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Vesicular-arbuscular mycorrhizae influence Mount St. Helens pioneer species in greenhouse experiments

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Vesicular-arbuscular mycorrhizae (VAM) are present in most terrestrial ecosystems and play a major role in community structure and function. However, their role in primary succession remains poorly understood. Two greenhouse studies examined the role of VAM in Mount St. Helens pioneer species under three nutrient regimes and four competitive scenarios. Nutrient levels were complete, complete without phosphorus (−P), and tap water (very low nutrient levels). In tap water a negative effect from VAM colonization was observed perhaps due to parasitic action of the VAM fungi. A weak but apparent benefit from VAM occurred in the −P treatment since plants in the −P treatment were usually not less in biomass than those in the complete nutrient treatment and VAM colonization levels were greater in the −P treatment. VAM colonization was more beneficial to plants under the complete nutrient treatment than under the tap water treatment. VAM assisted the facultatively mycotrophic *Hypochaeris radicata* in competition with the non-mycotrophic *Carex mertensii*. Lack of VAM improved the competitive ability of *Carex mertensii* when in competition with facultatively mycotrophic species. However, VAM did not significantly influence competitive outcomes between facultatively mycotrophic species.

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The 1980 eruption of Mount St. Helens produced a devastated landscape devoid of both plants and vesicular-arbuscular mycorrhizae (VAM) (Allen et al. 1992, J. H. Titus unpubl.). This catastrophic disturbance created a barren landscape and initiated primary succession. The role of VAM in primary succession is poorly understood and is the subject of this study.

The role of VAM in nutrient uptake, particularly phosphorus, is central to the symbiosis. Plants colonized by VAM fungi usually exhibit improved growth due to enhanced nutrient uptake (e.g., Smith et al. 1986). This is due to the additional absorbing surface provided by the external hyphae (Hattingh et al. 1973). However, in some situations the association may be neutral or even detrimental to the host plant (Allen and Allen 1986; Fitter 1986, Hetrick et al. 1986, Anderson and Liberta 1989). There are many reasons for a lack of benefits from VAM, these include high phosphorus levels (Fitter 1977, Schwab et al. 1983). Under nutrient-poor conditions, a parasitic effect may occur because VAM fungi continue to receive photosynthate from a plant but have little phosphorus to offer in return (Allen 1991, Boerner 1992). In addition, VAM may benefit the plant only during a brief period (Fitter 1989). Thus, the manner in which VAM act under different nutrient regimes is of interest.

Competitive interactions among plants can shape distribution patterns and relative species abundance and may also affect the adaptive traits of competing plant species (Keddy 1989). VAM may mediate com-

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Table 1. Percent VAM colonization under three fertilizer treatments. Comparisons were by the nonparametric Kruskal-Wallis test with chi-square correction for ties with P indicating significance. Different superscripts show mycorrhizal levels that differ at $\alpha = 0.05$ based on the nonparametric variant of Tukey's honestly significant difference test (mean ± standard deviation, $n = 12$).

Species	Nutrient addition levels			
	None	Complete minus P	Complete	P
Anaphalis margaritacea	10 ± 6^{a}	13 ± 15^{a}	4 ± 5^{a}	0.096
Carex mertensii	0^{a}	0^{a}	0^{a}	–
Epilobium angustifolium	37 ± 16^{b}	35 ± 9^{b}	16 ± 8^{a}	0.003
Epilobium brachycarpum	22 ± 18^{ab}	35 ± 17^{b}	8 ± 6^{a}	0.003
Hieracium albiflorum	27 ± 21^{a}	19 ± 19^{a}	25 ± 18^{a}	0.763
Hypochaeris radicata	11 ± 6^{a}	29 ± 21b	9 ± 12^{a}	0.007
Penstemon cardwellii	19 ± 6^{a}	12 ± 16^{a}	10 ± 16^{a}	0.066

Table 2. ANOVA tables for the biomass of seven pioneer species under three fertilizer and two mycorrhizal treatments (see Figs. 1A–G). Post-hoc shows the results of Tukey's honestly significant difference test at $\alpha = 0.5$ ($n = 12$). Fertilization treatment: 1 = no nutrient addition, 2 = complete without phosphorus addition, 3 = complete nutrient addition. Mycorrhizae treatment: 1 = inoculated, 2 = not inoculated.

Species	Source	DF	χ^2	P	post-hoc
Anaphalis	Fertilization	2	353.92	0.000	$1 < 2 = 3$
margaritacea	Mycorrhizae	1	0.65	0.422	
	Interaction	2	1.65	0.200	
Carex	Fertilization	2	292.40	0.000	$1 < 3 < 2$
martensii	Mycorrhizae	1	0.29	0.590	
	Interaction	2	1.28	0.283	
Epilobium	Fertilization	2	178.58	0.000	$1 < 2 < 3$
angustifolium	Mycorrhizae	1	2.18	0.145	
	Interaction	2	0.98	0.380	
Epilobium	Fertilization	2	277.47	0.000	$1 < 2 < 3$
brachycarpum	Mycorrhizae	1	4.15	0.046	$2 < 1$
	Interaction	2	0.60	0.549	
Hieracium	Fertilization	2	68.80	0.000	$1 < 2 < 3$
albiflorum	Mycorrhizae	1	1.62	0.207	
	Interaction	2	3.38	0.040	
Hypochaeris	Fertilization	2	117.59	0.000	$1 < 2 = 3$
radicata	Mycorrhizae	1	0.00	0.956	
	Interaction	2	3.13	0.050	
Penstemon	Fertilization	2	182.62	0.000	$1 < 2 < 3$
cardwellii	Mycorrhizae	1	7.47	0.008	$2 < 1$
	Interaction	2	14.24	0.000	

petitive interactions between plants and influence the resultant community structure. Most plants form the VAM mutualism; thus, in order for VAM to change the competitive balance between plants the relationship must affect competing plants differentially. These interactions are especially important in dynamic communities where both the density and type of VAM fungi and plant species are changing (Johnson et al. 1991). Studies of competition between early and late seral species have generally shown that late seral species exhibit both greater response to mycorrhizal colonization and greater competitive ability with mycorrhizal colonization (Allen and Allen 1990).

We conducted two experiments under greenhouse conditions: Experiment I tested for interactions between mycorrhizae and nutrient levels among common pioneer species that are found on the Pumice Plain of Mount St. Helens. The hypotheses were as follows: H_0: Levels of mycorrhizal colonization of host plants do not differ at different soil nutrient levels, and H_0: Non-mycotrophic and facultatively mycotrophic species do not differ in their response to mycorrhizal inoculum at different soil nutrient levels. Experiment II tested how VAM might affect competitive outcomes between four pioneer species. The hypotheses for this experiment were H_0: Mycorrhizal colonization levels of host plants do not change with increased number of competitors or with competitor species, and H_0: Non-mycotrophic and facultatively mycotrophic species differ in their competitive relationships with other species depending upon the presence or absence of VAM fungal inoculum.

