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Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species

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Abstract We were interested in the role of arbuscular mycorrhiza (AM) in the competition between plants of different sizes. A pot experiment of factorial design was established, in which AM root colonization and competition were used as treatments. Five-week-old *Prunella vulgaris* seedlings were chosen as target plants (i.e. plants whose response to competition was studied) and the following (13 replicates of each) were used as neighbours: (1) a large, 10-week-old *P. vulgaris*, (2) two *P. vulgaris* seedlings, and (3) a large, 10-week-old *Fragaria vesca*. In the experiment where small neighbours were grown together with small target plants, competition did not reduce target plant weight significantly, compared to the other two treatments. The competitive effects of large neighbours were significant, regardless of species (both older neighbours reduced the weights of target plants similarly), but there was a clear difference between intra- and interspecific competition when plants were mycorrhizal. In intraspecific competition with a large neighbour, the target plant shoot weight was reduced 24% when inoculated with AM. Thus, AM amplified rather than balanced intraspecific competition. In interspecific competition with old *F. vesca*, the shoot weights of target plants were 22% greater when inoculated with AM than when non-mycorrhizal. The results showed that, for given soil conditions, AM might increase species diversity by increasing competitive intraspecific suppression and decreasing the interspecific suppression of small plants by larger neighbours.

Key words Arbuscular mycorrhiza · Competition · *Fragaria vesca* · *Prunella vulgaris*

Introduction

Both greenhouse (Grime et al. 1987) and field experiments (Gange et al. 1990, 1993) have shown that mycorrhizal communities are more diverse (or more species rich) than ones with less mycorrhiza. On the other hand, high diversity of a low-mycorrhiza community has been observed where there were abundant non-mycorrhizal species (Newsham et al. 1995). Grime et al. (1987) suggested that the translocation of carbon and nutrients through common mycelia was the main mechanism by which mycorrhiza modify plant coexistence. The rate of carbon transfer depends on shading, which may suggest that assimilates move along a concentration gradient (Francis and Read 1984). If such a transfer occurs, it could be an important mechanism for enhancing coexistence and maintaining plant diversity, especially by promoting subordinates and/or juveniles.

Arbuscular mycorrhizal (AM) fungi might also play a direct role shifting the balance of competition between plants within a community (Bergelson and Crawley 1988; Allen and Allen 1990). Francis and Read (1994) reinterpreted the results of Grime et al. (1987), stressing the important influence of AM on plant fitness at the establishment phase. They also suggested that AM fungi may suppress chemically the growth of non-mycorrhizal plant species.

Competition experiments using AM fungal inoculation as a treatment can give more detailed information about the role of AM in plant coexistence. In the case of interspecific competition, the influence of AM has mostly been studied for species pairs, where one species is strongly AM dependent while the other is less dependent or non-mycorrhizal (Allen and Allen 1990). Typically, AM fungal inoculum confers a greater advantage on the mycorrhizal neighbour. Hartnett et al. (1993) distinguished between the influence of AM on competitive effect and response. AM significantly increased the competitive effect of a mycorrhiza-dependent species. The negative response of the same species

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to competition by neighbours was weaker when it was mycorrhizal, but the difference decreased as plant density increased. The competitive effect and response of less AM-dependent species were not significantly influenced by mycorrhiza. These results tend to show that AM fungi might decrease species diversity by benefitting one species. In cases of intraspecific competition, AM fungal root colonization has no effect on plant interactions, or even seems to amplify competition (Eissenstat and Newman 1990; Allsopp and Stock 1992; Hartnett et al. 1993). In the experiment performed by Koide et al. (1994), the positive effect of AM on plant fecundity vanished in crowded conditions.

Certain contradictions between individual- and community-level experiments could result from AM fungi influencing plant coexistence through an effect on the establishment phase, as suggested by Francis and Read (1994) and shown for cool-season grasses by Hartnett et al. (1994) and for Cape shrubs by Allsopp and Stock (1995). Survival at the seedling stage can be of crucial importance for plant coexistence (Grubb 1977; Tilman 1993), mainly due to severe light competition, which is always more asymmetrical than nutrient competition (Weiner 1986). In one experiment, the influence of AM fungi on intraspecific competition between adults and seedlings has been studied (Eissenstat and Newman 1990), but there was little competition for light.

