DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals

I Zobel, M. and Moora, M. 1995. Interspecific competition and arbuscular mycorrhiza: importance for the coexistence of two calcareous grassland species. — Folia Geobot. Phytotaxon. 30: 223–230.

II Moora, M. and Zobel, M. 1996. Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. — Oecologia 108: 79–84.

III Moora, M. and Zobel, M. 1998. Can arbuscular mycorrhiza change the effect of root competition between conspecific plants of different ages? — Can. J. Bot. (in print).

IV Zobel, M., Moora, M. and Haukioja, E. 1997. Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. — Oikos 78: 202–208.

INTRODUCTION

Plant species coexistence and the spatio-temporal pattern of species richness has traditionally been explained using the ecological time scale (Wilson 1990, Palmer 1994). More recently, the so-called species pool concept has evolved. This concept attempts to also include large-scale and long-term processes to explain the pattern of diversity in nature (Taylor *et al.,* 1990, Pärtel *et al.,* 1996, Zobel 1997). According to this concept, the pattern of species coexistence in any particular community is primarily determined by the migration of individuals from the regional and local species pools, the composition of which depends on evolutionary processes and vegetation history. However, even when an individual (diaspore) has successfully migrated to the community, it has to pass an environmental filter, consisting of abiotic factors and biotic interactions, which both work on an ecological time-scale.

Plant species coexistence and patterns of diversity have mostly been explained by patterns of the abiotic environment (Whittaker 1972, Grime 1979, Scheiner and Rey-Benayas 1994), and by the plant-plant interactions like competition and plant-herbivore interactions (Goldberg 1990, 1996, Huntly 1991, Goldberg & Barton 1992, Gurevitch *et al.,* 1992, Zobel 1992). Despite the fact that more than 90% of terrestrial plants are mycorrhizal (Smith and Read 1997), little attention has been paid to the the role of mycorrhizal fungi in plant community life. Arbuscular mycorrhiza (AM) is one of the most widespread types of endomycorrhiza. Approximately two thirds or more of vascular plant species form symbiotic relationships with arbuscular myccorhizal fungi (Trappe 1987, Gianinazzi 1991). AM fungi and terrestrial plants have evolved together since land colonization (Selosse and Le Tacon 1998).

Plant species of calcareous grassland communities, which are the target communities of the current work, are mostly arbuscular-mycorrhizal except orchids, a few ericaceous species and trees. The presence of AM mycelia is the norm for the calcareous grassland ecosystems. The influence of AM fungal infection on a single plant is quite well investigated by now. It is generally accepted that AM benefits host plants by promoting more efficient acquisition of mineral nutrients, mostly phosphorus (Harley and Smith 1983) and nitrogen (e.g. Ames *et al.,* 1984, Smith *et al.,* 1986, Barea *et al.,* 1989, Johansen *et al.,* 1994) from the soil. Also, AM symbiosis may enhance defences against herbivores (Gange and West 1994), improve water aquisition and may increase a plant's resistance to pathogens (Newsham *et al.,* 1995a). The cost of the benefit is the carbon flow from plant to fungus.

Since the number of AM forming fungal species (*ca* 150) is relatively low and the number of AM symbiosis forming plant species high (*ca* 225 000) (Sanders *et al.,* 1995), one may conclude that AM fungi are not host-specific.

This means that different plants are potential participitants in a common mycelial network which is present in the soil of a nonsuccessional grassland ecosystem. Consequently one might assume that AM will play an important role in the structuring of a grassland community.

Several reviews dealing with mycorrhizal symbiosis also include chapters about plant competition, community structure, and succession (Finlay and Söderström 1989, Allen 1991, Brundrett 1991, Chanway *et al.,* 1991, Ingham and Molina 1991, Read 1991, Goodwin 1992, Francis and Read 1994, Sanders *et al.,* 1995, Schönbeck and Raschen 1995). However, all these chapters share one common feature — the authors have been able to consider only a handful of case studies which have attempted to evaluate the role of AM on plant-plant interactions.

It is known from the experiments carried out on the community level, that the presence of AM fungi can increase plant species diversity in microcosm experiments (Grime *et al.,* 1987) or in early successional communities (Gange *et al.,* 1990, 1993). Different results have been obtained from a lichen-rich community, where the benomyl treatment resulted in an increase in vascular plant species richness (Newsham *et al.,* 1995b). There are some possible explanations for the higher plant species diversity in the presence of AM fungi. First, since AM fungi are not host-specific, they could form functional interconnections between plants (Newman 1988, Newman *et al.,* 1994). This means that carbohydrates could be transported along a concentration gradient from well illuminated to shaded plants. Grime *et al.,* (1987) used such an explanation, but see Bergelson and Crawley (1988). Gange *et al.,* (1990, 1993) explained the higher diversity of mycorrhizal communities by the different responses of plant species to AM — subordinate forb species benefitted more from AM than potential dominants (grasses). Indeed, species response to AM inoculation can be highly variable and depends also on the availability of soil phosphates (Koide 1991). However, some authors stress that mycorrhizal inoculum is important especially in the seedling establishment stage (Finlay and Söderström 1989, Hartnett *et al.,* 1994). Extramatrical mycelia can increase the absorbing surface area of seedling roots and thus reduce mortality in weaker species, which in turn increases diversity. Reconsidering the results of the experiments conducted by Grime *et al.,* (1987), Francis and Read (1994) claimed that mycorrhizal inoculum determined the species composition of the community by influencing plant fitness in the establishment phase, since there may be direct antagonistic interactions between the AM mycelium and noncompatible plant species.

However, the results of a few competition experiments, which have been conducted in the greenhouse, have demonstrated the opposite to the field or microcosm experiments. In the case of intraspecific competition, AM root colonization had no effect on plant interactions (Eissenstat and Newman 1990) or it even seemed to amplify competition (Allsopp and Stock 1992a, Hartnett *et* *al.,* 1993). In cases of interspecific competition, AM inoculum resulted in a greater advantage for more AM-dependent species in terms of increased biomass (Allen and Allen 1990, Hartnett *et al.,* 1993, Titus and del Moral 1998). In the last case, AM would tend rather to decrease than to increase diversity. Such a result can be explained by the fact that pot experiments have used plant species, which have clearly different mycorrhizal dependencies and/or a different successional status. Thus, these experiments are important in explaining the mechanism of succession, but tell us little if we want to know the impact of AM on plant-plant interactions (competition) in a nonsuccessional perennial grassland community. Consequently, it is important to study rather the interactions of common plant species with only slightly different rates of mycorrhizal root colonization (and presumably also mycorrhizal dependency), which are able to coexist within a limited space. Since seedling establishment can be of crucial importance for the performance of plant populations (Eriksson 1989, Weiher and Keddy 1995), it is also important to test how AM inoculation influences the performance of seedlings both in conspecific and multispecies stands.

The aims of the current work were:

1. To study whether AM influences interactions between individuals of naturally coexisting calcareous grassland plant species and if yes, then does this influence or maybe also change species diversity? (I, II)
2. To study whether the role of AM in structuring the plant community is dependent on plant age, i.e. does AM shift the balance of competition between adults and seedlings? (II, III)
3. To review our knowledge of the role of AM in determining plant species coexistence (IV).

MATERIAL AND METHODS

Plant species

Centaurea jacea L (*Compositae*), radiant cornflower is a polycarpic perennial with erect shoots and woody rhizome. *C. jacea* flowers in June to August, shed seeds in July to September. *C. jacea* is an arbuscular mycorrhizal (Harley and Harley 1987) dominant plant species in calcareous grassland (Kull and Zobel 1991).

Fragaria vesca L (*Rosaceae*), wild strawberry is a polycarpic perennial with broad leaved rosette and long arching runners. *F. vesca* is winter-green, flowers from May to June and bears fruits from June to July. *F. vesca* is an arbuscular mycorrhizal (Harley and Harley 1987) subordinate plant species in calcareous grassland (Kull and Zobel 1991).

Prunella vulgaris L. (*Labiatae*), self-heal is a stoloniferous polycarpic perennial with a broad leave overwintering semi-rosette. Shoots elongate in spring, flowers from June to September, seed set is from July to October. *P. vulgaris* is an arbuscular mycorrhizal (Harley and Harley 1987) subordinate plant species in calcareous grassland (Kull and Zobel 1991).

Hypericum perforatum L. (*Hyperiaceae*(*Guttiferae*)), common St John's wort is a rhizomatous, polycarpic perennial with erect branched shoots. *H. perforatum* flowers from June to September and shed seeds from late July to late October. Some seeds are overwintering in the dry inflorescence on plant. *H. perforatum* is an arbuscular mycorrhizal (Harley and Harley 1987) subordinate plant species in calcareous grassland (Kull and Zobel 1991).

Experimental design

Experiment 1 (Paper I): Two species — *Centaurea jacea* and *Fragaria vesca* — were grown in a pot experiment of factorial design. Both species were grown together in one pot (two individuals of *F. vesca* and one of *C. jacea*) and singly as a control, in both cases with and without AM fungal inoculaton. Initially, all treatments were represented by 20 replicates, but for various reasons some of the plants died during the experiment.

Experiment 2 (Paper II): 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 (all in 13 replicates) were used as neighbours: 1. a large, 10 — week old, *P. vulgaris*, 2. two *P. vulgaris* seedlings, 3. a large, 10 — week old, *Fragaria vesca*. In order to test the mycorrhizal dependency of *P. vulgaris* in the given soil conditions, we also grew single control plants with and without AM inoculation

Experiment 3 (Paper III): Three seedlings (one week old) and three adult (about 7 week old) *Hypericum perforatum L.* plants per pot were grown in a greenhouse experiment of factorial design where the presence of root competition and AM fungal inoculation were used as treatments. Both shoot and root competition occurred between the plants of *H. perforatum* in the pots. In half of the pots, root competition was eliminated by separating roots with 41 µm nylon mesh bags, which can be penetrated by AM hyphae but not by plant roots (see Jakobsen 1994). Both competition treatments were repeated in two variants — plants were arbuscular mycorrhizal or nonmycorrhizal. Thus four different competition treatments resulted. All treatments were represented by 30 replicates.

To determine the mycorrhizal dependency of the experimental plants at the given soil conditions in experiments 2–3 (I, II, III), single controls (both seedlings and adults in case of experiments 2 and 3) were grown alone in pots. Also, the effect of the root bag on mycorrhizal and nonmycorrhizal plants of different ages was controlled in experiment 3 (III).

Growth environment

Plants were grown in 4(depth)×13×18 cm pots. The soil used for seed germination and for experimentation was (I, II) three parts steam sterilized horticultural peat (pH 6) and one part fine sand. The resulting mixture had a relatively high P-level (the content of extractable P was 12 mg/100 g) (experiments 1, 2). In experiment 3 soil used in experimental pots was one part steam sterilized horticultural peat (pH 5.5) and two parts sterilized fine sand. The resulting mixture contained approximately of extractable P 0.89 mg/100 g.

Plants were grown in the greenhouse in full light (day length 16 h) for 59 (I), 60 (II), and 65 (III) days. Watering took place every day (I, II), and two-three times per week (III). Experiments 1 and 2 (I, II) were carried out in the experimental greenhouse of Satakunta Environmental Research Centre of Turku University. Experiment 3 (III) was carried out in the experimental greenhouse of Ruotsinkylä Forest Research Station of the Finnish Forest Research Institute.

AM inoculation

In experiments 1 and 2 (I, II) similar techniques were used. When the seedlings were transplanted in to the competition treatments, AM infection was achieved by adding 50 cm^3 of natural soil (Hayman *et al.,* 1981). The soil originated from the same calcareous grassland as the one from where the seeds of the experimental plants were collected. The advantage of this method is that plants are colonized by the natural community of fungi, which is important since different fungal species can have different roles in the association (Newsham *et al.,* 1995 c, Streitwolf-Engel *et al.,* 1997). In experiment 3 (III) we used the so-called donor plants for inoculation. The most rapid infection of plants occurs in the presence of living extramatrical hyphae (Eissenstat and Newman 1990). Because of this, experimental plants were first grown in the same pot with a naturally AM infected conspecific neighbour. Afterwards, the soil originating from the same calcareous grassland from which the seeds of experimental plants were collected, was also added to pots (20 cm^3).

Other soil microorganisms were not controlled. The species of AM fungi were not determined.

Fungicide application

The nonmycorrhizal variant received the same amount of natural soil (50 cm^3 and 20 cm^3 respectively) but was treated once with the fungicide benomyl (Benlate, 0.6 gr per pot) and once with iprodione (Rovral, 0.04 ml per pot) during the experiment. Benomyl has been claimed to be efficient in eliminating AM (Fitter and Nichols 1988) with no direct effect on vascular plants (Paul *et al.,* 1989, West *et al.,* 1993 a). We avoided the use of fumigated soil due to the changes this can induce in nutrient availability (Jakobsen 1994). However, due to uncertainties about benomyl's selective effect on zygomycetes (see Summerbell 1988), iprodione was also used, following Gange *et al.,* (1990) and West *et al.,* (1993 a).

Sampling

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, and the latter as root weight.

Statistical analysis

Plant biomass data was analysed by standard procedures of multifactor ANOVA (Systat). The effect of factors influencing the frequency of AM infection of individuals was investigated by using log-linear analysis (paper I). The significance of the efects of interest was assessed in a hierarchical sequence of models of increasing complexity (Haber 1984).

RESULTS

Influence of AM on the interactions between even-aged individuals of naturally coexisting plant species (paper I).