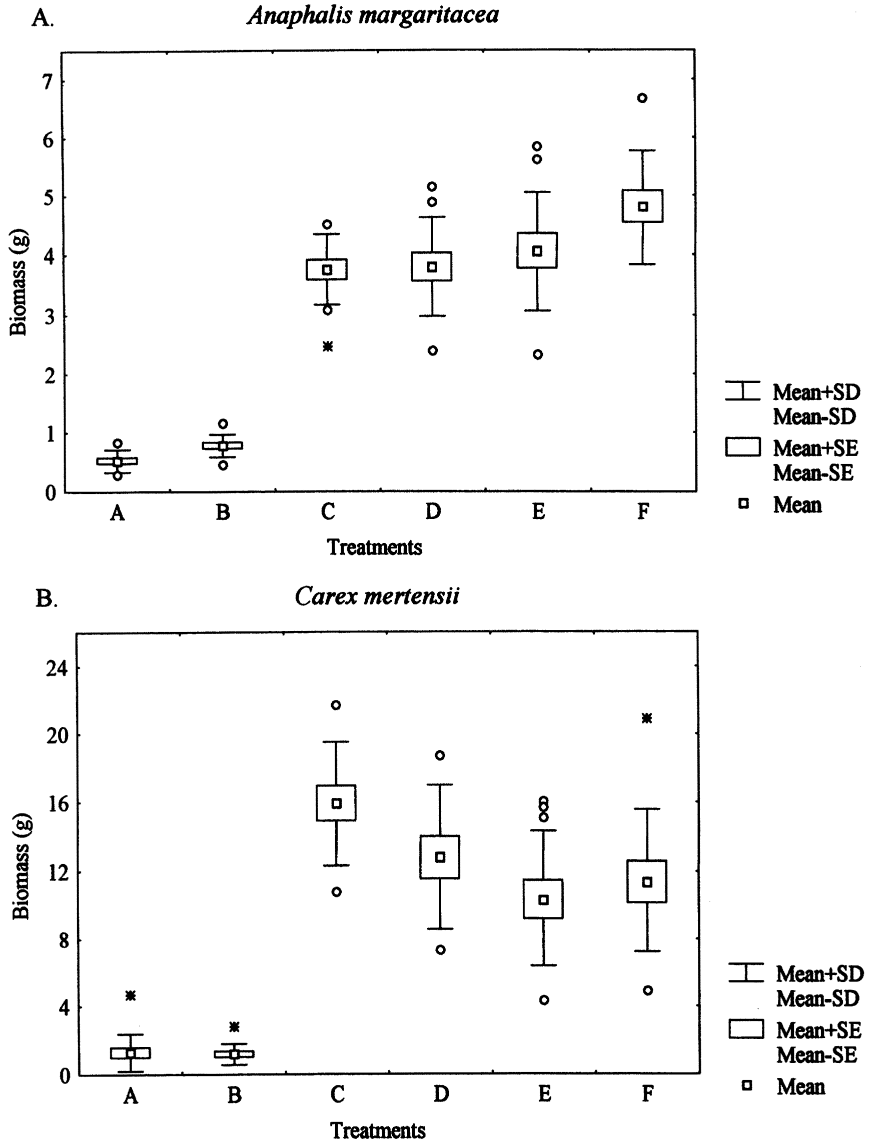


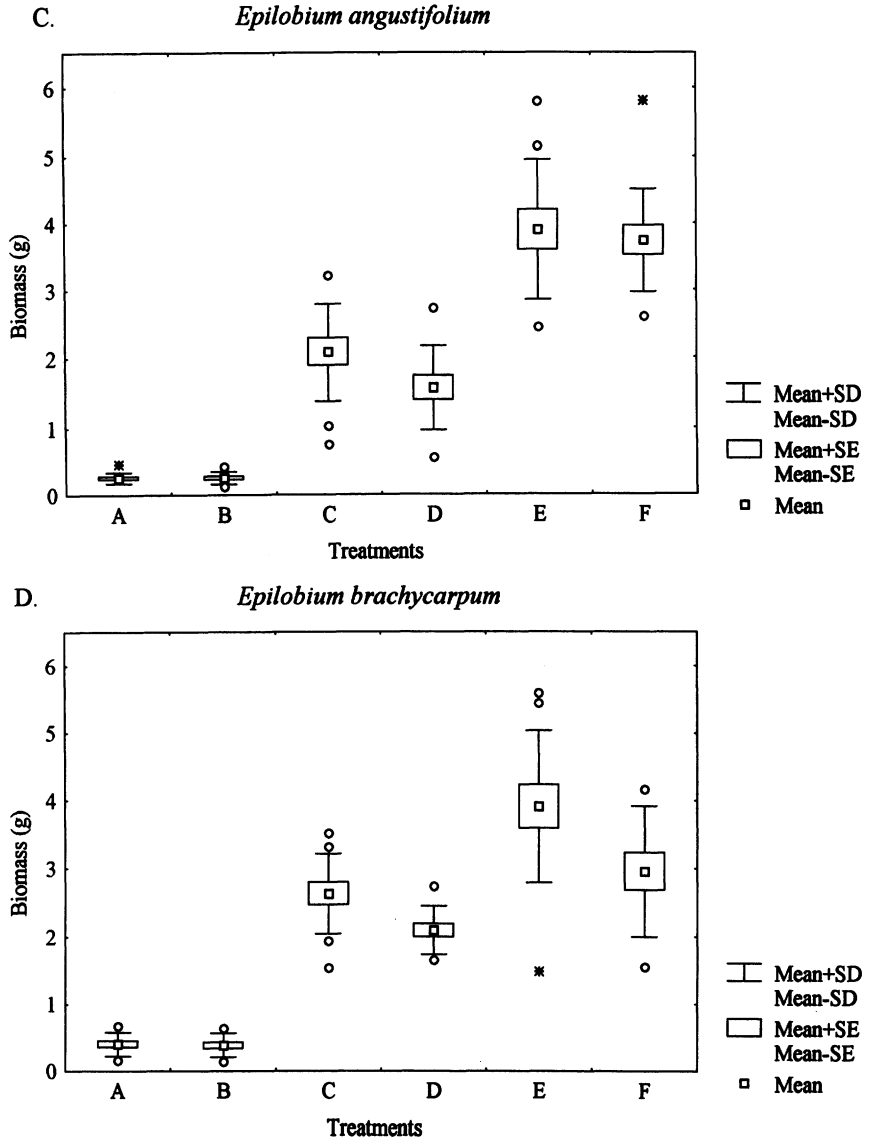
Fig. 1. Box and whisker plots of the biomass of seven pioneer species under three fertilizer and two mycorrhizal treatments. Treatment Abbreviations: A = inoculated, no nutrients added; B = not inoculated, no nutrients added; C = inoculated, complete nutrients −P; D = not inoculated, complete nutrients −P; E = inoculated, complete nutrients; F = not inoculated, complete nutrients. Inoculated = pots with soil containing mycorrhizal propagules added. Not inoculated = pots with sterilized soil added and mycorrhizal activity inhibited by benomyl ($n = 12$). See Table 2 for ANOVA tables. A. *Anaphalis margaritacea*, B. *Carex mertensii*, C. *Epilobium angustifolium*, D. *Epilobium brachycarpum*, E. *Hieracium albiflorum*, F. *Hypochaeris radicata*, G. *Penstemon cardwellii*.