The aim of the present work was to assess the role of mycorrhiza in the competition between naturally coexisting plants of clearly different sizes in a situation where larger plants shade smaller ones. We tried to answer the question whether a symbiotic interaction with AM can "help" young plants resist the competition of older ones with which they naturally coexist. We chose *Prunella vulgaris* L. as a target species and *Fragaria vesca* as a neighbouring species. Both are common subordinates in the lowest sublayer of the canopy of species-rich calcareous grasslands (Kull and Zobel 1991), and both species have AM (Harley and Harley 1987).

Materials and methods

P. vulgaris was grown in pot experiments of factorial design where competition and AM fungal root colonization were used as treatments. Since we were mainly interested in the growth of small *P. vulgaris* plants in competitive situations, we called this the target species although the meaning of this term is slightly different from that used by Goldberg and Landa (1991). Competition treatments

were established in three ways (see Table 1), each replicated 13 times:

Experiment 1: Intraspecific competition with one large neighbour. Four young *P. vulgaris* were planted in the corners of the pot with one large neighbour in the centre. We preferred to have more than one target individual per pot because we expected high mortality in shaded conditions. Due to the size differences between the target and neighbouring plants, we considered the competitive interaction to be initially rather unidirectional, i.e. the large neighbour was shading small targets, but not vice versa.

Experiment 2: Intraspecific competition with two small neighbours. The centre of the pot was filled with two young *P. vulgaris* plants. To begin with, plants were not shading each other, so we considered the competition to be initially relatively balanced.

Experiment 3: Interspecific competition with one large neighbour. A large *F. vesca* was planted in the centre of the pot, shading the young *P. vulgaris* plants

To test the mycorrhizal dependency of *P. vulgaris* in the given soil conditions, we also grew single control plants with and without AM inoculation.

Plants were grown in 4 (depth) × 13 × 18 cm pots. The soil used for seed germination and the experiments was three-parts steam-sterilized horticultural peat (pH 6) and one-part fine sand. The resulting mixture had a relatively high P level (extractable P was 12 mg/100 g). In the competition treatments, four 2-week-old target plants and a 7-week-old "adult" neighbour plant were transplanted into one pot. When the seedlings were transplanted in the competition treatments, AM infection was achieved by adding 50 cm³ natural soil (Hayman et al. 1981). In May 1993, when the root inoculum was collected, both species were infected with AM. The soil originated from the same calcareous grassland where the seeds of the experimental plants were collected. In previous experiments, adding soil with roots has proved more effective for inoculation than using spores only (Allen and Allen 1984). For the non-mycorrhizal treatment, the pots received the same amount of natural soil (without root pieces) but were treated once with the fungicide benomyl (Benlate, 0.6 g/pot) and once with iprodione (Rovral, 0.04 ml/pot). It has been claimed that benomyl efficiently eliminates AM (Fitter and Nichols 1988) and has no direct effect on those vascular plants tested (Paul et al. 1989; West et al. 1993a). We avoided autoclaved soil because of changes in nutrient availability (Jakobsen 1994). However, due to uncertainties about the selective effect of benomyl on zygomycetes (see Summerbell 1988), iprodione was also used, following Gange et al. (1990) and West et al. (1993a). Other soil micro-organisms were not controlled. The species of AM fungi were not determined.

Plants were grown in the greenhouse in full light (day-length 16 h) for 60 days, and watered every day. Root samples were taken from five pots of each treatment, from one target and one neighbouring plant. To quantify AM infection, root samples were stained according to Koske and Gemma (1989) and the percentage of colonized root segments was determined (Rajapakse and Miller 1992). The above- and below-ground parts of all plants were harvested, dried at 85 °C for 24 h and weighed. The former is referred to as shoot weight, the latter as root weight.