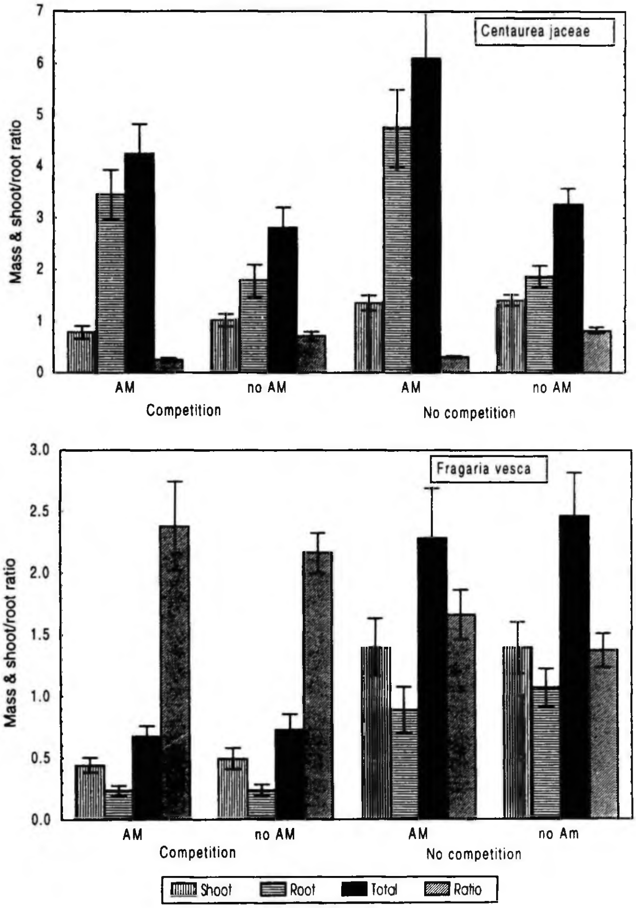

Fig. 1. The average dry mass of *C. jaceae* and *F. vesca* per plant. Shoot, root and total mass and shoot to root ratio of plants growing with and without AM inoculation in competition conditions, single control with and without AM inoculation.

The effects of competition were one-sided, i.e. the weight of *F. vesca* decreased relatively more than that of *C. jacea* as a result of competition. Competition reduced the biomass of *F. vesca* by approximately 70% and the biomass of *C. jacea* by approximately 25%. AM infection had no effect on the weight of

F. vesca but increased the total weight of *C. jacea* by approximately 42% (Fig. 1). The biomass difference between *C. jacea* and *F. vesca* growing together in one pot increased when plants were mycorrhizal, mostly due to the increase in the biomass of *C. jacea*.

Influence of AM on the competitive balance between adults and seedlings (papers II, III)

In experiment 2, competition did not reduce target plant (seedlings of *Prunella vulgaris*) weight significantly in the treatment, where small neighbours (*P. vulgaris*) were grown together with small target plants. The competitive effects of large neighbours (*P. vulgaris, F. vesca*) on target plants were significant, regardless of species (both older neighbours reduced the weights of target plants similarily), but there was a clear difference between intra- and interspecific competition when plants were mycorrhizal (Fig. 2). In the case of intra-specific

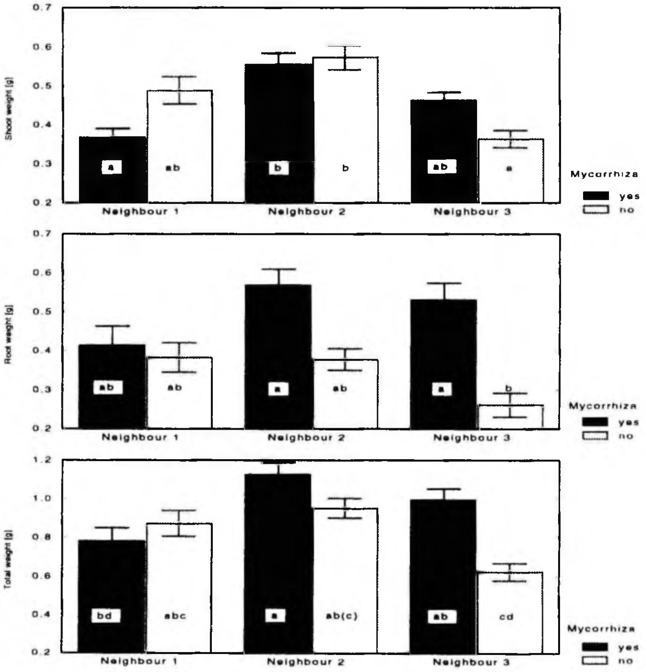

Fig. 2. The shoot, root and total weight (±SE) of target *P. vulgaris* plants in three neighbouring situation (1 — old *P. vulgaris*, 2 — young *P. vulgaris*, 3 — old *F. vesca*). Means with the same letter are not significantly different using Tukey's mean separation test (P≤0.05). The parenthesis in one case indicate that means were different on the probability level 0.060. (Modif. by paper II)

competition with a large neighbour, the target plant shoot weight was reduced on average by 24%, when plants were mycorrhizal. Thus, AM amplified rather than balanced intraspecific competition. In the case of interspecific competition with old *F. vesca,* the shoot weights of target plants were on average 22% higher in the AM inoculated case compared to the nonmycorrhizal one.

In experiment III the response of *Hypericum perforatum* to inoculation by arbuscular mycorrhiza in noncompetitive conditions was positive, while the positive response of seedlings was significantly stronger (see Paper III, Fig. 3). In the case on intraspecific root competition (Fig. 3), the positive effect of mycorrhiza on seedlings vanished — competing mycorrhizal and nonmycorrhizal seedlings were both of the same size. Without root competition, the shoots of mycorrhizal adults were much larger than those of nonmycorrhizal adults, but with root competition the shoot weights did not differ. Arbuscular mycorrhiza increased the biomass differences between competing seedlings and adults.

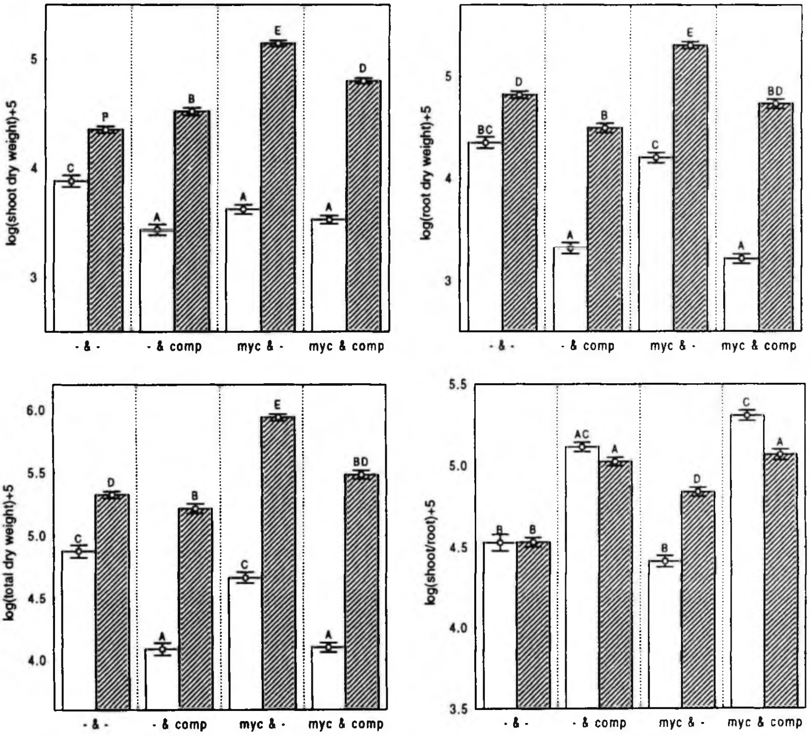

Fig. 2. Means (±SE) of the shoot, root and total weight and shoot to root ratio of *Hypericum perforatum* young (open bars) and old (filled bars) plants growing in competition experiment with (myc) or without (-) arbuscular mycorrhizal inoculation and with (comp) or without (bag) root competition. Means with the same letter are not significantly different using Tukey's mean separation test (P≤0.05).

The mycorrhizal dependency of the plant species used, in the given soil condition

Centaurea jacea (Paper I) showed a highly positive response to AM inoculation (Fig. 1). *Fragaria vesca* (Paper I, II) did not respond to the AM inoculation (Fig. 1). *Prunella vulgaris* (Paper II) responded positively to AM inoculation, it's total weight increased by approximately 55% ($P = 0.003$). All these experiments were conductedwith a relatively high level of soil P.

Hypericum perforatum (Paper III, Fig. 1) showed a significant increase in biomass in the case of AM inoculation. This experiment was conducted with a relatively low level of soil P.

Mycorrhizal colonization of roots

The mycorrhizal inoculation of experimental plants was successful in a qualitative sense — the roots of all plants tested in the mycorrhizal treatment were colonized by AM fungi. But there was a large variation in the rate of root colonization. In certain cases, the average root colonization remained low and did not exceed 8% for *C. jacea* and 4% *for F. vesca* in experiment 1. In experiment 2, the root colonization level of old *F. vesca* was 27% (Paper II). The average root colonization rate was 15% in the case of young and 22% in the case of adult *P. vulgaris* plants (Paper II). In the case of *Hypericum perforatum* (Paper III), the average colonization level was 46% for seedlings and 48% for adults. The fungicide treatment was efficient in all experiments — no AM root colonization was found in tested plants.

DISCUSSION

The results of the current study showed, that AM can change the balance of competition between naturally coexisting plant species. In the case of interspecific competition between even-aged plants, the balance of competition depended on the plant species-specific responsiveness to AM infection: *C. jacea*, which was clearly positively AM dependent, was a more successful competitor due to AM inoculation than *F. vesca,* which did not respond to AM inoculation at the given soil conditions (I). Since *C. jacea* is a predominating species and *F. vesca* a subordinate species in calcareous grasslands (Kull & Zobel 1991) one can argue that this may be due to 'one-sided' competition between these two species. The biomass of *F. vesca* decreased relatively more due to competition than the biomass of *C. jacea*, and the weight differences between the two competing species increased when plants were mycorrhizal. Goldberg (1987) argued that the relative size of a plant determines the outcome of competition. For the given soil conditions, AM inoculation can be the factor enhancing the predomination of *C. jacea* over *F. vesca* because of this differential growth response. We did not find any indirect evidence to support the interplant transfer of resources by AM. Consequently, our results are in agreement with earlier findings that AM amplifies interspecific competition. As in other experiments, where species of very different mycorrhizal dependencies have been used (Fitter 1977, Allen and Allen 1990, Hartnett *et al.,* 1993), our results showed that more unbalanced competition (larger differences in biomasses) resulted from AM infection. Hence the inconsistency with community-level experiments, which have shown higher species diversity in the mycorrhizal case (Grime *et al.,* 1987, Gange *et al.,* 1990, 1993) remains. Probably, the experiment with even-aged adult plants does not indicate clearly the real situation in the field, where coexisting plants have different ages and sizes. The experiment with even-aged plants does not give information about the role of competition and AM in the critical stages of plant life — i.e. seed germination and seedling establishment.

It has been shown that competition can have large negative impact in the seedling establishment stage (Goldberg and Werner 1983). On the other hand, AM infection can enhance seed germination and seedling establishment (Francis and Read 1994, Hartnett *et al.,* 1994). We found (paper III) that in a non-competitive environment, *H. perforatum* showed a clear positive mycorrhizal dependency in the given soil conditions — biomass increased significantly in the case of mycorrhizal inoculation. The positive influence of AM decreased as plants aged: seedlings showed a relatively greater increase in biomass due to the AM inoculation than adults. Thus, seedlings benefitted relatively more from the symbiosis with AM fungi than adults. The more rapid growth of the mycorrhizal seedlings with a root bag, compared to nonmycorrhizal seedlings in the same conditions, was an indication that extramatrical AM fungal mycelia functioned as an important nutrient absorber. Surprisingly, the positive effect vanished when seedlings grew in pots together with three adults — seedlings no longer showed any positive response to AM, as was the case in the single control. In the competition experiment, AM inoculation increased plant biomass, but only in the case of adult plants. The only explanation can be that the negative effect of the competition on the seedlings was stronger than the positive effect of the AM inoculation. The same result was received in an experiment with *P. vulgaris* seedlings (Paper II). Despite the fact that *P. vulgaris* seedlings performed better with mycorrhizal symbiosis in a non-competitive environment, the presence of a large conspecific neighbour eliminated this positive effect — target seedlings in the shade of a conspecific neighbour were significantly smaller when plants were mycorrhizal. Allsopp and Stock (1992) and Hartnett *et al.*, (1993) found that AM amplifies rather than balances intraspecific competition between even — aged plants. The same seems to be true when individuals of different ages and sizes are competing (II, III). Consequently, if there exists an age-specific positive effect of AM on seedlings in monospecific stands, it is more probably not due to the higher competitive ability of mycorrhizal seedlings, but rather due to the fact that mycorrhizal seedlings tolerate harsh environmental conditions better, which may be the main limitation for seedling recruitment in dry grasslands (Ryser 1993).

In the case of interspecific competition between seedlings and an adult of a different species (Paper II), the differences in shoot weights were the opposite compared to intraspecific competition, shoots of the target seedlings of *P. vulgaris* in the shade of *F. vesca* were larger when plants were mycorrhizal. Consequently, AM improved the performance of small *P. vulgaris* plants in the case of interspecific competition. This result is also in agreement with previous results from pot experiments which found that AM typically increases the competitive effect of the more mycorrhiza-dependent species (Allen and Allen 1990, Hartnett *et al.*, 1993, I). The competitive response of mycorrhiza-dependent species is smaller in the case of AM plants (Hartnett *et al.*, 1993), which is in accordance with our result since mycorrhizal target plants were relatively larger compared to nonmycorrhizal ones: AM decreased the response of *P. vulgaris* to interspecific competition. Thus, if a young *P. vulgaris* plant has established somewhere in a natural community, and has to compete with adults around in its vicinty, 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 may decrease and differences within a species may increase. Consequently, species diversity also increases. In the long run, this can also result in higher richness. Also, this results is in accordance with the results received from community level experiments where a positive correlation between species richness and arbuscular mycorrhizal inoculation has been observed (Grime *et al.,* 1987, Gange *et al.,* 1990, 1993).