Methods

Source and preparation of soil

Soil was collected from the Pumice Plain during August 1992. The Pumice Plain, which ranges in elevation from 1150 to 1300 m, occupies an area of approximately 20 km^2 immediately north of the Mount St. Helens crater. The area was formed in the volcanic eruption of 1980 by the deposit of over 100 m of pumice from the eruption. The material is extremely nutrient poor containing only trace levels of nutrients (del Moral and Bliss 1993). Pumice Plain soil rarely contains VAM spores except in specialized microsites (J. H. Titus unpubl.).

Soil was sifted in a 0.4-cm mesh sieve to remove all coarse particles. Plastic pots (10 cm × 10 cm) were filled with 80 g soil as well as 20 g of sterile perlite, to increase porosity. Mycorrhizal treatments were established by the addition of 30 g Bear Meadow soil (located 10 km northeast of the Pumice Plain, outside the blast zone, at a similar elevation as the Pumice Plain) to each pot to provide VAM inoculum. Only one morphological spore type was detected in Bear



Figs. 1C, D.

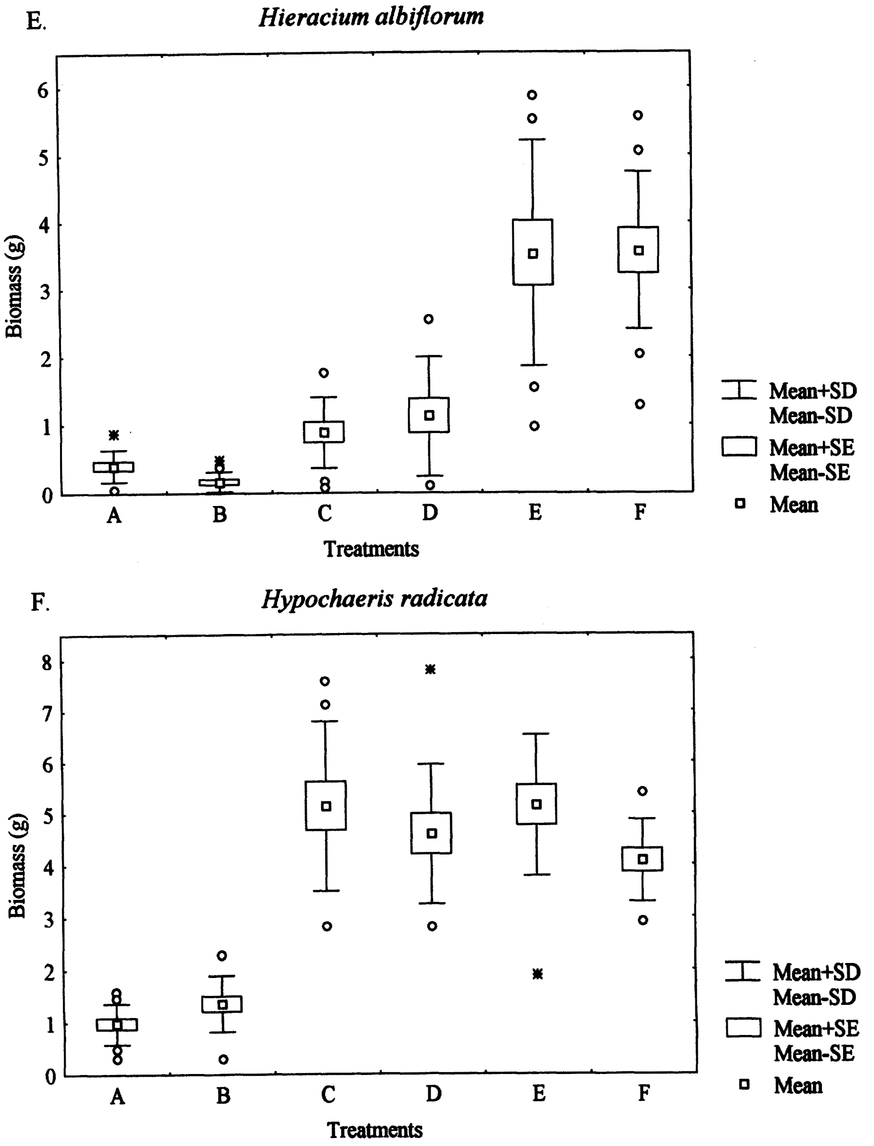
Meadow soil (14.6 ± 13.9 spores per 100 ml soil, determined to be *Glomus macrocarpum* (Tul. & Tul) (J. H. Titus unpubl.)). Mycotrophic species collected at Bear Meadow were VAM colonized and in the greenhouse, plants were readily VAM colonized when grown in Bear Meadow soil. Bear Meadow soil was steamed for 15 min, cooled and added to pots for the non-mycorrhizal treatment. Steaming effectively eliminates mycorrhizal inoculum potential (J. H. Titus unpubl.).

Maintenance of non-mycorrhizal conditions was assured by applying benomyl (benlate 50% active ingredient; Southern Mill Creek Products, Tampa, FL) at approximately 25 mg (active ingredient) per 1 kg of soil (dry mass). Benomyl was applied in 50-ml aliquots per pot 1 week after planting and every 4 weeks thereafter. Paul et al. (1989) found Benomyl to have no effect on plants in the absence of fungi and is often used to create and maintain non-mycorrhizal conditions (e.g. Fitter 1986, Fitter and Nichols 1988, Hetrick et al. 1989, Hartnett et al. 1993). Benomyl suppresses pathogenic fungi as well as mycorrhizal fungi. To the extent that pathogens are also suppressed, measured growth enhancement of untreated plants compared to those treated with fungicide may underestimate mycorrhizal benefit (Carey et al. 1992).

Design

Experiment I

This experiment was conducted to determine if nutrient levels affect the response of facultatively mycotrophic



Figs. 1E, F.

and non-mycotrophic pioneer species to mycorrhizal inocula. Plants in both mycorrhizal and non-mycorrhizal treatments were subjected to three different nutrient regimes: tap water (i.e., very low nutrient levels), 10% Colwell's solution without phosphorus, and 10% Colwell's solution. Colwell's solution resembles natural proportions of nutrients (Colwell 1943, R. B. Walker, Univ. of Washington, pers. comm.). The dilute solution (i.e., 10%) was used to simulate nutrient poor conditions on the Pumice Plain. All pots were watered daily with tap water. Fertilizer was applied in 50-ml aliquots per pot at planting and at weekly intervals throughout the experiment. Sample size was twelve pots per nutrient regime per species.

The following five facultatively mycotrophic perennial species were used: *Anaphalis margaritacea* (L.) Benth & Hook., *Epilobium angustifolium* L., *Hieracium albiflorum* Hook., *Hypochaeris radicata* L., and *Penstemon cardwellii* Howell. The non-mycotrophic perennial *Carex mertensii* Prescott and the facultatively mycotrophic annual *Epilobium brachycarpum* C. Presl were also used (Allen et al. 1992, Chapin 1995, J. H. Titus unpubl.). These are common pioneer species on the Pumice Plain (del Moral and Bliss 1993). Seeds were collected August and September of 1992 from the Pumice Plain. On 21 February, 1993 seeds were placed in Petri plates on filter paper and watered with tap water. Seedlings were transferred into pots on 28 February, 1993. Plants were harvested on 4 and 5 July, 1993.