For statistical analysis of target plant biomass data, the standard procedures of multifactor ANOVA (Systat) with one competition factor, three treatment levels and one AM inoculation factor with two treatment levels were used. To estimate the differences between the three competition treatments, the Tukey HSD multi-

Table 1 The three competition treatments

Experiment	Number of target plants	Number of neighbours	Species of neighbours
1	4	1	<i>P. vulgaris</i> (adult)
2	4	2	<i>P. vulgaris</i> (young)
3	4	1	<i>F. vesca</i> (adult)

ple-comparison test (Systat) was used. A one-way ANOVA was applied to study the effect of AM inoculation on the weight of the neighbouring plants and on the weight of the non-competing single control.

Results

Single control

The weight of *P. vulgaris* plants growing singly in pots was greater when they were mycorrhizal. Shoot weight was increased by approximately 30% ($P = 0.018$), root weight by 87% ($P = 0.003$) and total weight by 55% ($P = 0.003$).

Target plant weight

AM fungal inoculation had no significant effect on target plant shoot weight. However, the effects of the different competition treatments were statistically significant (Table 2). When old *P. vulgaris* and *F. vesca* were neighbours (experiments 1 and 3), both reduced the shoot weights of target plants, compared to the variant with two small conspecific neighbours (experiment 2; Fig. 1). The interaction between AM inoculation and different competition treatments was also significant. In experiment 2, AM inoculation did not affect the target plant shoot weight. In experiment 1, target plant shoot weight was lower in the mycorrhizal case, and was approximately 21% lower than the mycorrhizal target plant shoot weight in experiment 2 (Fig. 1). There was no difference in target plant shoot weights between experiments 1 and 2 when plants were non-mycorrhizal. In experiment 3, target plant shoot weight was lower when plants were non-mycorrhizal. In this experiment, non-mycorrhizal target plants had an approximately 26% lower shoot weight than non-mycorrhizal plants in experiment 2. There was no difference in target plant shoot weights between experiments 2 and 3 when plants were mycorrhizal.

Table 2 Results of multifactor ANOVA: weight of target plant with or without AM inoculation (MYC) and growing with different neighbours in experiments 1–3 (COMP)

Parameter	Source of variation	df	F-ratio	P
Shoot weight	MYC	1	0.184	0.669
	COMP	2	9.262	0.000
	MYC × COMP	2	3.955	0.020
Root weight	MYC	1	13.567	0.000
	COMP	2	1.328	0.267
	MYC × COMP	2	2.453	0.088
Total weight	MYC	1	4.873	0.028
	COMP	2	4.765	0.009
	MYC × COMP	2	3.789	0.022