According to classical competition theory, for species to coexist it is necessary that intraspecific competition is greater than interspecific. We can conclude that, at least for certain soil conditions and certain species pairs, AM might reinforce this difference (II). If this relationship is universal, it could be an important mechanism increasing species diversity in natural grassland communities.

However, we have no reason to assume that our results represent a general relationship only — very little and relatively diverse information is available on this topic (Paper IV). The responsiveness of plant species to AM infection is very variable (Koide 1991, Sanders *et al.,* 1995). The role of AM in plant coexistence is dependent on the species-specific response of plants to AM at the given soil fertility conditions. One of the most common effects of AM infection on the physiology of the host plant is an increase in phosphate absorption. Although external AM hyphae deliver up to 80% of plant phosphorus in experimental chambers (Marschner and Dell 1994), some species do not seem to be P-limited in the field (West *et al.,* 1993 b, Streitwolf-Engel *et al.,* 1997). Most experiments trying investigate the role of AM in competition have been made at one soil-P level only, as we also did. Considering that plant species have clearly different mycorrhizal dependencies at different soil-P levels, one can assume that the possible (balancing or unbalancing) effect of AM on competition is dependent on the particular species and on the soil-P level.

The impact of AM fungi on plant species coexistence has been studied mostly in the context of plant vegetative growth, i.e. by comparing the biomass differences between competing species. There are a few works which have attempted to research the influence of AM on plant fecundity (i.e. Sanders and Koide 1994, Shumway and Koide 1994, Chanrashekara *et al.,* 1995) . Results of these studies have shown that the influence of AM symbiosis on plant fecundity or offspring vigour may be positive — increases both the quality and number of offspring. This means that AM can have a long-term impact on plant community composition. Since vegetative growth and generative reproduction in plants often compete (Waller 1990), then the controversial results of experiments studying the role of AM in plant growth and reproduction need the further investigation.

AM symbiosis and competition are not the only biotic interactions influencing the plant community, but their influence must viewed in the contecst of other interactions. Indeed, AM can mediate plant-herbivore, plant pathogens and plant — symbiont (e. g. *Rhizobium*, mycophyllae) interactions (Finlay and Söderström 1989, Allen 1991, Ingham and Molina 1991, Clay 1992, Fitter and Sanders 1992, Jarstfer and Sylvia 1992, Lussenhop 1992, Gange and West

1994, Fitter and Garbaye 1994, Gehring and Whitham 1994, Newsham *et al.*, 1994, 1995a, Sanders *et al.*, 1995, Azcon-Aguilar and Barea 1996). All such interactions can influence the competitive ability of plants by changing their carbon allocation pattern, and thus also the species composition and diversity of plant communities.

The influence of plant — AM fungal symbiosis on the plant and plant interactions has mostly been studied in greenhouse conditions. This is understandable due to the difficulties in conducting well designed experiments in the field. However, the effect of AM on plant life should be evaluated in the field, since the results may be different from these found in the greenhouse. In conditions of constant management, calcareous grasslands in Estonia represent stable and species rich communities (Kull and Zobel 1991). Though vegetative regeneration clearly prevails over regeneration by seeds in grasslands(Hein 1968, see also Eriksson 1989), the latter is extremely important for species migration over greater distances than a few centimeters. The success of the establishment of a new plant individual is evidently dependent on interactions with AM mycelium. Future studies have to explain, what is the role of AM fungi in seedling establishment in calcareous grasslands.

Consequently, if we are able to ascertain the role of AM in field experiments, and if we know (from pot-experiments) whether and how the soil-fertility gradient influences the competitive effect and response of AM host-plants, considering both vegetative and reproductive characteristics, we shall come closer to answering the question: “How does AM influence plant competition and, through it, plant coexistence in stable communities?”.

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ARBUSKULAAR-MÜKORIISSE SÜMBIOOSI MÕJU LUBJARIKKA NIIDU TAIMELIIKIDE KONKURENTSILE JA KOOSEKSISTEERIMISELE

Kokkuvõte

Klassikaline taimeökoloogia on uurinud taimeliikide kooseksisteerimist, võttes põhiliselt arvesse taimede ja taimede-herbivooride interaktsioone. Seni on veel väga vähe uuritud, kas ja kuidas mükoriissed seened, mis on evolutsioneerunud koos taimeliikidega, määravad taimekoosluse struktuuri ja mõjutavad taimeliikide kooseksisteerimist. Ligikaudu 90% maismaataimedest on mükoriissed, enamus endomükoriissed. Arbuskulaarne mükoriisa (AM) on üks endomükoriisa vorme ja esineb põhiliselt rohttaimedel. Enamik lubjarikka niidu taimeliike on arbuskulaar-mükoriissed (AM) liigid.

AM seente mõju taimele on üsna hästi uuritud. Seenehüüf suurendab juurte aktiivset pinda, aitab taimel mullast toitaineid kätte saada, parandab veega varustatust, võtab taimelt süsivesikuid. Kas ja kuidas mõjutab AM taimekoosluse struktuuri, on keeruline ja vastakaid arvamusi põhjustanud küsimus.

Praeguseks on koosluse tasandil tehtud katsetest teada, et AM suurendab niidukoosluse liigirikkust. Selle selgitamiseks on kolm põhiseisukohta: 1) et AM seened pole liigispetsiifilised, võivad seenehüüfid moodustada peremeestaimede vahel sildu, mille kaudu süsinik ning mineraalained kantakse ühelt taimelt teisele; 2) mükoriissuse mõju eri taimeliikide kasvule ja selle kaudu konkurentsivõimele on erisugune, mistõttu AM muudab kogu koosluse konkurentsi tasakaalu; 3) AM muudab koosluse struktuuri mõjutades taimepopulatsioonide uuenemist. Arenemisjärgus taimisendid on eriti vastuvõtlikud mükoriissele infektsioonile ja AM positiivse mõju korral suudavad rohkemate liikide isendid läbida edukamalt juveniilse arengustaadiumi.

Kui võrrelda koosluse tasandil tehtud eksperimentide ja valdavalt kasvuhoones sooritatud potikatsete tulemusi, on näha vastuolu. Potis tehtud konkurentsikatsetes on leitud, et AM pigem tugevdab kui leevendab liikide konkurentsi. Teooria kohaselt peaks koosluse liigirikkus sellisel juhul pigem vähenema. Liigisisese konkurentsi korral AM kas ei mõjuta konkurentsi või tugevdab selle intensiivsust. Enamus konkurentsikatseid on tehtud taimeliikidega, mis on juba ette teada selgelt erineva mükotroofsusega ja vahel ka erisuguse suktsessioonilise staatusega. Sellised eksperimendid annavad meile informatsiooni näiteks suktsessiooni võimalikest toimemehhanismidest, kuid ütlevad vähe, milline on AM roll stabiilses niidukoosluses.

Käesoleva doktoritöö eesmärgid: (1) Kontrollida, kas AM mõjutab looduslikult kooseksisteerivate taimeliikide interaktsioone. Kui jah, siis kas AM mõju muudab ka koosluse liigirikkust. (2) Kontrollida, kas AM mõju taimekooslusele sõltub taimede vanusest (suurusest). Kas AM muudab vanade ja noorte taimede konkurentsi tasakaalu? (3) Üldistada eksperimentidest saadud tulemusi ning luua teoreetiline raamistik mõistmaks AM rolli taimeliikide kooseksisteerimisel.

Doktoritöö koosneb kahest osast: eksperimentaalsest (vastused küsimustele 1 ja 2) ja teoreetilisest (vastused küsimusele 3).

Kontrollimaks, kas ja kuidas mõjutab AM niidutaimeliikide konkurentsisuhteid, sooritati seeria kasvuhoonekatseid: kasvatati eri liiki taimi ja eri vanusega isendeid mitmesugustes kombinatsioonides, kasutades arbuskulaarse mükoriisa olemasolu ja puudumist ning erinevate konkurentsivormide olemasolu ja puudumist kui eksperimentaalseid töötlusi.

Saadud tulemused näitasid, et AM mõjutab looduslikult kooseksisteerivate taimeliikide konkurentsi tasakaalu. Konkurentsi tasakaal sõltub taimede liigispetsiifilisest mükotroofsusest. Üheealiste taimede puhul leiti, et *Centaurea jacea,* mis katses kasutatud mullatingimustel sõltus selgelt AM-ist, on konkurentsis edukam, kui taimed kasvavad mükoriisses sümbioosis. *Fragaria vesca*, mis antud mullatingimustel ei reageerinud AM olemasolule, jäi konkurentsis rohkem alla siis, kui taimed olid mükoriissed. Seega suurendab AM liikide konkurentsi. Selline tulemus ei anna põhjust arvata, et AM mõjuks positiivselt liikide arvule koosluses.

Tulemused erinevad, kui eksperimendis kasutati erineva vanusega taimisendeid. Liikide konkurentsi korral, kui koos kasvasid *F. vesca* suur taim ja *Prunella vulgaris*'e juveniilid, olid noored taimed suhteliselt edukamad mükoriissel juhul. Kui samas katses uuriti liigisisest konkurentsi, olid *P. vulgaris*'e idandid suhteliselt edukamad mittemükoriissel juhul. Analoogiline tulemus saadi ka siis, kui uuriti *Hypericum perforatum*'i juveniilide ja suurte taimede liigisisese juurkonkurentsi ja mükoriisse sümbioosi mõju. Tulemused näitasid, et AM sümbioos suurendas väikeste ja suurte taimede biomassi erinevust, ehkki kasvades üksi, ilma konkurentsita, reageerisid juveniilid AM sümbioosile oluliselt tugevamini kui vanad taimed: idandite biomass suurenes tunduvalt rohkem. Seega võib järeldada, et AM muudab erivanuseliste taimede konkurentsi tasakaalu. Liigisisese konkurentsi korral AM suurendab, liikidevahelise konkurentsi korral (*P. vulgaris*'e ja *F. vesca* näitel) vähendab konkurentsi tugevust.

Kui kirjeldatud eksperimentide tulemustest teha üldine järeldus, saab öelda, et AM suurendab liigisisest ja tasakaalustab liikidevahelist konkurentsi ning see võib olla üheks kõrget liigirikkust tagavaks mehhanismiks niidukoosluses. Siiski, toetudes varasematele uurimustele, pole põhjust arvata, et selline järeldus kehtib igas olukorras. Teave AM mõjust taimeliikidele ja taimekooslustele on liiga vähene ja küllalt vastakas. Tuleb arvestada, et AM roll taimeliikide kooseksisteerimises sõltub taimeliigi reaktsioonist AM sümbioosile antud mullatingimustel. Seega sõltuvad ka eksperimentide tulemused palju taimeliigipaaride ning substraadi omadustest. AM sümbioosi olulisim mõju peremeestaimede füsioloogiale on fosfaatide adsorptsiooni suurendamine. Suur osa eksperimente, mis on tehtud uurimaks AM rolli taimede konkurentsis, on tehtud ainult ühel mulla fosforisisaldusel. Võttes arvesse, et taimede mükoriisasõltuvus erineb selgelt mulla erinevate toitainete sisalduse juures, võime eeldada, et AM (mitte)tasakaalustav roll konkurentsis sõltub liigi spetsiifikast ja mulla fosforisisaldusest, üldisemalt mulla viljakusest.

AM rolli taimede elus on seni uuritud, võttes arvesse põhiliselt taimede vegetatiivset kasvu iseloomustavaid parameetreid: on võrreldud konkureerivate liikide biomassi erinevusi. Samas aga võib AM-il olla pikaajalisem mõju taimede kooseksisteerimisele koosluses, mõjutades taimede ja nende järglaskonna seksuaalset paljunemise kvaliteeti ja kvantiteeti. Seega peaks lisaks vegetatiivsetele parameetritele uurima ka konkurentsikatsetes kasutatavate taimede reproduktiivseid parameetreid.

Ka on seni liiga vähe teada, kuidas AM seened interakteeruvad teiste taime elutsüklit mõjutavate elusolenditega — maapealsete ja -aluste herbivooridega, mügarbakteritega, maapealsete ja -aluste patogeenidega, mis kõik põhjustavad süsiniku allokatsiooni muutusi taimes ja seega mõjutavad nii taimedevahelisi kui ka taimede ja seente interaktsioone.

Arvestades potikatsete piiratud võimalusi, tuleks tulevikus rohkem tähelepanu pöörata manipulatiivsetele eksperimentidele looduslikes taimekooslustes. Sealjuures peaks eriti arvestama kahte aspekti: a) AM mõju taimede seemneproduktsiooni kvaliteedile ja kvantiteedile ning b) AM mõju seemnete idanemisele ja idandite arengule. Arvatavasti võib AM mängida olulist rolli just koosluse seemnelist uuenemist mõjutades.

Käesolev töö annab esialgse vastuse küsimusele “Kuidas AM mõjutab taimede interaktsioone ja seega taimede kooseksisteerimist stabiilses niidukoosluses?” Täiuslikum vastus eeldab lisauurimusi, kus hinnatakse, kuidas mulla P- (viljakuse-) gradient mõjutab AM taimede konkurentset efekti või vastust konkurentsile, võttes arvesse nii vegetatiivseid kui ka reproduktiivseid parameetreid. Samuti on väga oluline hinnata AM rolli manipulatiivsetes väliEksperimentides.