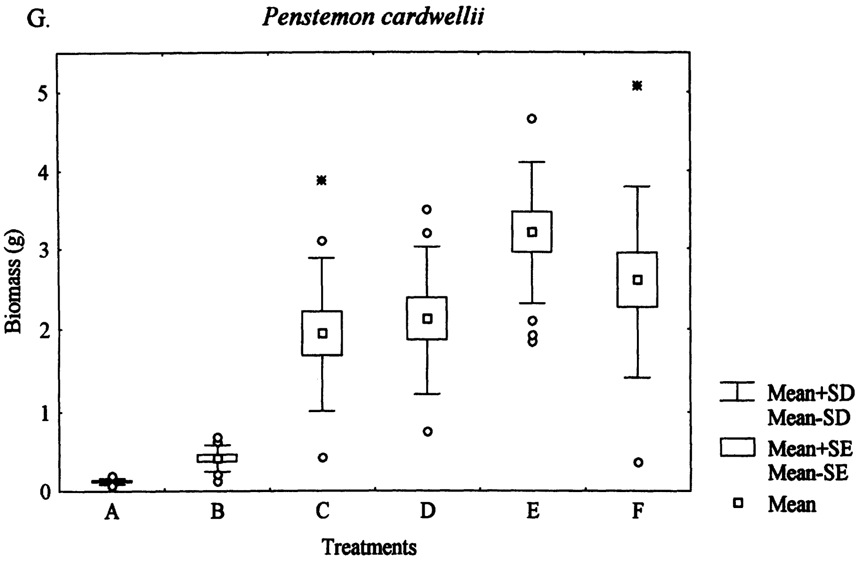


Fig. 1G.

Experiment II

This experiment was conducted to determine if VAM mediates competitive interactions between pioneer species common on the Pumice Plain. More specifically, we investigated how VAM affected intra- and interspecific competitive relationships among four pioneer species. An additive experiment, using three facultatively mycotrophic species and one non-mycotrophic species, was designed to determine the competitive effects of 'neighbor' plants on a 'target'. The slopes of the regressions of target plant performance (e.g., biomass) with increasing neighbor density provide a quantitative estimate of competitive effect and allow statistical comparisons of the effects of different treatments, such as mycorrhizae, on competitive ability (Goldberg and Scheiner 1993). Zero slopes indicate no significant interactions or effects; significant negative slopes indicate competitive effects; and significant positive slopes indicate direct or indirect beneficial effects. This additive study was conducted at low nutrient levels to approximate conditions actually experienced by the target species on the Pumice Plain.

Seeds of *Carex mertensii*, *Anaphalis margaritacea*, *Epilobium angustifolium* and *Hypochaeris radicata* were collected August and September, 1993 from the Pumice Plain. On 24 January, 1994 seeds were placed in Petri plates on filter paper and watered with tap water. Seedlings were transferred into pots on 1 February, 1994. Single target seedlings were planted centrally in each pot and surrounded by 0, 2, 4, and 8 evenly spaced seedling neighbors of the same age in each possible intraspecific and interspecific target neighbor combination with five replicates (Fitter 1977, Hartnett et al. 1993). Plants were watered daily with tap water and a 10% Colwell's solution without phosphorus was applied in 50-ml aliquots at planting, one week after planting and at 2-week intervals thereafter. Plants were harvested on 4 and 5 July, 1994, after five months of growth.

Experiments I and II

Pots were arranged in a randomized block design and maintained at 20–25°C in the Univ. of Washington Botany Greenhouse. Natural lighting was supplemented by sodium lamps to provide a 16-h photoperiod. Flats were rotated at 2-week intervals. After harvest, roots were washed free of soil and frozen until examination. Plants were dried for 3 d at 80°C; and root, shoot and reproductive dry weights measured to the nearest 0.01 g.

Roots were washed, cleared and stained with trypan blue (Brundrett et al. 1994). Percent VAM colonization was estimated by placing a grid of 1-cm squares below a Petri plate which contained the root sample under a dissecting microscope. One hundred locations in which a root crossed a line on the grid were scored for mycorrhizae. Many samples were examined under higher power to ascertain that the fungi were indeed VAM. Root segments containing vesicles, arbuscles, hyphae or intercellular hyphal coils were recorded as colonized. The number of mycorrhizal "hits" is used as an estimate of percent root colonized (Brundrett et al. 1994).

Table 3a. Percent VAM colonization under four competitive regimes with four competitors. Data were from the mycorrhizal addition portion of the mycorrhizal treatment only (mean ± standard deviation, $n = 5$). See Table 3b for statistical analysis. *Carex* is not included as a target species due to lack of mycorrhizal colonization.

Target species	Density of competitors	Competing species			
		Anaphalis margaritacea	*Carex mertensii*	*Epilobium angustifolium*	*Hypochaeris radicata*
Anaphalis margaritacea	0	9 ± 1	9 ± 1	9 ± 1	9 ± 1
	2	8 ± 6	5 ± 4	9 ± 5	10 ± 4
	4	8 ± 9	11 ± 11	8 ± 7	15 ± 4
	8	12 ± 7	5 ± 3	14 ± 5	18 ± 6
Epilobium angustifolium	0	22 ± 9	22 ± 9	22 ± 9	22 ± 9
	2	5 ± 3	15 ± 8	16 ± 7	12 ± 5
	4	18 ± 3	10 ± 5	10 ± 5	1 ± 1
	8	11 ± 5	6 ± 4	2 ± 1	1 ± 1
Hypochaeris radicata	0	25 ± 26	25 ± 26	25 ± 26	25 ± 26
	2	5 ± 2	2 ± 1	13 ± 7	3 ± 3
	4	8 ± 4	14 ± 7	11 ± 6	3 ± 2
	8	11 ± 7	9 ± 6	24 ± 19	1 ± 1

Data analysis

Experiments I and Experiment II

To determine if nutrient level or neighbor species or density affected mycorrhizal colonization, the degree of VAM colonization of each species was assessed by the nonparametric Kruskal-Wallis test with a chi-square correction for ties (Zar 1984, Norusis 1993). Post-hoc tests were conducted by using the nonparametric variant of the Tukey's honestly significant difference test (Zar 1984: p. 199).

The root:shoot ratio was determined using the biomass of each. Root, shoot, and total dry biomass and the root:shoot ratio of mycorrhizal and non-mycorrhizal treatments were compared by two-way ANOVA. Biomass and ratios were log transformed to improve normality and homoscedasticity. Post-hoc comparisons were conducted using Tukey's honestly significant difference test (Zar 1984, Norusis 1993). Due to the paucity of reproductive individuals, flowers were included with total aboveground biomass.

Experiment II

For each treatment combination the relationship between plant performance and neighbor density was examined using linear regression for each biomass measure of target plant performance. The relationship between target plant biomass and neighbor density varied among treatments and were nonlinear (negative exponential) because as the number of neighbors increased, they compete more intensely with one another and their per-individual effect on the target plant decreases. Therefore, log transformation of the target plant biomass produced linear relationships and homoscedastic variances. Hartnett et al. (1993) found that using either number of neighbors or total neighbor biomass as the independent variable yielded the same results; in this analysis we used the number of neighbors.