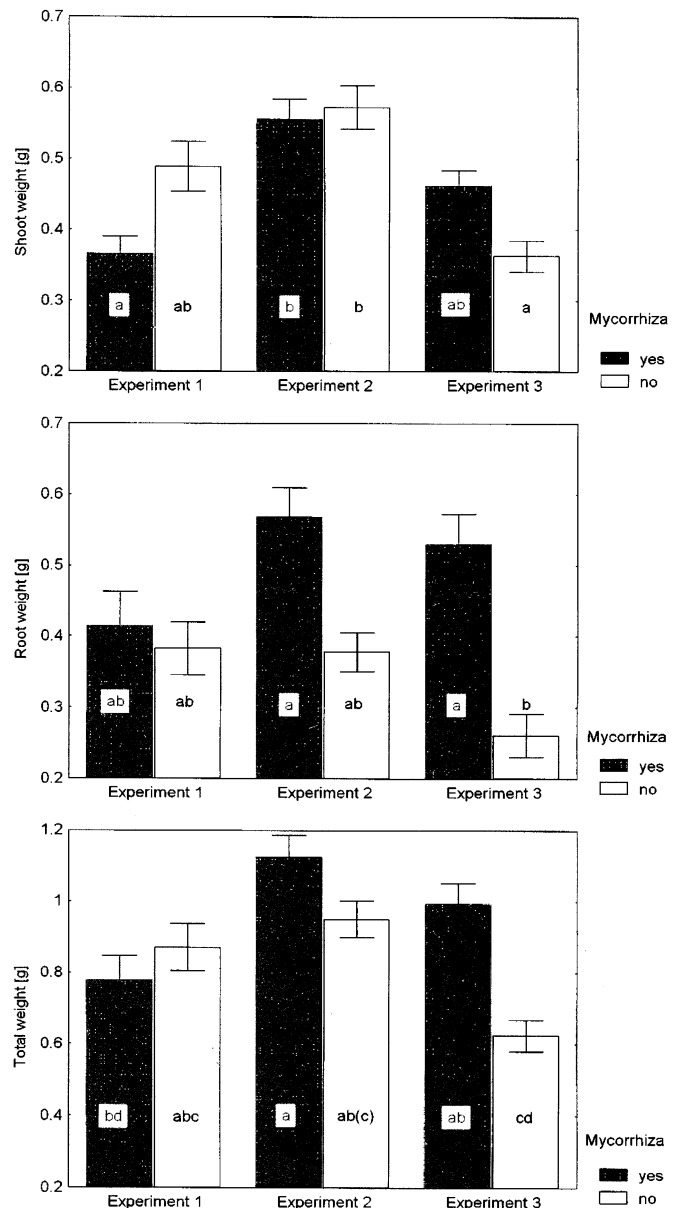


Fig. 1 Means (\pm SE) of the shoot, root and total weight of target *Prunella vulgaris* plants in three competition experiments. Means with the same letter are not significantly different using Tukey's mean separation test ($P \leq 0.05$). The parentheses in one case indicate that means were different on the probability level of 0.060

AM fungal inoculation increased root weight, but neither the competition treatments nor their interaction with inoculation was statistically significant (Table 2).

AM inoculation significantly increased the target plant total weight, and competition treatments and the interaction term also had a significant effect (Table 2, Fig. 1). In experiments 1 and 3, the target plant total weight was smaller than in experiment 2. When competition was intraspecific, AM inoculation decreased total plant weight compared with experiment 2, but when *F. vesca* was the neighbour, mycorrhizal plants