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I

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INTERSPECIFIC COMPETITION AND ARBUSCULAR MYCORRHIZA: IMPORTANCE FOR THE COEXISTENCE OF TWO CALCAREOUS GRASSLAND SPECIES

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Abstract: Two naturally coexisting grassland species - *Centaurea jacea* (often predominating) and *Fragaria vesca* (subordinate) were grown together in a pot experiment of factorial design, where competition and arbuscular mycorrhiza (AM) inoculation were used as treatments. The effects of competition were one-sided, i.e. the mass of *F. vesca* decreased relatively more than that of *C. jacea* as a result of competition. The root and total mass of *C. jacea* increased with AM inoculation while *F. vesca* did not respond. The mass difference between *C. jacea* and *F. vesca* in a particular pot increased when plants were mycorrhizal, mostly due to the mass increase of *C. jaceae*. This can be explained by the differential response of these species to AM. We did not find any indirect indication of the interplant transfer of resources. The results of this experiment show the more unbalanced competition (larger differences in biomass) resulting from AM infection of plants.

INTRODUCTION

Plant species coexistence has mainly been considered in the context of plant-plant or plant-herbivore interactions (GOLDBERG 1990, WILSON 1990, ZOBEL 1992). Only a few studies consider the role of mycorrhizal symbiosis. GRIME et al. (1987) and GANGE et al. (1990, 1993) showed that arbuscular mycorrhiza (AM) can influence plant coexistence: mycorrhizae increased the species equitability and/or richness of the microcosm and early successional communities. The results of the few competition experiments in the greenhouse have, in contrast, demonstrated the opposite. AM inoculum resulted in a greater advantage for more AM-dependent species in terms of increased biomass (earlier works reviewed by ALLEN & ALLEN 1990, HARTNETT et al. 1993).

Two possibilities have been cited in the literature to explain how AM can influence the outcome of plant competition and thus coexistence. (a) AM mycelia can form functional interconnections between plant species and individuals; phosphate (CHIARIELLO et al. 1982, WHITTINGHAM & READ 1982) and carbon (FRANCIS & READ 1984) can be transferred via shared arbuscular mycorrhizal hyphae. Carbon transfer is assumed to occur along a carbohydrate concentration gradient, i.e. from an illuminated to a shaded plant. This explanation was adopted by GRIME et al. (1987), when interpreting the results of a microcosm experiment. (b) Another explanation could be the differential response of species to AM (e.g.

BERGELSON & CRAWLEY 1988). Indeed, the response of species to AM inoculation can be very variable (KOIDE 1991) and also depends on the availability of phosphates. This explanation was used by GANGE et al. (1990, 1993).

Whether or not the presence of AM balances competition and enhances coexistence can be tested in a pot experiment. If two plants of different species and size are grown together, a smaller mass difference in mycorrhizal plants than in nonmycorrhizal plants will indicate the occurrence of a balancing effect. If the smaller plant shows significant positive and/or the larger plant significant negative mycorrhizal dependency (i.e. improved or decreased growth when mycorrhizal, respectively), the mechanism responsible could be a differential response to AM. If AM does not improve the growth of the smaller plant when growing alone, but the mass difference decreases in the mycorrhizal case, interplant transport of carbohydrates could be the explanation.

The purpose of the present study was to ascertain the role of AM in interspecific competition and thus species coexistence. All the studies of which we know have been conducted with species of clearly different mycorrhizal dependency. In contrast, we chose two naturally-coexisting rich calcareous grassland forb species that are both arbuscular-mycorrhizal (HARLEY & HARLEY 1987), although we had no information about the magnitude of their responses to AM. Both perform well without AM in the greenhouse.

MATERIAL AND METHODS

Two species with different-sized individuals were grown in a pot experiment of factorial design. *Centaurea jacea* L. is relatively large and a typical predominating species in rich calcareous grassland communities (KULL & ZOBEL 1991). *Fragaria vesca* L. is relatively small and a common subordinate species in the same communities. Both species were grown together in one 4 × 13 × 18 cm pot (two individuals of *F. vesca* and one of *C. jacea*) or as single as a control, in both cases with and without AM fungal inoculation. Because of *C. jacea* located between two individuals of *F. vesca* and thus the physical contact between *F. vesca* individuals was absent, we assumed that intraspecific competition was negligible compared to interspecific. Initially, all treatments were represented by 20 replicates, but some of the plants died during the experiment.

The substrate used for seed germination was three parts steam-sterilized horticultural peat (pH = 6) and one part fine sand. The soil used for inoculation was a mesic rendzic leptosol with a pH of around 6.5. The content of extractable P in the growth substrate was 12 mg/100 g. Five-week-old seedlings were transplanted to pots containing the same substrate. When the seedlings were planted, AM infection was achieved following the standard procedure (HAYMAN et al. 1981), of adding 50 ml of natural soil containing spores, hyphal fragments and infected root segments. In experiments, soil treatment has been a more efficient method for inoculation than using spores only (ALLEN & ALLEN 1984). Nonmycorrhizal treatments received the same amount of natural soil (but without root pieces) but having been treated once with the fungicide benomyl (0.6 g per pot) and once with iprodione (Rovral, 0.04 ml per pot). Benomyl is claimed to be efficient in eliminating AM (FITTER 1986) and has no direct effect on vascular plants (PAUL et al. 1989). Because benomyl may have a selective effect on phycomycetes (see SUMMERBELL 1988), iprodione was also used, as previously suggested by GANGE et al.

Table 1. Results of ANOVA - influence of competition (comp), AM inoculation (myc) and their interaction (comp*myc) on the mass of *C. jacea* and *F. vesca* (per plant) in a pot experiment.

Parameter	Source of variation	F-ratio		Significance level	
		C. jacea	*F. vesca*	*C. jacea*	*F.vesca*
shoot mass	comp	14.78	48.98	0.00	0.00
	myc	1.32	0.03	0.25	0.86
	comp*myc	0.50	0.04	0.48	0.50
root mass	comp	2.53	65.70	0.11	0.00
	myc	27.90	1.09	0.00	0.96
	comp*myc	2.00	0.93	0.16	0.53
total mass	comp	4.77	26.80	0.03	0.00
	myc	16.06	0.31	0.00	0.57
	comp*myc	1.72	0.08	0.19	0.48
shoot/root ratio	comp	1.69	6.67	0.20	0.01
	myc	53.38	0.77	0.00	0.39
	comp*myc	0.26	0.01	0.61	0.91

(1990). Species of AM fungi were not determined. Other soil microorganisms were not controlled.

Plants were grown in full light (day length 16 h), and watered daily, for 59 days. The above- and below-ground parts of all plants were then harvested, dried at 85 °C for 24 h and weighed. The first is referred to as shoot mass, although it consisted mainly of leaves, and the second is referred to as root mass. Total mass per plant, total mass per pot and the mass difference between *C. jacea* and *F. vesca* were calculated for each pot. Root samples were taken from each plant in 5 pots of each treatment and the percentage of AM fungal colonization was estimated on the basis of 30-50 1 cm root segments. To quantify AM infection, roots were stained according to Koske & Gemma (1989), and the percent of colonized root segments determined (Rajapakse & Miller 1992).

To analyse the effect of the experimental treatments on plant biomass, standard procedures of multifactor ANOVA (Systat) were used. One-way ANOVA was applied to study the effect of AM infection on the difference in species mass and on the total mass per pot. The effect of factors influencing the frequency of AM infection of individuals was investigated using log-linear analysis (Statgraphics). The significance of the effects of interest was assessed in a hierarchical sequence of models of increasing complexity (Haber 1984).

RESULTS

Centaurea jacea

The effects of competition and AM infection on the dry mass of *C. jacea* are characterized in Tab. 1 and Fig. 1. Competition reduced shoot mass and total mass by approximately 35% and 25% respectively but had no effect on root mass and on the shoot to root ratio. Mycorrhizal

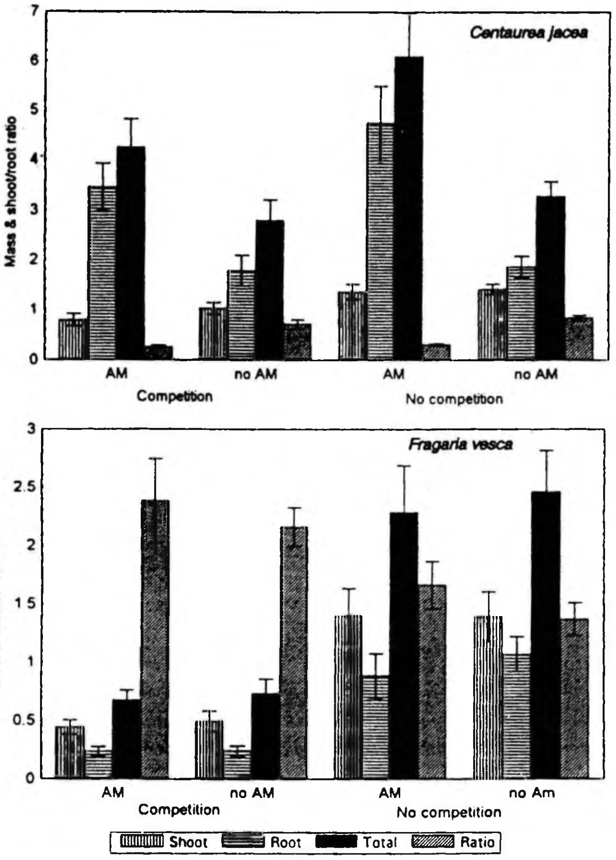

Fig. 1. The average dry mass of *C. jaceae* and *F. vesca* per plant. Shoot, root and total mass and shoot to root ratio of plants growing with and without AM inoculation in competition conditions, single control with and without AM inoculation.

infection increased root and total mass by approximately 56% and 42%. The slight decrease of shoot mass was statistically nonsignificant. Due to the marked increase of root mass, mycorrhizal inoculation significantly decreased the shoot to root ratio. The interaction between competition and mycorrhizal inoculation was nonsignificant.

Fragaria vesca

The effect of competition and AM infection on the dry mass of *F. vesca* (per plant) is characterized in Tab. 1 and Fig. 1. Competition reduced shoot, root and total biomass by approximately 70% and significantly increased shoot to root ratio. AM inoculation had no effect on the mass and on the shoot to root ratio of *F. vesca*. The interaction between competition and mycorrhizal inoculation was nonsignificant.

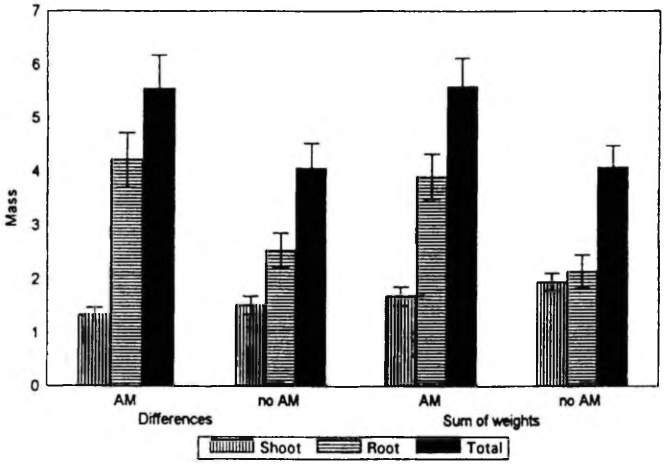

Fig. 2. The differences in shoot, root and total mass between *C. jacea* and *F. vesca* (AM) with and (no AM) without AM inoculation. The mass per pot (shoot, root and total) with and without AM inoculation.

Mass differences between *C. jacea* and *F. vesca* and mass per pot

The effect of AM inoculation on the mass differences between *C. jacea* and *F. vesca* and on mass per pot is characterized in Tab. 2 and Fig. 2. A significant increase in mass differences was observed for root and total mass due to AM inoculation. This was mostly due to the large increase in the root mass of *C. jacea* caused by AM inoculation and the lack of response by *F. vesca.* Similarly, only the root mass and total mass per pot significantly responded to mycorrhizal inoculation.

Mycorrhizal infection of roots

The mycorrhizal inoculation of experimental plants was successful in a qualitative sense - almost all the plants in the mycorrhizal treatment were infected. But there was a large variation in the infection rate - alongside plants with a root infection of 30-40%, there were several individuals where only 1-2% of roots were infected. Thus, average infection remained low and did not exceed 7-8% for *C. jacea* and 3-4% for *F. vesca.* In the case of *C. jacea,* loglinear analysis indicated a significant effect of competition ($P = 0.013$) on the frequency on infected plants - when plants were competing, the number of infected individuals was lower. In the case of *F. vesca,* this effect was not significant ($P = 0.083$).

DISCUSSION

Of the two species studied, only *C. jacea* responded to AM inoculation - root mass was higher for inoculated plants. More typically, root to shoot ratio decreases when plants are arbuscular-mycorrhizal (SMITH & GIANINAZZI-PEARSON 1988, HETRICK 1991), but the opposite has been demonstrated before, for example, by AZCON & OCAMPO (1981), ALLSOPP & STOCK (1992), BAON et al. (1993 a,b), and PENG et al. (1993). Responses in root mass and structure

Table 2. Results of the one-way ANOVA - influence of AM inoculation on the mass difference between *C. jacea* and *F. vesca* and on mass per pot.