Competition coefficients for each of the seven species growing in competition in each treatment combination were calculated as the slope of the regression of log target plant biomass against number of individuals of the neighbor species. Regression parameters were compared between mycorrhizal and non-mycorrhizal treatments using analysis of covariance. Significant differences in slopes indicate that mycorrhizae have altered competitive relationships (Goldberg and Scheiner 1993, Hartnett et al. 1993).

Results

Experiment I

Mycorrhizal colonization

Benomyl effectively suppressed mycorrhizal colonization in the non-mycorrhizal treatments. In the mycorrhizal treatments, *Carex* was not colonized (Table 1). For *E. angustifolium*, *E. brachycarpum*, and *Hypochaeris*, the −P treatment had significantly higher VAM colonization levels.

Table 3b. Percent VAM colonization under four competitive regimes with four competitors. Comparisons were by the two-way nonparametric Kruskal-Wallis test and the nonparametric variant of Tukey's honestly significant different test at $\alpha = 0.5$ ($n = 5$). *Carex mertensii* is not included as a target species due to lack of mycorrhizal colonization. Competing species: 1 = *Anaphalis margaritacea*, 2 = *Carex mertensii*, 3 = *Epilobium angustifolium*, 4 = *Hypochaeris radicata*. Density of neighbors: 1 = 0 neighbors, 2 = 2 neighbors, 3 = 4 neighbors, 4 = 8 neighbors.

Species	Source	DF	χ^2	*P*	post-hoc
Anaphalis	Competing species	3	10.20	0.017	$2 = 1 = 3 < 4$
margaritacea	Density of neighbors	3	4.62	0.202	
	Interaction	9	4.17	0.118	
Epilobium	Competing species	3	17.23	0.001	$4 = 3 = 2 < 1$
angustifolium	Density of neighbors	3	37.43	0.000	$4 < 3 = 2 < 1$
	Interaction	9	26.59	0.003	
Hypochaeris	Competing species	3	14.71	0.002	$4 < 2 = 1 = 3$
radicata	Density of neighbors	3	20.39	0.000	$2 = 4 = 3 < 1$
	Interaction	9	2.34	0.825	

Biomass response

Root and shoot biomass responses were similar to those of total biomass. Therefore, we discuss only total biomass results to improve clarity. Root:shoot ratio results were not significant and will not be discussed. Biomass significantly increased with increased nutrient level for five species, but not for *Carex* and *Hypochaeris* (Table 2, Fig. 1A–G). *Epilobium brachycarpum* and *Penstemon* had greater biomass in the mycorrhizal treatment.

Interactions occur due to a differential response to the presence of mycorrhizae across nutrient input levels (Zar 1984). Interactions occurred in *Hypochaeris* and *Penstemon* because biomass was greater under mycorrhizal conditions for the complete fertilizer and −P treatments, but biomass was lower in the tap water treatment under mycorrhizal conditions than under non-mycorrhizal conditions. This effect implies a beneficial mycorrhizal effect with nutrient additions and a negative effect at low nutrient levels. The interaction for *Hieracium* illustrated a different effect, that is, biomass was greater in the tap water treatment and lower in the −P treatment under mycorrhizal conditions than under nonmycorrhizal conditions.

Experiment II

Mycorrhizal colonization

Plants in the non-mycorrhizal treatment lacked VAM. In the mycorrhizal treatment, all plants were VAM except for *Carex* (Table 3a, b). VAM colonization in *Anaphalis* was influenced by the identity, but not by the density of neighbor species. VAM colonization of *Anaphalis* was least in competition with the non-VAM species *Carex* and greatest in competition with *Hypochaeris*. For *E. angustifolium*, VAM colonization was greatest when in competition with *Anaphalis* and decreased with increased neighbor density. There was also a strong interaction between neighbor species identity and density. *Hypochaeris* showed significant differences in VAM colonization level in relation to both identity and density of neighbor species. VAM colonization levels were lowest when in competition with conspecifics, and pots with single *Hypochaeris* plants had significantly greater VAM colonization levels than those in which *Hypochaeris* plants were subjected to competition.

Biomass

As in experiment I only the results for total biomass are described here. Significant biomass decreases with increasing neighbor density were observed for all species (Tables 4 and 5, Figs 2–5). At the conclusion of the experiment plants were small and, with the exception of singly grown plants, rarely achieved dry weights greater than 1 g.

Mycorrhizal *Anaphalis* plants were larger than non-mycorrhizal plants when in competition with *Carex* (Fig. 2B). In addition, when *Anaphalis* plants were in competition with *Carex* under mycorrhizal conditions, biomass decreased significantly with increased *Carex* density. However, under non-mycorrhizal conditions there was no significant competitive effect, i.e., slope = 0. Thus there was competition under mycorrhizal conditions, but not under non-mycorrhizal conditions. However, the competitive intensity was not significantly different between the two treatments. An opposite trend occurred when *Anaphalis* was in competition with *E. angustifolium* (Fig. 2C). That is, the slope was steeper under non-mycorrhizal conditions than under mycorrhizal conditions, meaning that competition was more intense without mycorrhizae.

When *Carex* was in competition with *Hypochaeris*, plants in the non-mycorrhizal treatment were significantly greater in biomass (Fig. 3D). In addition, the slope was 0, indicating no competitive effects. Under mycorrhizal conditions with *Hypochaeris*, biomass decreased significantly with increased neighbor number. The difference in competitive intensity was not significant at $p = 0.08$. However, this low value of p is suggestive that competition may be more intense under mycorrhizal conditions and that non-mycorrhizal *Hypochaeris* plants were less competitive. When *Carex*

Table 4. ANOVA tables for log biomass under four competitive regimes with four competitor species. Post-hoc shows the results of Tukey's honestly significant difference test at $\alpha = 0.5$ ($n = 5$). Inoculated = pots with soil containing mycorrhizal propagules added. Not inoculated = pots with sterilized soil added and mycorrhizal activity inhibited by benomyl. Density of neighbors: 1 = 0 neighbors, 2 = 2 neighbors, 3 = 4 neighbors, 4 = 8 neighbors. Mycorrhizae treatment: 1 = soil with VAM propagules added, 2 = sterilized soil added.