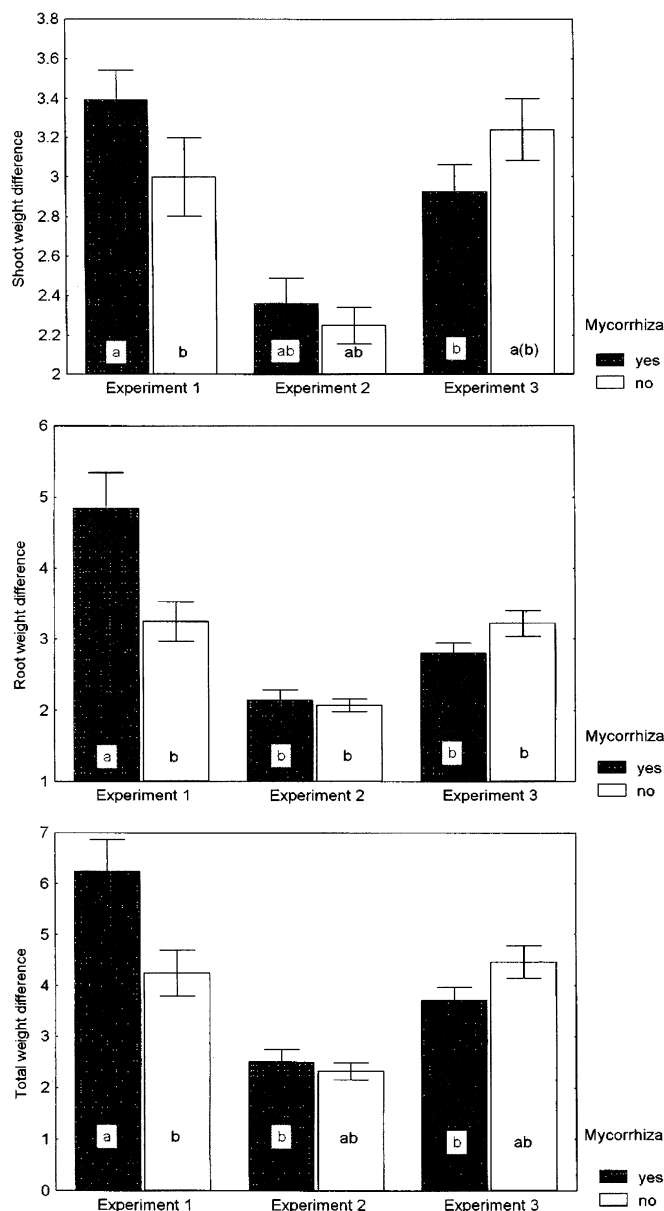


Fig. 2 Mean difference (\pm SE) between the average neighbouring and average target plant in three competition experiments. Results with the same letter are not significantly different using Tukey's mean separation test ($P \leq 0.05$). The parentheses in one case indicate that means were different on the probability level of 0.06

were approximately 37% larger than non-mycorrhizal ones and did not differ from plants in experiment 2.

Neighbours

Old *P. vulgaris* as a neighbour had marginally non-significantly larger roots ($P = 0.061$) when mycorrhizal. The weight of young *P. vulgaris* plants as neighbours was not significantly influenced by AM fungal inoculation. The weight of old *F. vesca* as a neighbour was

not significantly influenced by AM, though mycorrhizal plants were always slightly smaller.

Weight differences between neighbours and target plants

The weight differences between the average neighbour and target plant are characterized in Fig. 1. The effects of AM inoculation on shoot weight differences were converse in experiments 1 and 3 – when competition was intraspecific, mycorrhiza increased the weight difference, while when competition was interspecific, mycorrhiza decreased the weight difference. In experiment 2, shoot weight differences were negligible. When the total weight was considered, only the mycorrhizal variant with a conspecific neighbour produced a significant difference – the mycorrhiza increased the weight difference.

AM fungal root colonization

The colonization of the roots of experimental plants by AM fungi was successful – all plants were infected. The average colonization level was 14–15% in the case of young and 21–22% in the case of adult *P. vulgaris* plants. The root colonization of old *F. vesca* was 26–27%. The fungicide treatment was efficient, only 1–2% of the root length of old *P. vulgaris* and 0.8% of the root length of the *F. vesca* plants were colonized in fungicide-treated variants, while roots of young *P. vulgaris* plants were not colonized at all.

Discussion

The single control demonstrated that the target plant under investigation, *P. vulgaris* responded positively to AM inoculation in the given soil conditions. This confirms that the positive effect of benomyl on small target plants in experiment 1 cannot be due to the suppression of pathogenic fungi, which might have been possible in some cases (cf. Newsham et al. 1994). Furthermore, Zobel and Moora (1995) have shown that the other species used, *F. vesca*, does not demonstrate mycorrhizal dependency in similar conditions.

The effect of competition treatments on the target plants was most clearly expressed by shoot weight. Although both old neighbours decreased the shoot weight of target plants compared with young neighbours, AM inoculation also changed the responses of target plants to different old neighbours. In intraspecific competition with small neighbours, AM did not affect target plant shoot weights, but in the presence of a large conspecific neighbour, the shaded target plants were significantly smaller when plants were mycorrhizal. Allsopp and Stock (1992) and Hartnett et al. (1993)

found that AM amplifies rather than balances intra-specific competition between similarly aged plants. The same seems to be true when individuals of different ages and sizes are competing.

We observed different reactions in individuals of different ages – large conspecific neighbours were larger and small target plants smaller when they were mycorrhizal. Interplant translocation of carbon cannot be occurring here. The results indicate that there is probably a certain resource pre-emption by larger individuals when they are mycorrhizal, possibly because of the relatively slow root infection of the small target plants – the percentage AM root colonization was almost twice as high in adult plants. In this experiment, the competitive response of the small *P. vulgaris* target to the old conspecific neighbour was increased (i.e. target plants were relatively smaller) by AM inoculation. Though the extent of root infection is not necessarily an indication of the ability of the endophyte to enhance plant growth (Roldan-Fajardo 1994), this seems to be the case in experiment 1.