Parameter	Mass differences		Mass per pot	
	F-ratio	Significance level	F-ratio	Significance level
shoot mass	0.64	0.43	1.17	0.29
root mass	8.46	0.01	12.12	0.00
total mass	3.92	0.06	5.57	0.02

can be related to changes in meristematic activity and fungal-produced hormones (HOOKER et al. 1992), but the exact mechanisms are presently unknown. Higher root mass of AM plants is typically observed at high soil-P levels. In such conditions, shoot and total mass can even decrease due to AM - i.e. mycorrhizal growth depression occurs (GRAHAM & EISSENSTAT 1994). HETRICK (1991) called this evidence of "an imbalance in the symbiosis".

The lack of response to AM in *F. vesca* and the increase of root mass in *C. jacea* were evidently connected with the abundance of extractable P in the soil (12 mg/100 g). In natural calcareous soils in western Estonia the average content of available P is also relatively high (8-14 mg/100 g, REINTAM et al. 1962), but the typical deficit of moisture decreases the real availability of P. During the present experiment, watering took place every day, hence the availability of P was probably greater than in natural soils.

The low root colonization by AM fungi was probably also the result of high soil-P. Percentage colonization is typically lower at high P levels (BRUCE et al. 1994, HETRICK et al. 1994, MIRANDA & HARRIS 1994). Also, the time scale of the experiment was probably too short to realize full infection, as occurs in the field (MEJSTŘÍK 1972, DAFT & NICHOLSON 1974). Finally, the most rapid infection typically occurs in the presence of living intramatrical hyphae (NEWMAN 1988, EISSENSTAT & NEWMAN 1990, FRANCIS & READ 1994), which were not present here. The "soil inoculation technique" used here, was probably responsible for the lower frequency of infection for plants in pots containing three individuals than for control plants in *C. jacea*. In both cases, pots received approximately the same amount of AM fungal diaspores, thus the relative concentration of diaspores per plant was simply lower in pots containing 3 individuals.

What does the present experiment tell us about the coexistence of two species at the given level of soil-P, where the increase of root and total mass of *C. jacea* were the only responses to AM? First, competition between the predominating and subordinate species was clearly "one-sided", i.e. the biomass of *F. vesca* decreased relatively more due to competition than the biomass of *C. jacea*. Second, the mass differences between the two competing species increased when plants were mycorrhizal. Consequently, our results are in agreement with earlier findings that AM amplifies interspecific competition. GOLDBERG & WERNER (1983) argue that the relative size of a plant determines the outcome of competition. For the given soil conditions, AM inoculation can be the factor enhancing the predomination of *C. jacea* over *F. vesca*.

Quite clearly, this effect is due to the differential responses of two plant species to AM. We did not find any indirect indication to support interplant transfer of resources. Like other experiments, where species of very different mycorrhizal dependency have been used (see

ALLEN & ALLEN 1990, HARTNETT et al. 1993), our results showed more unbalanced competition (larger differences in biomasses) resulting from AM infection. So the inconsistency with community-level experiments, which show higher species diversity in the mycorrhizal case (GRIME et al. 1987, GANGE et al. 1990, 1993) remains. FRANCIS & READ (1994), reconsidering the results of GRIME et al. (1987), pointed out the significance of AM for the plant at the seedling stage. Indeed, competition experiments with larger plants may not include the critical stages of plant development, when the plant may be more dependent on AM. As a working hypothesis for the future we would claim that AM has a community-level effect on plant coexistence just through its influence on seedlings while, at least in nonsuccessional communities, the effect on adult plants does not alter the outcome of interspecific competition.

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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*

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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 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 cm^3 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	*P. vulgaris* (adult)
2	4	2	*P. vulgaris* (young)
3	4	1	*F. vesca* (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

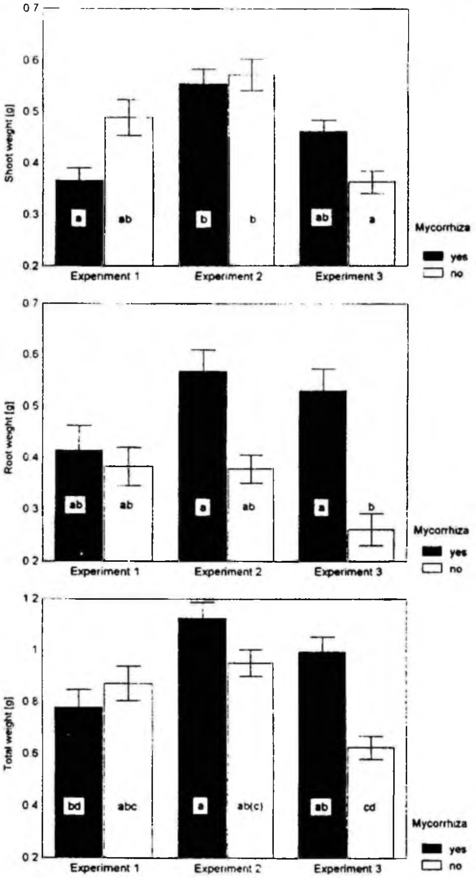

Fig. 1 Means (±SE) of the shoot, root and total weight of target *Prunella vulgaris* plants in three competition experiments. Means with the same letter are not significantly different using Tukey's mean separation test ($P \leq 0.05$). The parentheses in one case indicate that means were different on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

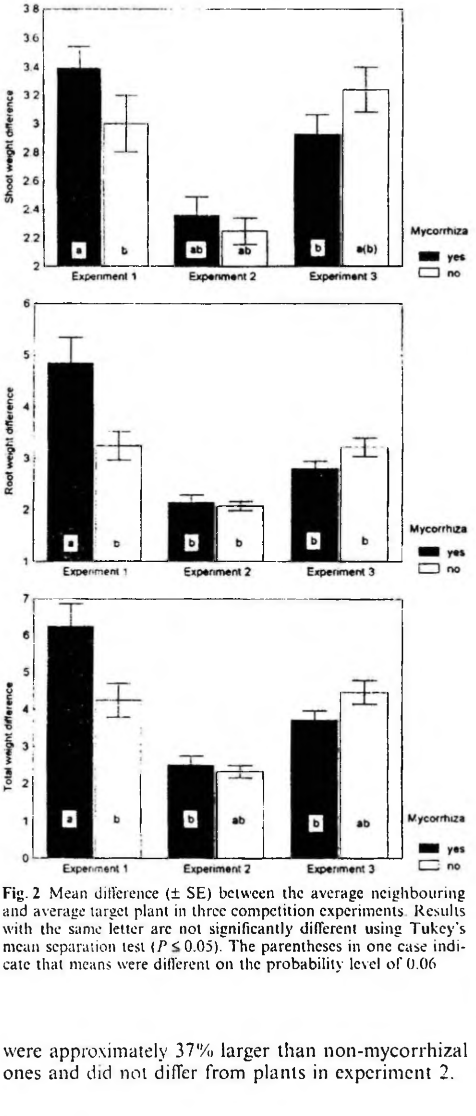

Fig. 2 Mean difference (± SE) between the average neighbouring and average target plant in three competition experiments. Results with the same letter are not significantly different using Tukey's mean separation test ($P \leq 0.05$). The parentheses in one case indicate that means were different on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

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Can arbuscular mycorrhiza change the effect of root competition between conspecific plants of different ages? —
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Can arbuscular mycorrhiza change the effect of root competition between conspecific plants of different ages?

Mari Moora and Martin Zobel

Abstract: Seedlings and adults of *Hypericum perforatum* L., common St. John's wort, were grown together in an experiment of factorial design, where the presence of root competition and arbuscular mycorrhizal inoculation were used as treatments. There was moderate shoot competition, the intensity of which was not manipulated. To check the response of plants to arbuscular mycorrhiza in noncompetitive conditions, adults and seedlings were also grown singly in pots. Single individuals of seedlings and adults responded positively to mycorrhizal inoculation, with the response of seedlings significantly greater. In the competition experiment the positive effect of mycorrhizal colonization on seedling growth vanished, since with root competition, both mycorrhizal and nonmycorrhizal seedlings were of the same size. Without root competition, the shoots of mycorrhizal adults were much larger than of nonmycorrhizal adults, but under root competition the shoot weight did not differ. Arbuscular mycorrhiza increased the biomass differences between competing seedlings and adults. We did not confirm our hypothesis that mycorrhiza makes competition between seedlings and adults more balanced because of the stronger positive response of seedlings to inoculation. The positive effect of arbuscular mycorrhizae on growth vanishes in more crowded conditions. It was concluded that if mycorrhizal inoculation has age-specific positive effect of seedlings in field conditions, it is more probably due to higher tolerance to abiotic stress than due to higher competitive ability of seedlings.

Key words: arbuscular mycorrhiza, intraspecific root competition, seedlings, *Hypericum perforatum*.

Résumé : Les auteurs ont cultivé ensemble les plantules et les plantes adultes de l'*Hypericum perforatum* L. dans un dispositif expérimental factoriel, où la présence de compétition racinaire et l'inoculation mycorhizienne constituaient les traitements. La compétition entre les tiges était modérée et son intensité n'a pas été manipulée. Pour vérifier la réaction de la plante aux mycorhizes arbusculaires, dans des conditions de non compétition, les plantules et les plantes adultes ont été également cultivées séparément dans des pots. Les individus isolés des plantules et des plantes adultes ont réagi positivement à l'inoculation mycorhizienne, la réaction des plantules étant significativement plus importante. Dans l'expérience en compétition l'effet positif de la colonisation mycorhizienne sur la croissance des plantules disparaît, les plantules mycorhizées et non-mycorhizées ayant la même dimension. Sans compétition racinaire, les tiges des plantes adultes mycorhizées sont beaucoup plus grosses que celles des adultes non-mycorhizées, mais en compétition, les poids des tiges ne sont pas différents. Les mycorhizes arbusculaires augmentent la différence de biomasse entre les plantules et les plantes adultes en compétition. Les auteurs n'ont pas pu confirmer leur hypothèse à l'effet que les mycorhizes rendraient la compétition entre les plantules et les plantes adultes mieux balancée à cause de l'effet positif plus marqué de l'inoculation sur les plantules. L'effet positif des mycorhizes arbusculaires sur la croissance disparaît dans des conditions de surpopulation. Les auteurs concluent que si l'inoculation mycorhizienne à un effet positif lié à l'âge des plantules en conditions naturelles, ce serait probablement à cause d'une meilleure tolérance aux stress abiotiques plutôt qu'à une meilleure capacité compétitive des plantules.

Mots clés : mycorhizes arbusculaires, compétition racinaire intraspécifique, plantules, *Hypericum perforatum*.

[Traduit par la rédaction]

Introduction

The influence of arbuscular mycorrhizal (AM) fungal infection on a single plant has been quite well investigated by now. It is generally accepted that AM benefits host plants by promoting a more efficient acquisition of mineral nutrients, mostly phosphorus (Harley and Smith 1983) and nitrogen (e.g., Ames et al. 1984; Smith et al. 1986; Barea et al. 1989; Johansen et al. 1994) from the soil. Also, AM symbiosis may improve defense against herbivores (Gange and West 1994), enhance the acquisition of water, and increase a plant's resistance to pathogens (Newsham et al. 1995). The cost of the advantage is the carbon flow from plant to fungus. However, certain environmental conditions such as low light, low temperature, and high phosphate level (Smith and Smith 1996) may produce negative growth responses to mycorrhiza in plants resulting from too large a carbon cost under these circumstances.

However, in nature, plants grow in mono- or multi-specific stands and interact in many ways: compete for soil resources, for space, or even for resources of fungal inoculum. There are only a handful of studies that have attempted to ascertain the joint effects of competition (a negative interaction) and AM (in most of cases a positive interaction) on plant population

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dynamics and plant species coexistence (Zobel et al. 1997). In previous experiments, it has been shown that the positive effect of AM on the mass of a mycorrhizal plant will disappear when plants compete in even-aged monospecific stands. The cost of being mycorrhizal increases as plant density increases, while the benefit decreases (Allsopp and Stock 1992; Hartnett et al. 1993; Shumway and Koide 1995), although AM may still increase plant fecundity. When studying plants of different age, Eissenstat and Newman (1990) found that AM did not alter markedly the competitive balance between conspecific individuals. However, in their experiment, plant density was low, and competition for light was weak or altogether absent. Moora and Zobel (1996) found that AM made the competition between conspecific adults and seedlings more unbalanced (biomass differences increased). This experiment was set apart by a relatively high level of soil phosphorus.

Plant size might have a great influence on competitive ability (Goldberg 1987). In natural communities, seedling establishment often takes place near larger plants, and competition is considered to be a major factor limiting seedling establishment in grasslands (Goldberg and Werner 1983). In these conditions, AM infection may develop rather quickly (Fitter and Nichols 1988), and the early integration of the seedling into the mycelial network would provide the plant with an absorptive surface at a relatively low energy cost (Read 1991; Francis and Read 1994). Thus, one can conclude that if AM enhances the establishment of seedlings and increases their mass, it will also influence their competitive ability and will make competition between seedlings and adults more balanced. Since the results of previous experiments conducted with plants of different age are contradictory and the setup of experiments did not fully follow the ecological situation in low-productivity European calcareous grasslands (small plant density in Eissenstat and Newman 1990, relatively high soil phosphorous content in Moora and Zobel 1996), the question of the role of AM in seedling establishment in conspecific stands still remains open.

Both greenhouse (Wilson 1988; Weiner 1990; Aerts et al. 1991) and field experiments (Tilman and Wedin 1991; Wilson and Tilman 1993; Belcher et al. 1995; Gerry and Wilson 1995) have shown that in grassland root competition is usually the more important source of a reduction in biomass than shoot competition. We were interested in testing whether mycorrhizal seedlings are better root competitors than nonmycorrhizal ones. For this, we grew seedlings of *Hypericum perforatum* L. (Hyperiaceae), common St. John's wort, in a monospecific stand, where both shoot and root competition were present. Because of the low mobility of phosphorus in the soil, especially in the presence of an abundance of calcium, phosphorus is important for determining early seedling growth (Fenner and Lee 1989) we hypothesized that AM symbiosis makes root competition between adults and seedlings in nutrient (phosphorus) poor soil conditions (where relatively greater mycorrhizal dependency is expected) more balanced. In this case, weight differences between seedlings and adults, which compete for nutrients, are expected to be smaller when plants are mycorrhizal.

