bødker 2001). Secondly, *A. euteiches* infection and AMF colonisation were negatively correlated in the non-carbendazim treated plots. Thirdly, low levels of AMF colonisation in the control plots infested with *A. euteiches* but not treated with carbendazim had approximately the same effect on oospore infection as low levels of AMF due to treatment with carbendazim.

The mechanisms of pathogen suppression by AMF are poorly understood. Perrin (1990) proposed several protection mechanisms for the interaction between AMF and soil-borne pathogens but there is still a lack of knowledge about the effect of AMF on oospore formation and mycelium growth inside roots or in the rhizosphere. In the present experiment, there was no indication of an induced resistance factor as suggested by Rosendahl (1985) and Bødker et al. (1998). The mode of interaction between AMF and *A. euteiches* is more likely to be competition for nutrients rather than for physical space, because only oospore formation, the final stage in the pathogen life cycle, was influenced. This hypothesis is supported by the results of Larsen and Bødker (2001), who found that the *G. mosseae*–pea symbiosis had no effect on disease severity caused by *A. euteiches* but reduced the number of oospores, the biomass and the level of energy reserves of the pathogen.

The reduction in colonisation of AMF did not influence plant growth until pod setting, which can be explained by the high phosphorus status of the soil (27 mg P kg^{-1} soil). According to Jakobsen (1986), the reduction in AMF could be important at low P levels and at pod filling.

The results of recent studies have suggested that the activity of *A. euteiches*-specific G6PD can be used as an indicator of mycelium activity of this pathogen (Kjøller and Rosendahl 1997, 1998; Bødker et al. 1998). The present field study showed for the first time that it is possible to measure pathogen enzyme activity in roots from field samples even before oospores can be seen in the root tissue. The infection process of *A. euteiches* is characterised by a peak in activity followed by a rapid decline. This agrees with the observations from controlled experiments, which show a quick switch from the vegetative to the resting stage of the pathogen, leading to the production of numerous oospores in the roots (Kjøller and Rosendahl 1996; Bødker et al. 1998).

The results from the present study question the beneficial effect of AMF on the suppression of *A. euteiches*

root rot disease in field-grown pea. However, the rate of increase in pathogen infection potential will likely be lower in fields with high than with low levels of indigenous AMF. The existence of a certain specificity among AMF isolates in their ability to suppress diseases caused by *A. euteiches* in pea should be investigated by more field trials and controlled experiments testing a number of different fungal species. This study clearly demonstrates the importance of field experiments for validating the significance of AMF for plant health. Effects which seem of major importance under controlled conditions may well be of minor importance in the field.

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