Target species	Competitor	Source	DF	*F*	*P*	post-hoc
Anaphalis margaritacea	*Anaphalis margaritacea*	Density	3	17.47	0.000	4 = 3 < 2 < 1
		Mycorrhizae	1	0.32	0.578	
		Interaction	3	1.14	0.346	
	Carex mertensii	Density	3	14.67	0.000	4 = 3 = 2 < 1
		Mycorrhizae	1	4.42	0.044	2 < 1
		Interaction	3	1.33	0.281	
	Epilobium angustifolium	Density	3	7.38	0.001	4 < 1, 3 < 1, 2 = 1, 4 = 3 = 2
		Mycorrhizae	1	1.75	0.195	
		Interaction	3	0.77	0.519	
	Hypochaeris radicata	Density	3	26.00	0.000	3 = 2 < 1, 4 = 3, 4 < 2
		Mycorrhizae	1	1.37	0.249	
		Interaction	3	0.18	0.910	
Carex mertensii	*Anaphalis margaritacea*	Density	3	6.31	0.000	4 = 3 < 2 = 1
		Mycorrhizae	1	3.66	0.065	
		Interaction	3	0.92	0.442	
	Carex mertensii	Density	3	12.27	0.000	4 = 3 < 2 < 1
		Mycorrhizae	1	0.30	0.589	
		Interaction	3	0.13	0.944	
	Epilobium angustifolium	Density	3	11.90	0.000	4 < 3, 3 = 2, 3 < 1, 2 = 1
		Mycorrhizae	1	0.96	0.335	
		Interaction	3	0.11	0.956	
	Hypochaeris radicata	Density	3	11.20	0.000	4 = 3, 4 = 2, 3 < 2, 2 < 1
		Mycorrhizae	1	12.20	0.001	1 < 2
		Interaction	3	2.29	0.097	
Epilobium angustifolium	*Anaphalis margaritacea*	Density	3	6.24	0.002	4 = 3, 4 < 2 = 1, 3 = 2, 3 < 1
		Mycorrhizae	1	6.21	0.018	1 < 2
		Interaction	3	0.62	0.607	
	Carex mertensii	Density	3	10.38	0.000	4 = 3, 4 < 2 < 1, 2 = 3
		Mycorrhizae	1	1.07	0.309	
		Interaction	3	0.45	0.720	
	Epilobium angustifolium	Density	3	6.94	0.001	4 = 3 = 2 < 1
		Mycorrhizae	1	18.45	0.000	1 < 2
		Interaction	3	1.03	0.392	
	Hypochaeris radicata	Density	3	8.48	0.000	4 = 3 = 2 < 1
		Mycorrhizae	1	7.23	0.011	1 < 2
		Interaction	3	0.66	0.581	
Hypochaeris radicata	*Anaphalis margaritacea*	Density	3	13.00	0.000	4 = 3 < 1, 4 < 2 = 1, 3 = 2
		Mycorrhizae	1	8.97	0.005	2 < 1
		Interaction	3	1.21	0.324	
	Carex mertensii	Density	3	15.25	0.000	4 = 3 = 2 < 1, 4 < 2 < 1
		Mycorrhizae	1	37.16	0.000	2 < 1
		Interaction	3	4.76	0.007	
	Epilobium angustifolium	Density	3	6.82	0.001	4 = 3 < 1, 4 = 2, 2 = 1
		Mycorrhizae	1	29.93	0.000	2 < 1
		Interaction	3	0.89	0.458	
	Hyochaeris radicata	Density	3	22.59	0.000	4 = 3, 4 < 2 = 1, 3 = 2, 3 < 1
		Mycorrhizae	1	3.33	0.078	
		Interaction	3	0.31	0.821	

was competing intraspecifically, with *Anaphalis* and with *E. angustifolium*, slopes of both mycorrhizal and non-mycorrhizal treatments were significant and the slopes did not differ (Fig. 3A–C). Constants showed a significant negative mycorrhizal effect, i.e., when grown singly *Carex* plants were greater in biomass under non-mycorrhizal conditions (Table 5).

Epilobium angustifolium biomass was greater for non-mycorrhizal treatment plants, except when in competition with *Carex* (Fig. 4A–D). Slopes of *E. angustifolium* competing intraspecifically and with *Anaphalis*, *Carex* and *Hypochaeris* were significant under both mycorrhizal and non-mycorrhizal treatments. The slopes were not significantly different. Thus, *E. angustifolium* plants were larger when non-mycorrhizal but the intensity of competition did not change with mycorrhizal status.

In all cases, the mycorrhizal *Hypochaeris* plants were larger than the non-mycorrhizal plants (Fig. 5A–D). When *Hypochaeris* was subjected to competition with *Carex*, both the mycorrhizal and non-mycorrhizal slopes were significant (Fig. 5B). Total biomass de-

Table 5. Competition coefficients for target species growing in intra- and interspecific competition calculated as the slope of the regression of log target plant biomass against number of neighbors. Inoculated = plants with soil containing mycorrhizal propagules added. Not inoculated = plants with sterilized soil added and mycorrhizal activity inhibited by benomyl. Regression parameters were compared by analysis of covariance. Asterisks indicate slopes different from zero at $\alpha = 0.05$. Within each species combination, different letter superscripts indicate that slopes or constants of the inoculated and not inoculated treatments differ at $\alpha = 0.05$. The P value shows the significance of the comparison between the two slopes or constants.

Target species	Competing species	Competition coefficients			Constants		
		Inoculated	Not inoculated	P	Inoculated	Not inoculated	P
Anaphalis margaritacea	*Anaphalis margaritacea*	-0.24^{*a}	-0.072^{*a}	0.55	0.32^{a}	-0.0027^{a}	0.90
	Carex mertensii	-0.11^{*a}	-0.077^{*a}	0.51	-0.088^{a}	-0.49^{a}	0.63
	Epilobium angustifolium	-0.061^{*a}	-0.071^{*a}	0.72	0.079^{a}	0.0026^{a}	0.39
	Hypochaeris radicata	-0.12^{*a}	-0.13^{*a}	0.88	-0.12^{a}	-0.29^{a}	0.39
Carex mertensii	*Anaphalis margaritacea*	-0.062^{*a}	-0.038^{*a}	0.48	0.35^{a}	0.44^{b}	0.0028
	Carex mertensii	-0.050^{*a}	-0.061^{*a}	0.66	0.31^{a}	0.38^{b}	0.0004
	Epilobium angustifolium	-0.088^{*a}	-0.098^{*a}	0.68	0.31^{a}	0.43^{b}	0.0003
	Hypochaeris radicata	-0.15^{*a}	-0.048^{*a}	0.079	0.85^{a}	0.22^{a}	0.64
Epilobium angustifolium	*Anaphalis margaritacea*	-0.086^{*a}	-0.91^{*a}	0.91	-0.42^{b}	-0.94^{a}	0.003
	Carex mertensii	-0.12^{*a}	-0.14^{*a}	0.67	-0.37^{b}	-0.45^{a}	0.030
	Epilobium angustifolium	-0.076^{*a}	-0.045^{*a}	0.28	-0.42^{a}	-0.16^{b}	0.0001
	Hypochaeris radicata	-0.16^{*a}	-0.10^{*a}	0.35	-0.53^{a}	-0.27^{a}	0.007
Hypochaeris radicata	*Anaphalis margaritacea*	-0.052^{*a}	-0.029^{*a}	0.10	0.29^{b}	0.093^{a}	0.0000
	Carex mertensii	-0.010^{*a}	-0.076^{*b}	0.013	0.097^{b}	0.086^{a}	0.0004
	Epilobium angustifolium	-0.019^{*a}	-0.039^{*a}	0.28	0.22^{b}	0.020^{a}	0.0006
	Hypochaeris radicata	-0.063^{*a}	-0.062^{*a}	0.87	0.18^{b}	0.093^{a}	0.0009

creased significantly more under non-mycorrhizal conditions with increasing density of *Carex* neighbors than it did under mycorrhizal conditions. This was the *only* case in this experiment where a significant difference in competitive intensity was found between the mycorrhizal and non-mycorrhizal treatments. In addition, competition between *Carex* as the target species and *Hypochaeris* was a non-significant $p = 0.08$. In that situation, competition was more intense under mycorrhizal conditions. Significant interactions were also found with *Carex* as competitor. The interaction effect occurred with the mycorrhizal treatment, where biomass decreased with two *Carex* competitors but then increased with four competitors and then decreased again with eight *Carex* competitors. Thus, the interaction effects are due to the unusual biomass characteristics of the *Hypochaeris* plants with four *Carex* competitors under mycorrhizal conditions.