Materials and methods

Hypericum perforatum, a rhizomatous, polycarpic perennial with erect shoots, was used in a greenhouse experiment. *Hypericum perforatum* is a common subordinate arbuscular mycorrhizal plant species in the species-rich calcareous grasslands of Estonia, with average AM fungal root colonization in mid-July 1994 of 90% (unpublished data). Seeds of *H. perforatum* were collected from a calcareous grassland in western Estonia in August and preserved in a refrigerator (at 2 ± 1°C) to break seed dormancy before the start of experimentation.

The soil used in experimental pots was one part steam-sterilized horticultural peat (pH 5.5) and two parts sterilized fine sand. The resulting mixture contained approximately 8.9 mg/kg extractable P. Pots were watered two to three times per week, so the soil was kept relatively dry to simulate natural conditions.

Competition experiment

Three large plants (about 7 weeks old, mean dry weight 0.067 g, hereafter called adults) and three young plants (about 1 week old, mean dry weight 0.005 g, hereafter called seedlings) were transplanted into one 4 × 13 × 18 cm (depth ×width × length) pot. Plants were arranged alternatively into the two rows so that both age-classes had two corner and one central position.

Both shoot and root competition occurred between the plants of *H. perforatum* in the pots. In half of the pots, roots were separated with 41-μm nylon mesh bags (4 cm depth and 9 cm diameter) to prevent root competition. This mesh can be penetrated by AM hyphae but not by plant roots (see Jakobsen 1994). Both competition treatments were repeated in two variants: plants were arbuscular mycorrhizal or nonmycorrhizal. Thus, four different competition treatments resulted. All treatments were represented by 30 replicates.

In addition to competing through the exploitation of shared resources, plants may also compete by interference, which most likely takes the form of suppression by allelochemicals (Crawley 1997). Though the only work we know about *H. perforatum* (Clark 1953) claimes that root exudates had no allelopathic effect, we cannot fully exclude this possibility in the present experiment.

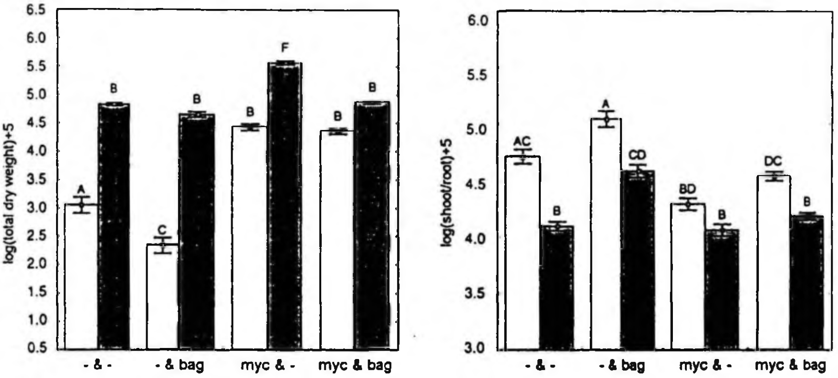
To determine the mycorrhizal dependency of the *H. perforatum* at the given soil conditions, single controls (both seedlings and adults) were grown alone in 4 × 13 × 18 cm pots. To check the effect of the root bag (identical to that used in competition experiment), single mycorrhizal and nonmycorrhizal plants of both age-classe were grown singly with and without bags. All treatments were represented by 15 replicates.

Plants were grown in the greenhouse in full light (daylength 16 h) for 65 days. 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, and the latter, as root weight.

AM inoculation

Typically, so-called soil inoculation, where natural soil with root pieces, hyphal fragments, and spores is added to pots (Hayman et al. 1981), is used for greenhouse experiments. However, the most rapid infection occurs in the presence of living extramatrical hyphae (Eissenstat and Newman 1990). Because of this, for 2 weeks before the experiment, mycorrhizal adult plants were grown in the same pot with a naturally AM infected conspecific neighbour. After these 2 weeks, there was still no biomass difference between mycorrhizal and nonmycorrhizal adults. At the beginning of a competition experiment, the soil originating from the same calcareous grassland from which the seeds of experimental plants were collected, was added to pots (20 cm^3). The nonmycorrhizal treatment received the same amount of natural soil but was treated once with fungicide benomyl (Benlate, 0.6 g per pot) and once with iprodione (Rovral, 0.04 mL per pot) during the experiment. Benomyl has been claimed to be efficient in eliminating AM (Fitter and Nichols 1988) and has no direct effect on vascular plants (Paul et al. 1989; West et al. 1993). However, because of uncertainties about benomyl's selective effect on zygomycetes (see

Fig. 1. Means (± SE) of the total weight and shoot to root ratio of *Hypericum perforatum* young (open bars) and old (filled bars) plants growing singly with (myc) or without (–) arbuscular mycorrhizal inoculation and with (bag) or without (–) root bag. Means with the same letter are not significantly different using Tukey's HSD test ($P \leq 0.05$).



Summerbell 1988), iprodione was also used, following Gange et al. (1990) and West et al. (1993). We avoided the use of fumigated soil because of changes in nutrient availability (Jakobsen 1994). Other soil microorganisms were not controlled. The species of AM fungi were not determined.

Root samples were taken at the end of competition experiment from each individual in five pots of inoculated treatment and from three fungicide-treated pots; percentage of AM fungal colonization was estimated on the basis of thirty to fifty 1 cm long root segments. To quantify AM infection, roots were stained according to Koske and Gemma (1989), and the percentage of colonized root segments was determined (Rajapakse and Miller 1992).

Data analysis

Since the root bag may have an effect on the mass of plants, we calculated the coefficient of the bag effect (BEC) using weight data from the experiment of growing plant singly:

BEC = mass of a plant without root bag/mean mass of the plants with root bag

AM-inoculated and nonmycorrhizal seedlings and adults had different values of BEC. All biomass data from the competition experiment were weighted by the proper BEC before the statistical analysis. The mean biomass was calculated on the basis of three even-aged plants for each pot prior to statistical analysis.

For statistical analysis of the log-transformed plant biomass data the standard procedures of three-way ANOVA (SYSTAT) with age with two levels, root competition with two levels, and AM inoculation with two levels were used. For analysis of biomass of singly growing plants, AM inoculation with two levels, plant age with two levels, and root bag with two levels were used. For total biomass data of pot, AM inoculation and competition factors with two levels were used in the standard procedure of two-way ANOVA.

To estimate the degree of difference between different treatments the Tukey HSD multiple comparison test was used.

Results

AM fungal colonization of roots

The colonization of the roots of experimental plants by AM fungi was successful; all sampled plants in mycorrhizal variants were infected. Average colonization levels were 43–46% in the case of seedlings and 45–48% in the case of adults. The fungicide treatment was efficient, practically all treated plants were noninfected. There were no statistically significant differences in the root colonization rates between different competition treatments.

Single control plants

Absence of AM reduced total mass and increased shoot to root ratio of *H. perforatum* ($P < 0.001$) (Fig. 1). The root bag decreased total mass and increased shoot to root ratio ($P < 0.001$). The presence of root bag had no effect on mycorrhizal or nonmycorrhizal adults and seedlings ($P > 0.05$). AM inoculation had a differential effect on the total mass of the adults and seedlings. The relative increase of biomass due to AM inoculation was larger in the case of seedlings, compared with adults ($P < 0.001$). There was a significant three-way interaction between AM inoculation, plant age, and root bag on total mass ($P < 0.002$). The negative effect of the root bag was more evident in the case of seedlings, when plants were nonmycorrhizal, and in the case of adults when plants were mycorrhizal.

Competition experiment

In the competition experiment, shoot, root, and total mass decreased, and shoot to root ratio increased significantly (Table 1) for all plants subjected to root competition. AM inoculation increased shoot, root, and total mass and the shoot to root ratio of all plants (Table 1). Interactions between root competition and AM inoculation were never significant. Plant age interacted significantly with root competition, which had a stronger negative effect on the shoot, root, and total growth of seedlings (Fig. 2). The mass of adults decreased relatively less because of root competition. In the presence of root competition, the increase of the shoot to root ratio was more evident in the case of seedlings (Fig. 2). The interaction of AM inoculation and plant age was significant; mycorrhizae increased the shoot, root, and total mass and shoot/root ratio of adults. In seedlings there were no significant increases.

In seedlings, root competition decreased the shoot mass of

Fig. 2. Means (± SE) of the shoot, root and total weight and shoot to root ratio of *Hypericum perforatum* young (open bars) and old (filled bars) plants growing in competition experiment with (myc) or without (–) arbuscular mycorrhizal inoculation and with (comp) or without (bag) root competition. Means with the same letter are not significantly different using Tukey's HSD test ($P \le 0.05$).

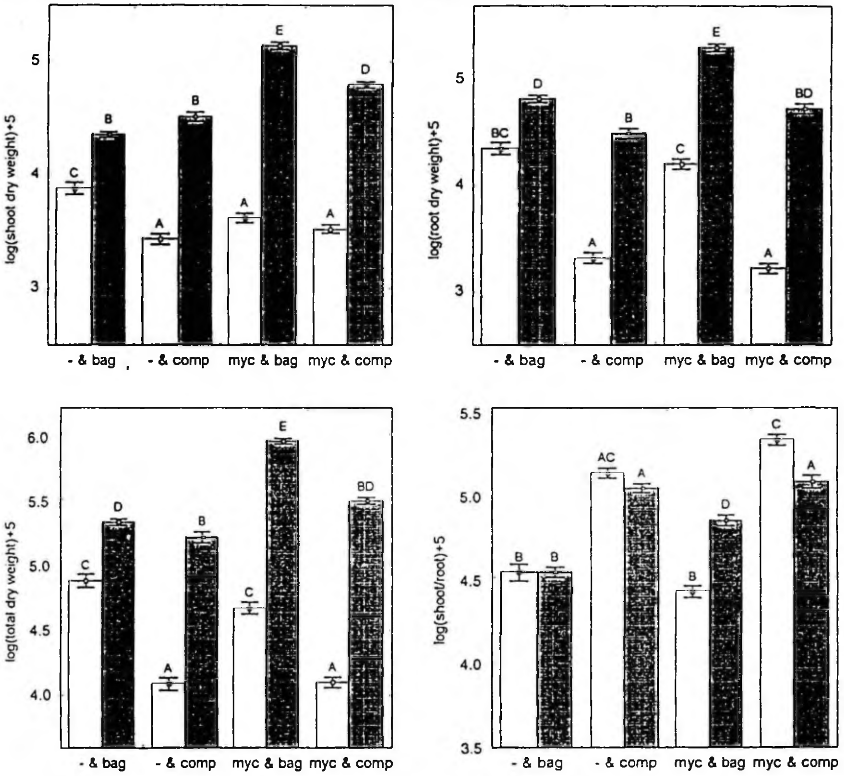


Table 1. Results of multifactor ANOVA for weight of different aged (age) *H. perforatum* with or without AM inoculation and growing in different competititive situations.

		Shoot weight		Root weight		Total weight		Shoot/root ratio	
Source of variation	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Age (A)	1	811.41	<0.001	544.55	<0.001	737.43	<0.001	0.48	0.489
AM inoculation (M)	1	35.29	<0.001	6.84	0.01	19.6	<0.001	10.35	< 0.00
Competition (C)	1	22.29	<0.001	255.89	<0.001	153.23	<0.001	270.32	<0.001
A × M	1	66.07	<0.001	28.34	<0.001	48.39	<0.001	4.08	0.044
A × C	1	5.61	0.018	37.47	<0.001	25.78	<0.001	31.91	<0.001
M × C	1	1.07	0.301	1.24	0.265	0.68	0.41	0.12	0.734
A × M × C	1	31.98	<0.001	2.58	0.108	13.33	<0.001	18.21	<0.001

nonmycorrhizal plants, while in mycorrhizal seedlings the negative effect was nonsignificant (Table 1, Fig. 2). When the root and total mass was considered, root competition decreased the biomass of seedlings despite their mycorrhizal status. When adults were considered, root competition statistically significantly decreased shoot mass of mycorrhizal plants, while shoots of nonmycorrhizal plants did not react. Root and total mass were decreased by root competition in both mycorrhizal treatments. Shoot to root ratio of seedlings increased more because of root competition when they were mycorrhizal. Shoot to root ratio of adults increased more because of root competition when plants were nonmycorrhizal.

The total biomass per pot (i.e., the sum of all six plants) was significantly larger when there was no root competition ($P <$ 0.001). When mycorrhizal and nonmycorrhizal pots were considered separately, it became evident that, in the case of mycorrhizal plants, the decrease due to root competition was significant ($P < 0.001$), while in the case of nonmycorrhizal plants it was still evident but nonsignificant ($P > 0.05$).