Considering interspecific competition, the differences in shoot weights were reversed – shoots of the target *P. vulgaris* in the shade of *F. vesca* were larger when plants were mycorrhizal, i.e. AM improved the performance of small *P. vulgaris* in the situation of interspecific competition. When similarly aged plants are competing, AM typically increases the competitive effect of the more mycorrhiza-dependent species (Allen and Allen 1990; Hartnett et al. 1993; Zobel and Moora 1995). The competitive response of mycorrhiza-dependent species is smaller in the case of AM plants. This correlates with our result, since mycorrhizal target plants were relatively larger than non-mycorrhizal ones: AM decreased the response of *P. vulgaris* to interspecific competition.

Competition treatments did not have any substantial effect on root weight, but AM fungal inoculation increased root weight significantly. This result is evidently connected with the relatively high P level in the growth substrate. The content of extractable phosphorus (12 mg/100 g) is within the limits of the variation in natural calcareous soils in north and west Estonia (8–14 mg/100 g; see Reintam et al. 1962), but in relatively dry field conditions, phosphate chemistry tends to be dominated by a precipitation reaction with calcium ions. In the greenhouse, watering took place every day and so the availability of phosphorus was evidently better than in natural soils. At high soil P levels, the root weight of mycorrhizal plants is typically enhanced, while above a certain P level, mycorrhizal growth depression can occur (Graham and Eissenstat 1994).

Considering the lack of variation in root weights between competition treatments and also the high nutrient level of the soil used, we can conclude that root competition was not significantly different between treatments. For total weight, the interaction of AM and competition was significant, but in a slightly different

way than for shoots: mycorrhizal target plants were larger in the experiment with old *F. vesca*, but the weight differences in the experiment with the old conspecific neighbour were non-significant.

In contrast to several other individual-level experiments, our results do not contradict the results from community-level experiments. Thus, if a young *P. vulgaris* plant has established itself somewhere in a natural gap, and has to compete with adults around it, the presence of AM inoculum might make intraspecific competition more severe, but may decrease the strength of interspecific competition (at least where *F. vesca* occurs as a neighbour). In terms of biomass, this means that differences in shoot weight between species can decrease and differences within a species increase. Consequently, species diversity also increases. In the long run, it can also result in a higher plant species richness.

Classical competition theory predicts that for coexisting species, intraspecific is greater than interspecific competition. We can conclude that, at least for certain soil conditions and certain species pairs, AM might reinforce this difference. If this relationship is universal, it could be an important mechanism increasing species diversity in natural grassland communities. Still, there is no reason to assume that our result represents a general relationship. The relatively diverse results of previous experiments studying the interaction between competition and AM (Allen and Allen 1990; Eissenstat and Newman 1990; Allsopp and Stock 1992; Hartnett et al. 1993) are probably the result of the different (sometimes undetermined) soil P levels used. AM can depress growth in high-P soils due to the carbon costs of the AM fungus (Peng et al. 1993; Graham and Eissenstat 1994), but there is considerable variability in responsiveness to AM infection at different soil P levels among plant taxa (e.g. Koide 1991). Like the response of carbon allocation to fertilization (Berendse 1994), the response of allocation to AM inoculation depends on the morphological and functional attributes of particular plant species. Furthermore, the effect of AM fungi can be dependent on their interactions with other soil micro-organisms. West et al. (1993b) state clearly that some species may not be P limited in the field and if there is any benefit from mycorrhiza, it is not due to improved P nutrition.

Consequently, in each case, the role of AM in plant coexistence is dependent on the response of plants to AM in given soil conditions and in the presence of given soil micro-organisms. If the species under investigation has a positive mycorrhizal dependency in the presence of the natural microbial community, AM can amplify intraspecific competition due to resource pre-emption by older and larger individuals, when root colonization of young plants is slow. The effect of AM on interspecific competition is a function of the differences in the mycorrhizal dependencies of the taxa studied.

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