Discussion

Experiment I

VAM colonization levels were higher at lower nutrient levels for most species. Due to the smaller size of the roots in the tap water treatment the percent total root examined was much greater than in the fertilization treatments. Thus, the absolute quantity of VAM fungi was probably much less. In any case, the evidence supports the hypothesis that on per unit of root basis the colonization density does not remain constant across nutrient levels (Sparling and Tinker 1978).

Hetrick et al. (1986) found that VAM fungi are suppressed in non-sterile soil. From this evidence they concluded that presumed benefits from VAM as measured in sterilized soils were overestimated. This supports the hypothesis that applying benomyl to the non-mycorrhizal treatment underestimates VAM benefit, because the pathogens are eliminated from the non-mycorrhizal treatment but not from the mycorrhizal treatment (Carey et al. 1992). In this experiment, VAM fungal propagules were added to Pumice Plain soil in the form of non-sterile Bear Meadow soil possibly containing fungal pathogens, and the non-mycorrhizal treatment had potential fungal pathogens eliminated. Therefore, the presence of pathogenic fungi may lead to an underestimate of mycorrhizal benefit. However, the roots examined contain no signs of fungi other than VAM.

As expected, fertilization generally increased plant biomass. Two exceptions of this were: the lack of a significant difference for *Hypochaeris* between −P and complete fertilizer treatments, and significantly greater biomass *Carex* plants in the −P treatment. These species appear to be adapted to low phosphorus environments (Turkington and Aarssen 1983).

Significant increases in biomass in VAM over non-VAM plants were observed in *E. brachycarpum* and *Penstemon*. *Epilobium brachycarpum* is a rapid growing facultatively mycotrophic annual of disturbed environments. Such growth forms are not expected to respond to mycorrhizal colonization (Allen et al. 1992, Boerner 1992). *Penstemon* responds positively to mycorrhizal colonization as would be expected from a woody perennial subalpine species.

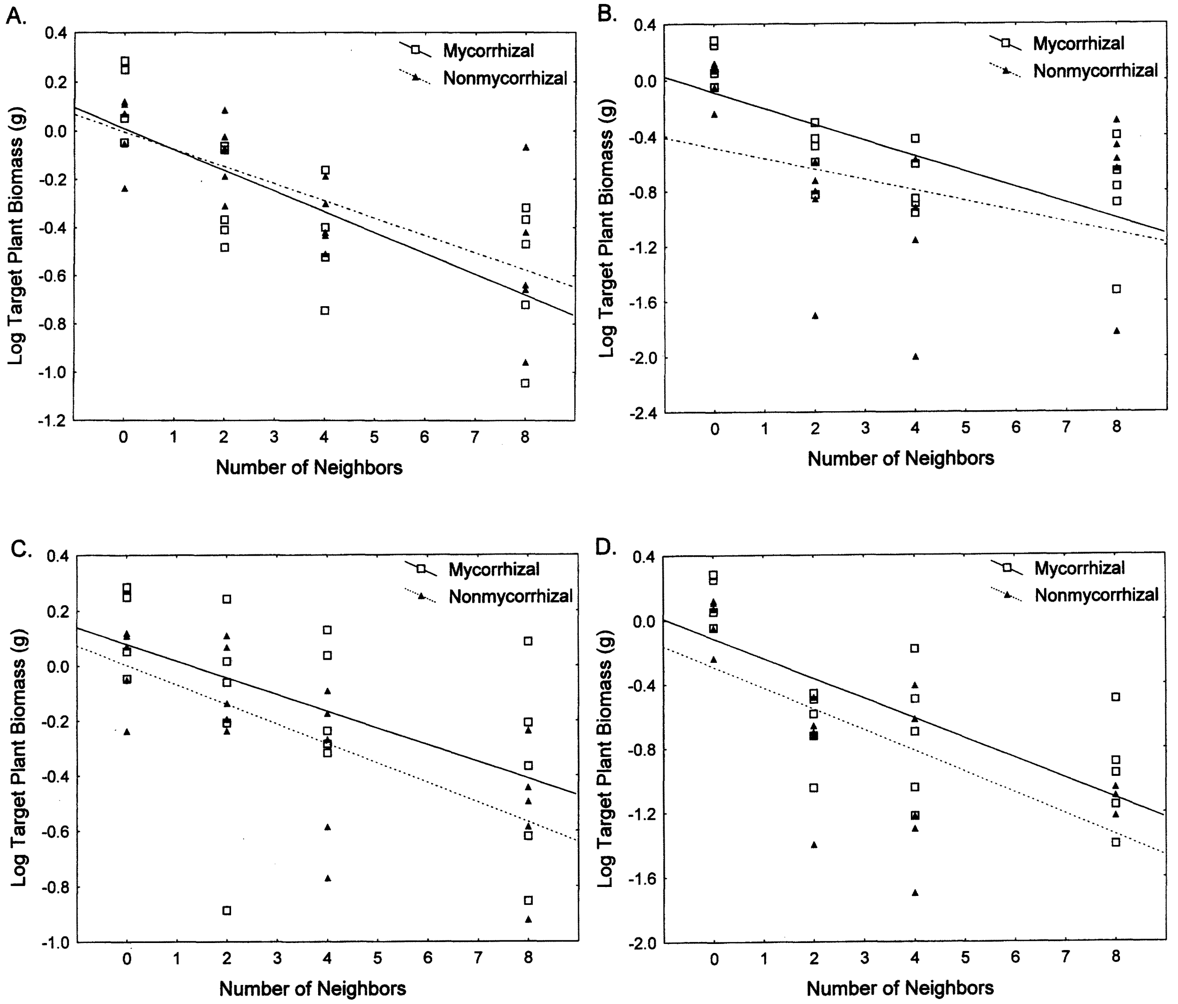


Fig. 2. The relationship between log target plant biomass and number of neighbors. Open squares and solid lines indicate the inoculated with mycorrhizae (+myc) treatments. Closed triangles and dashed lines indicate the not inoculated with mycorrhizae (−myc) treatments. Equations of the lines are in braces. A. *Anaphalis margaritacea* in competition with *Anaphalis margaritacea.* +myc $r^2 = 0.61$, $P = 0.0000$ {$Y = 0.032 + -0.24X$}; −myc $r^2 = 0.55$, $P = 0.0002$ {$Y = -0.0027 + -0.071X$}. B. *Anaphalis margaritacea* in competition with *Carex mertensii.* +myc $r^2 = 0.53$, $P = 0.0003$ {$Y = 0.088 + -0.11X$}; −myc $r^2 = 0.12$, $P = 0.14$ {$Y = -0.49 + -0.077X$}. C. *Anaphalis margaritacea* in competition with *Epilobium angustifolium.* +myc $r^2 = 0.28$, $P = 0.016$ {$Y = 0.079 + -0.061X$}; −myc $r^2 = 0.51$, $P = 0.0004$ {$Y = 0.0026 + -0.071X$}. D. *Anaphalis margaritacea* in competition with *Hypochaeris radicata.* +myc $r^2 = 0.52$, $P = 0.0003$ {$Y = -0.12 + -0.12X$}; −myc $r^2 = 0.51$, $P = 0.0004$ {$Y = -0.29 + -0.13X$}.