Discussion

Hypericum perforatum showed clear positive mycorrhizal dependency in terms of increased biomass when grown singly in the experimental pots. The positive influence of AM on biomass decreased as plants aged. Thus, seedlings gained more from the symbiosis with AM fungi than adults. This is in accordance with the expectation that mycorrhizal symbiosis is more evident in the seedling stage (e.g., Francis and Read 1994). The better growth of the mycorrhizal seedlings with a root bag, compared with nonmycorrhizal seedlings in the same conditions, was an indication that extramatrical AM fungal mycelia was functioning as an important nutrient absorber. However, the positive effect vanished when seedlings grew in pots together with three adults, since in contrast to single controls, seedlings no longer showed any positive growth response to AM. In the competition experiment, AM inoculation increased plant biomass, only in the case of adult plants. The only explanation can be that the negative effect of the competition on the seedlings was stronger than the positive effect of the AM inoculation. Consequently, if there exists an age-specific positive effect of AM on seedlings, as claimed by Gange et al. (1993, see also Read 1991; Francis and Read 1994), it is more probably not due to the greater growth and thus also better competitive ability (Goldberg 1987) of mycorrhizal seedlings, but was rather due to the fact that mycorrhizal seedlings may tolerate harsh environmental conditions better, which may be the main limitation for seedling recruitment in dry grasslands (Ryser 1993).

Previous experiments have given conflicting results, indicating that competitive ability increases with (Ross and Harper 1972; Gaudet and Keddy 1988; Grace et al. 1992) or is independent of (Newbery and Newman 1978; Wilson 1988; Wilson 1994) initial plant size. In our experiment, there was a significant interaction between root competition and plant age: the biomass of seedlings decreased relatively more because of root competition than the biomass of adults; competition was asymmetric in the sense of Weiner (1990). Since the reduction of root weight was greater than the reduction of shoot weight, shoot to root ratio also increased. This is not in accordance with the expectation that, when soil resources are scarce, allocation to roots increases (Tilman 1988). This may be explained by the fact that the carbon allocation pattern should not necessarily reflect other important responses to resource deficiency such as changes in nutrient allocation pattern or changes in overall plant structure (e.g., Olff et al. 1990; Ryser 1996; Fitter 1997).

According to our working hypothesis, we expected competition to be more balanced when plants are mycorrhizal. Indeed, there was a significant three-way interaction of root competition, AM inoculation, and plant age. The shoot mass of mycorrhizal seedlings did not decrease because of root competition, while in the case of nonmycorrhizal seedlings the decrease was significant. In turn, the shoot mass of adults did not decrease because of root competition when plants were nonmycorrhizal, but in the case of mycorrhizal plants the decrease was significant. However, it is not easy to say whether AM definitely had an effect on the balance of competition between adults and seedlings. On one hand, AM made competition more balanced, since, when situations with and without root competition are compared, the size difference between seedlings and adults decreased because of competition in the mycorrhizal case and increased in the nonmycorrhizal case. However, the absolute size difference between seedlings and adults was always larger when plants were mycorrhizal. Thus, we have to reject the working hypothesis that weight differences between seedlings and adults, which compete for nutrients, are smaller when plants are mycorrhizal. In this respect, AM made root competition more unbalanced. If we assume that the final biomass of plants indicates their competitive response (sensu Goldberg and Landa 1991), one can say that mycorrhizal status did not change the response of seedlings, but increased the competitive response (i.e., caused a relatively larger loss of biomass) of adults.

The last result is in agreement with previous experiments. Allsopp and Stock (1992), Hartnett et al. (1993) from greenhouse, and Shumway and Koide (1995) from field experiments reported that AM increased the intensity of intraspecific competition. However, these authors worked with plants of the same age. Moora and Zobel (1996) found that AM increased the weight differences between the seedlings and adults of *Prunella vulgaris* L., which is also a strongly positively mycorrhiza dependent species like *H. perforatum* in this experiment.

Earlier explanations of the effect of AM on the balance of plant competition considered the possibility of interplant carbon transfer, which was assumed to occur along a carbohydrate concentration gradient (Grime et al. 1987). Though we did not measure interplant carbon transfer directly, our results did not give any indirect evidence for its occurrence. When root competition was eliminated by a nylon mesh, AM hyphae were still able to penetrate the mesh and carbon translocation was potentially possible. In the mycorrhizal case, adults were much larger than in the nonmycorrhizal case, but seedlings were significantly smaller than in the nonmycorrhizal case. If carbon transfer from well-illuminated adults to shaded seedlings did occur, one would expect the opposite: larger seedlings and smaller adults in the mycorrhizal case.

The competitive effect of adult plants is positively dependent on plant biomass (Goldberg 1987; Wilson 1994), while the competitive response may be smaller when their biomass is larger (McLellan et al. 1997). If AM increases the plant mass, one may expect that it also effects competitive ability. Since AM root infection takes place at an early stage of seedling development, and AM mycelia provide the plant with an enormous increase in absorptive surface at a low energy cost, it has been seen to be of potentially profound importance for the recruitment of seedlings and thus also for the community as a whole (Fitter and Nichols 1988; Read and Birch 1988; Finlay and Söderström 1989; Read 1991). Since in our experiment the positive effect of AM on seedling biomass vanished in crowded conditions, the possible age-specific positive effect on seedlings in field conditions is more probably due to a higher tolerance of abiotic stress than the higher competitive ability of seedlings.

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IV

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Plant coexistence in the interactive environment:
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Oikos 78: 202–208.

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Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind

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Community diversity and plant coexistence

Mechanisms responsible for species diversity in communities constitute a central topic in ecology. Most of the theories explaining the coexistence of plant species in a community share two basic assumptions. First, they recognize the importance of "ecological phenomena", i.e. of contemporary forces which – at least in theory – can be experimentally studied. Accordingly, historic and phylogenetic explanations of species diversity have only superficially been taken into account (Ricklefs 1987, Zobel 1992, Eriksson 1993). Second, among the biotic interactions influencing species diversity, plant–plant interactions (mainly competition) have received most attention (see, for example, reviews of Goldberg and Barton 1992, Gurevich et al. 1992). The importance of herbivory for plant coexistence and species diversity has also been recognized for a long time (Whittaker 1972, Huntly 1991), although the true importance of less visible below-ground herbivory has only recently been fully recognized (Brown and Gange 1989a, b).

Among biotic interactions the role of micro-organisms in particular has recently gained recognition: "a plant out in the field is not simply a plant, but rather a merger of fungal cells with plant tissues" (Wilson 1993: 379). Besides pathogenic fungi and leaf endophytes, mycorrhizal fungi may also have an important influence on plants.

Several reviews concerning mycorrhiza–symbiotic relationships between plant roots and fungi also include chapters considering plant competition, community structure, and succession (Finlay and Söderström 1989, Allen 1991, Brundrett 1991, Chanway et al. 1991, Ingham and Molina 1991, Goodwin 1992, Sanders et al. 1995, Schönbeck and Raschen 1995). This topic has even been included in the new edition of a textbook (Silvertown and Lovett Doust 1993: 131). Thus, the possible importance of mycorrhiza in plant coexistence is recognized in principle at least. Some experimental studies have also claimed that the presence of arbuscular mycorrhiza (AM) increases plant species diversity in microcosm experiments (Grime et al. 1987) or in early successional communities (Gange et al. 1990, 1993). Different results have been obtained from a lichen-rich community, where benomyl treatment resulted in an increase in vascular plant species richness (Newsham et al. 1995a). Consequently, we can ask how important is the presence of mycorrhiza for plant coexistence and does it contribute to the variation of plant species diversity in time and space?

Approximately two thirds or more of vascular plant species form symbiotic relationships with AM fungi (Trappe 1987, Gianinazzi 1991). Since the number of AM forming fungal species (ca 150) is relatively low and the number of AM forming plant species high (ca 225 000) (Sanders et al. 1995), one may conclude that the host specificity of AM fungi is low. In the case of ectomycorrhiza (EC), the situation is almost the opposite (Read 1991). Since we are mostly interested in herbaceous communities, where very high species richness but also considerable variation in richness are encountered (e.g. Grime 1979), we have focused on the role of AM.

How can AM influence plant coexistence?

In principle, AM can influence the coexistence of plants directly or indirectly. Direct ways include the modification of plant traits by AM and, if it occurs in a large enough quantity, the interplant transfer of resources. Both of these may have a direct influence on the outcome of competitive interactions and hence on plant coexistence. Indirect ways include the possible impact of AM on ecological interactions between plants and other organisms, e.g. plant–herbivore or plant–pathogen interactions.

AM and plant competition

It is generally assumed that AM benefits host plants by promoting a more efficient acquisition of phosphate ions from the soil, resulting in increased plant weight and a decrease in root:shoot ratio (Harley and Smith 1983). The improvement of nitrogen acquisition has been also discussed (e.g. Ames et al. 1984, Smith et al. 1986, Barea et al. 1989, Johansen et al. 1994). These effects can be expected to increase the competitive ability of a plant. Plant species differ in their growth response to mycorrhizal inoculation. The measure of positive response in terms of biomass increase for particular soil conditions is sometimes called mycorrhizal dependency. This has been related to morphological properties of the roots, such as root diameter or root hair length (Baylis 1970. 1975, Hayman 1983, Graham and Syvertsen 1985. Graham et al. 1991). However, certain environmental conditions such as low light and low temperature may produce negative growth responses to mycorrhiza (Smith and Smith 1996). Mycorrhizal-induced growth depression can also occur at high phosphate levels; this is attributed to the effects of carbon expenditure for the construction of mycorrhizal roots and their maintenance (Graham and Eissenstat 1994). Schweiger et al. (1995) are probably the first to have studied the growth response of mycorrhizal and non-mycorrhizal plants along a phosphorus gradient.

With regard to interspecific competition, the influence of AM has mostly been studied in species pairs where one species is strongly AM dependent but the other is non-mycorrhizal (Allen and Allen 1990). Typically, AM inoculum confers a greater advantage to the mycorrhizal competitor. Sanders and Koide (1994) obtained similar results when studying experimental communities containing three plant species. Goldberg (1990, Goldberg and Landa 1991) has shown that individual competitive ability can be compared between species in two distinct ways: in their competitive effect, or ability to suppress other individuals, and in their competitive response. or ability to avoid being suppressed. Such a dissection of the interaction into effect and response is useful because it highlights the mechanism underlying the interaction. Hartnett et al. (1993) first distinguished the influence of AM on competitive effect and response. The role of AM was more conspicuous in the competitive effects of a mycorrhiza-dependent species; the competitive response was less dependent on AM when plant density increased. The competitive effect and response of less AM dependent species were not significantly influenced by mycorrhiza.

In cases of intraspecific competition, AM root colonization has no effect on plant interactions, or possibly even seems to amplify competition (Eissenstat and Newman 1990, Allsopp and Stock 1992a, Hartnett et al. 1993, Moora and Zobel 1996). In the experiment performed by Koide et al. (1994) the positive effect of AM on plant fecundity vanished at high plant densities.

From this review, a clear gap in our knowledge emerges. The responsiveness of plant species to AM infection is very variable (Koide 1991. Sanders et al. 1995). Although the external AM hyphae deliver up to 80% of plant P in experimental chambers (Marschner and Dell 1994), some species do not seem to be P-limited in the field (West et al. 1993). Thus. to understand the general pattern of the relationship between plant competition and AM, a more systematic approach is needed, where the mycorrhizal dependence of any particular species, for different levels of soil phosphate, is taken into account first. To explain the coexistence of many herbaceous plant species within a limited space, it is not so important to study the interactions of mycorrhizal and non-mycorrhizal species (that may be more important when the successional replacement of plant species is considered – see Allen and Allen 1984, Gange et al. 1990). Instead. it is more important to study the interactions of rather more common plant species with only slightly different rates of mycorrhizal root colonization (and presumably also mycorrhizal dependences) which is usually the case. for example, in temperate grasslands (Fitter 1989). This should include experimental work examining the interrelationships between the mycorrhizal dependence of the coexisting plant species and the level of soil-P (and ideally also taking other soil resources into account). Further, when competition between species of known responses to AM at certain soil-P levels is studied, both competitive effect and competitive response should be taken into account.

Hyphal connections and interplant transfer

The low level of host specificity of AM fungi permits intraspecific (Hirrel and Gerdemann 1979) and interspecific (Newman et al. 1994) connections. The possibilities of interplant transport of phosphorus have been discussed by Chiariello et al. (1982) and Whittingham and Read (1982). However, Newman et al. (1993) and Newman and Eason (1993) claimed that phosphorus movement between plants, even when they are mycorrhizal. is too slow to influence substantially the nutrient status of the shoots. Instead, they discuss the possibility that nutrients pass from dying roots to living plants via mycorrhizal links. Furthermore, Francis and Read (1984) presented autoradiographic evidence of direct hyphal transfer of carbon. Transfer of labelled assimilate was enhanced by inducing carbon sinks in receiver plants by shading. However, Read et al. (1985) showed that if net carbon transfer between plants occurs, it is a very small. Ledgard et al. (1985) found no significant transfer of nitrogen between mycorrhizal plants in the field. although they did find it in a pot experiment. Later experiments. both in the field and in the greenhouse. have shown that the role of hyphal bridges in N-transfer between plants is not significant (Hamel and Smith 1991. Hamel et al. 1991, Frey and Schuepp 1992)

Grime et al (1987) showed that mycorrhiza increased plant species diversity in the microcosm and concluded that: "... export of assimilate from 'source' (canopy dominants) to 'sink' (understorey components) through a common mycorrhizal network may be an important element of the mechanism maintaining species-rich communities in infertile soils". However, later interpretations of the results of this experiment (Bergelson and Crawley 1988, Newman et al. 1993, Francis and Read 1994) have focused more on other explanations, like species-specific or size-specific differences in the response of plants to AM.

None of the competition experiments – even those which have been made with plants of similar mycorrhizal dependences – have produced indirect evidence of the transfer of assimilates. On the contrary, AM increased plant size differences under intraspecific competition (Allsopp and Stock 1992a) or did not influence size inequality (Shumway and Koide 1995), whereas assimilate transfer should result in a more uniform size distribution. Similarily, in the case of interspecific competition, the presence of mycorrhizal inoculum did not result in the more uniform distribution of biomass between competing species (Zobel and Moora 1995).

AM and plant fecundity

AM can have long-term effects on plant community structure by changing the quantity and/or quality of seeds (Sanders and Koide 1994). Eriksson and Ehrlen (1992) have shown that in certain plant communities, seed limitation may be a more important factor inhibiting community regeneration than microsite limitation. There are several papers which show that AM root colonization increases seed quality, i.e. weight and/or phosphorus content (Lu and Koide 1991, 1994, Sanders and Koide 1994, Shumway and Koide 1994, Chandrashekara et al. 1995, Koide and Lu 1995). The results have been more controversial when the number of seeds per plant has been considered – Bryla and Koide (1990), Lu and Koide (1994) and Shumway and Koide (1995) report an increase in the number of seeds, while West et al. (1993) and Newsham et al. (1994) report the opposite. In the last case, the negative result may have occurred because benomyl shifted the competitive balance between arbuscular mycorrhizal and pathogenic fungi. Also, maternal mycorrhizal infections positively influence offspring vigour (Koide and Lu 1992, 1995, West 1995).

However, since the experiments cited have used only a handful of species, general conclusions about the influence of AM on plant fecundity cannot be made. Interestingly, Shumway and Koide (1995) demonstrated that AM increased the inequality in fecundity between the individuals of the same plant species. At the same time, Allsopp and Stock (1992b, 1995) have shown that seed size and phosphorus content of the seed are inversely related to the mycorrhizal dependence of the particular species. If these results were general, there would be a possibility that AM amplifies intraspecific competition, but makes the regenerative abilities (and hence competitive abilities) of different species more even.

The effect of AM on seedlings

Seedling establishment can be of crucial importance for the performance of plant populations (Eriksson 1989) and thus for maintaining species richness. For example, more productive grasslands are also less species rich mostly due to accumulated litter and lower light penetration which inhibit seed germination and/or seedling survival (Tilman 1993). Compared to competition for nutrients, competition for light always tends to be more one-sided (Weiner 1986). However, there is considerable variation between the requirements for seedling emergence and establishment between species (van Tooren 1990, Rusch 1992, Ryser 1993, Rusch and Fernández-Palazios 1995).

Integration of young seedlings into an AM mycelial network may be of great importance in situations where access to light is restricted by established plants (Finlay and Söderström 1989). AM can also increase the survival and growth rate of the seedlings of certain species in non-competitive environments (Hartnett et al. 1994). Consequently, the study of the role of AM in seedling establishment should be of primary interest. Eissenstat and Newman (1990) investigated the role of AM when old and young individuals were grown together. They found that adult plants suppressed seedlings despite the presence of AM. But, as light competition was practically absent in this experiment, the relevance of this result to field conditions remains unclear. Moora and Zobel (1996) were not able to show the positive effect of AM on seedlings growing in the shade of an adult.

However, it is known that due to its low mobility in the soil, phosphorus is important for determining early seedling growth (Fenner and Lee 1989). Francis and Read (1994) stress that AM inoculum plays a role in determining species composition in the community by influencing plant fitness in the establishment phase. Still, Merryweather and Fitter (1995) bring a different example – seedlings of *Hyancinthoides non-scripta* are supplied with a P-rich endosperm and become increasingly dependent on AM as the bulbs of adult plants reach a depth of approximately 20 cm. The increased fitness may not be only due to AM root colonization of seedlings, but also due to higher fecundity and the better developed offspring of mycorrhizal mother plants (see above). Indeed, the competition experiments referred to above all consider adults or late-seedling stages. This can also be one of the reasons why the results of individual-level and community-level experiments have been controversial. Greenhouse experiments, which have studied the effect of AM on intra- or interspecific competition, demonstrate that the presence of the AM inoculum makes competition more unbalanced (weight differences increase), or that it has no effect on competition. Several community-level experiments, in turn, show that the presence of AM root colonization results in higher diversity and consequently in more balanced competition. If the community-level effect of AM is mostly due to effects on plant fecundity or offspring vigour, competition experiments with established plants alone are not sufficient to explain the role of AM. In order to establish the role of AM in plant coexistence, further studies must include competition between plants of clearly different sizes and or ages.

AM mediation of other ecological interactions

The structure of plant communities can be dependent on interactions between AM and herbivores. Grime et al. (1987) found that the interaction of simulated above-ground herbivory (clipping) and AM inoculation was significant in a microcosm experiment. Gange and Brown (1992) demonstrated that a clear mycorrhizal benefit of a perennial by significant interaction between fungicide and insecticide treatments for a second-year successional community – the reduction of the number of soil-dwelling insects – resulted in an increase in the cover of perennial grasses, but that this effect virtually disappeared if mycorrhizas were reduced as well.

Indeed, AM can mediate plant–herbivore, plant–pathogen and plant–symbiont (e.g. *Rhizobium*) interactions (Finlay and Söderström 1989, Allen 1991, Ingham and Molina 1991, Fitter and Sanders 1992, Jarstfer and Sylvia 1992, Lussenhop 1992, Fitter and Garbaye 1994, Gehring and Whitham 1994, Newsham et al. 1994, 1995b, Sanders et al. 1995). All such interactions can influence the competitive ability of plants and thus also the species composition and diversity of plant communities. Newsham et al. (1995b) stress that the evidence for a general role of AM fungi in plant P-relations under field conditions in temperate regions has been overestimated. They claim that in many cases, the protection of a plant's root system against pathogenic fungi may be at least as important a function of AM association. This function seems to be more important for plants with fine roots.

Again, to reveal possible generalities in the above-mentioned interactions and their significance for plant coexistence, more attention should be paid to carbon expenditure in interactions at defined levels of soil-P (and other soil resources) and in the presence of a defined microbial community (see Newsham et al. 1995c). This approach has been tried by considering the costs and benefits of mycorrhiza in a general framework (Fitter 1991, Jones and Last 1991). The consideration of total costs and benefits may enable predictions about the outcomes of a particular set of interactions for a plant to be made.

The recent results of Gange and West (1994) show that AM infection can lead to an increased allocation to carbon-based defences, which in turn can reduce the rate of herbivory. Consequently, it is also necessary to consider the qualitative aspects of overall quantitative changes in allocation patterns.

Conclusions

Knowledge of the possible role played by AM fungi in plant coexistence is growing rapidly. So far this knowledge does not allow the formulation of a general theory. First, individual-level experiments have focused only on the role of AM in the coexistence of plants of one or a few species at only a few levels of soil-P, without previous knowledge about the variation in mycorrhizal dependences and carbon expenditure of different species along the whole soil-P gradient. Second, the results of individual- and community-level experiments are contradictory. This may be, at least partly, because individual-level experiments have considered adults or at least established plants, while in the case of plant communities AM could in fact influence just the fecundity and the establishment phases of participating plants. Third, attempts to study the significance of AM in mediating other ecological interactions have mostly overlooked not only the general pattern of species-specific AM dependence (the significance of soil-P and plant age) but, until recently, also qualitative aspects of the changes in allocation patterns, e.g. the production of chemical defences against herbivory, etc.

Consequently, we cannot yet provide a good answer to the question "what is the role of AM in plant coexistence?" However we think that we are not very far from this answer. Knowing the costs and benefits of AM symbiosis for particular soil conditions for a particular species of a particular age will increase the possibility of predicting the ability of a plant to coexist with others in an interactive environment including AM fungi. Knowing the influence of AM on plant fecundity and offspring vigour will increase this possibility even more.

The finding that positive interactions are common is likely to change our views on how plant communities are structured (Bengtsson et al. 1994). Better knowledge of the role of interactions between plants and AM fungi will hopefully contribute some interesting insights into this changing theory.

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CURRICULUM VITAE

MARI MOORA

Born in Rapla, Estonia, March 19th, 1966. Married, two sons (Mart, born in 1987 and Hendrik, born in 1990).

Education

Nõo Secondary School (Tartumaa, Estonia): graduated in 1984
Tartu University: Graduated in biology (genetics) in 1989

Previous professional apointments

1983	Research assistant in the Estonian Zootechnical and Veterinarian Research Institute
1989–1992	Researcher in the Estonian Agricultural Biocentre
1992–	Research assistant in the Department of Botany and Ecology, Tartu University
1994–	PhD student in the Department of Botany and Ecology, Tartu University

Teaching experience

Tartu University
  Lectures in experimental methods in plant ecology — from 1995
  Field course in plant ecology — from 1995
  Lectures in community ecology — from 1997
  Laboratory courses in mycorrhizal studies — from 1997

Work as a visiting lecturer
  University of Rio Cuarto — 1998

Membership in scientific societies

International Association of Vegetation Science (IAVS) — 1993
Nordic Ecological Society Oikos — 1996

Received awards

Sience award of the goverment of The Estonian Republic — 1998

Participitations in international conferences and workshops.

Symposium “Species coexistence and diversity maintenance in temperate grassland ecosystems” — Bedrichov, Chech Republic, 1993.
Symposium “Community ecology and conservation biology” — Bern, Switzerland, 1994.
Workshop “Current topics in plant ecology and evolution” — Kronlund, Sweden, 1995.
Workshop on root ecology, Tartu, Estonia, 1995.
Workshop “The importance of complex interactions for plant community structure”, Kronlund, Sweden, 1996.
Workshop “Biodiversity as an important parameter in restoration ecology” — Groningen, The Netherlands, 1997.
IAVS’97 Symposium — České Budějovice, Czech Republic, 1997.

Current scientific work

The role of mycorrhizal symbiosis in vascular plant community life.

Experimental study of the role of arbuscular mycorrhiza in plant competition and seedling establishment in calcareous grassland.

Analysis of vegetation structure and community regeneration in calcareous grasslands. Experimental study of the effect of seed rain and seed germination on the pattern of calcareous grassland community.

Publications

Zobel, M. and Moora, M. 1995. Interspecific competition and arbuscular mycorrhiza: importance for the coexistence of two calcareous grassland species. — Folia Geobot. Phytotaxon. 30: 223–230.
Moora, M. and Zobel, M. 1996. Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. — Oecologia 108: 79–84.
Zobel, M., Moora, M. and Haukioja, E. 1997. Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. — Oikos 78: 202–208.

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Moora, M. and Zobel, M. Can arbuscular mycorrhiza change the balance of root competition between conspecific plants of different ages? (accepted for publication in Can. J. Bot.).

Pärtel, M., Moora, M. and Zobel, M. Species richness in alvar grasslands — the role of core and satellite species. (submitted).

Knowledge in foreign languages

English (good), Russian (good), Finnish.

CURRICULUM VITAE

MARI MOORA

Sündinud 19. märtsil 1966 Eestis, Raplas. Abielus, kaks poega (Mart, s. 1987 ja Hendrik, s. 1990).

Haridus

Nõo Keskkool (Eesti, Tartumaa): lõpetanud 1984
Tartu Ülikool: lõpetanud bioloogia (geneetika) 1989

Varasemad töökohad

1983	Eesti Loomakasvatus- ja Veterinaaria Instituudi laborant
1989–1992	Eesti Agrobiotsentri noorem-teadur
1992–	Tartu Ülikooli botaanika ja ökoloogia instituudi vanemlaborant
1994–	Tartu Ülikooli botaanika ja ökoloogia instituudi taimeökoloogia õppetooli juures doktorant.

Õppetöö

Tartu Ülikoolis
- Eksperimentaalsed meetodid taimeökoloogias, loengud alates 1995. a.
- Taimeökoloogia välipraktikum, alates 1995. a.
- Sünökoloogia, loengud alates 1997. a.
- Mükoriisaõpetus, praktikumid alates 1997. a.

Külalisloengud
- Rio Cuarto Ülikool, Argentiina 1998

Osalus rahvusvahelistes organisatsioonides

Rahvusvahelise Taimkatteteadlaste Assotsiatsiooni (IAVS) liige 1993. a.
Põhjamaade Ökoloogiaseltsi “Oikos” liige 1996. a.

Autasud

Eesti Vabariigi teaduspreemia 1998. a.

Osalemine rahvusvahelistel konverentsidel ja sümpoosiumitel

Sümpoosion "Species coexistence and diversity maintenance in temperate grassland ecosystems", Bedrichov, Tšehhi Vabariik, 1993.

Sümpoosion "Community ecology and conservation biology", Bern, Šveits, 1994.

Workshop "Current topics in plant ecology and evolution", Kronlund, Rootsi, 1995.

Workshop juure ökoloogiast, Tartu, Eesti, 1995.

Workshop "The importance of complex interactions for plant community structure" — Kronlund, Rootsi, 1996.

Workshop "Biodiversity as an important parameter in restoration ecology", Groningen, Holland, 1997.

Rahvusvahelise Taimkatteteadlaste Assotsiatsiooni 1997. aasta sümpoosion, České Budějovice, Tšehhi Vabariik, 1997.

Käimasolev teadustöö

Mükoriisse sümbioosi osatähtsus maismaa taimekoosluste elus.

Mükoriisse sümbioosi ja konkurentsi eksperimentaalne uurimine lubjarikka niidu taimekoosluses.

Taimekoosluse struktuuri ja uuenemise uurimine lubjarikkal niidul. Seemnevihma ja seemnete idanemise mustri eksperimentaalne uurimine lubjarikkal niidul.

Teaduspublikatsioonid

Zobel, M. and Moora, M. 1995. Interspecific competition and arbuscular mycorrhiza: importance for the coexistence of two calcareous grassland species. — Folia Geobot. Phytotaxon. 30: 223–230.

Moora, M. and Zobel, M. 1996. Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. — Oecologia 108: 79–84.

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Pärtel, M., Moora, M. and Zobel, M. Species richness in alvar grasslands — the role of core and satellite species. (Submitted.)

Võõrkeelte oskus

Inglise keel (hea), vene keel (hea), soome keel.

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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