The absence of a significant positive biomass response to the mycorrhizal treatment for most species is consistent with the facultatively mycotrophic nature of these species. It is possible that nutrient levels were not high enough for mycorrhizal mutualism to benefit the host. At very low nutrient levels, the VAM symbiosis can be parasitic on mycotrophic plants (Koide and Elliott 1989). However, most species showed non-significant increased biomass with VAM. The exceptions, *Hypochaeris* and *Penstemon*, occurred in tap water where biomass was less under mycorrhizal conditions than under non-mycorrhizal conditions. The significant interaction effects seen in these two species imply a possible parasitic effect by mycorrhizae at low nutrient levels.

The trend observed for most of the species was for the maximum benefit from VAM to occur in the −P treatment. This is in accordance with many mycorrhizal models, i.e., the mycorrhizal effect is greatest under low phosphorus conditions (e.g., Smith et al. 1986, Mullen and Schmidt 1993). Phosphorus is the principal benefit plants receive from the mycorrhizal mutualism, therefore increased biomass in low phosphorus environments appears to be due to the fungi supplying the nutrient to the plant.

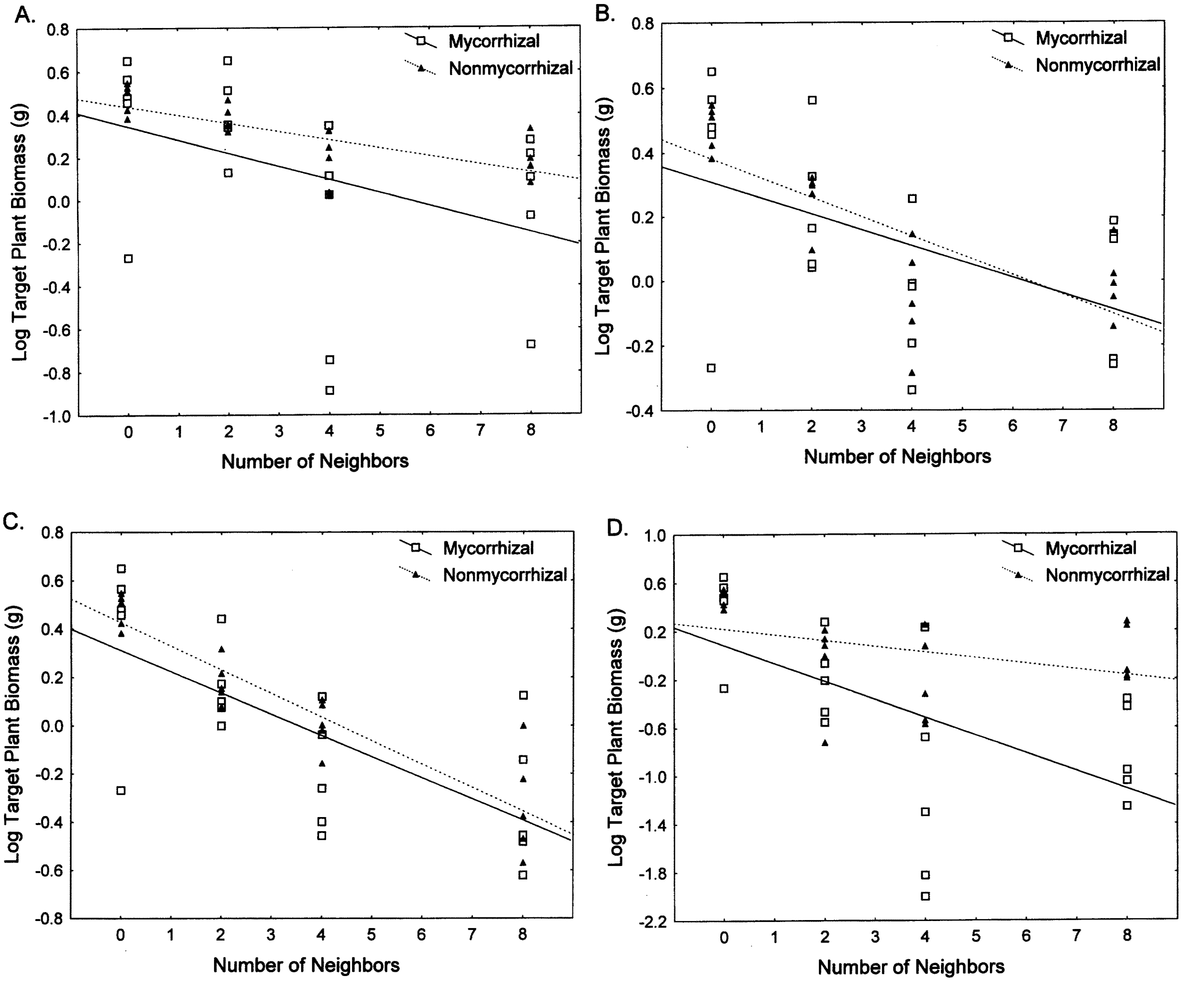


Fig. 3. The relationship between log target plant biomass and number of neighbors. Open squares and solid lines indicate the inoculated with mycorrhizae (+myc) treatments. Closed triangles and dashed lines indicate the not inoculated with mycorrhizae (−myc) treatments. Equations of the lines are in braces. A. *Carex mertensii* in competition with *Anaphalis margaritacea*. +myc $r^2 = 0.17$, $P = 0.070$ $\{Y = 0.35 + -0.062X\}$; −myc $r^2 = 0.53$, $P = 0.0003$ $\{Y = 0.44 + -0.038X\}$. B. *Carex mertensii* in competition with *Carex mertensii*. +myc $r^2 = 0.25$, $P = 0.027$ $\{Y = 0.31 + -0.050X\}$; −myc $r^2 = 0.56$, $P = 0.0001$ $\{Y = 0.38 + -0.061X\}$. C. *Carex mertensii* in competition with *Epilobium angustifolium*. +myc $r^2 = 0.48$, $P = 0.0007$ $\{Y = 0.31 + -0.088X\}$; −myc r^2 0.84, $P = 0.0000$ $\{Y = 0.43 + -0.098X\}$. D. *Carex mertensii* in competition with *Hypochaeris radicata*. +myc $r^2 = 0.34$, $P = 0.007$ $\{Y = 0.085 + -0.15X\}$; −myc $r^2 = 0.15$, $P = 0.093$ $\{Y = 0.22 + -0.048X\}$.

No negative effects by VAM propagules on *Carex* biomass was observed. In other studies negative impacts of VAM on non-mycotrophic species have been found (Allen et al. 1989). Propagule densities may be too low in Bear Meadow soil or VAM fungus species from Bear Meadows are not as aggressive as those in which a negative effect by VAM on non-mycotrophic species was observed.

At the conclusion of both experiments plants were small due to nutrient poor conditions. In comparing the −P treatment in the two experiments (that is, plants with no competitors in the competition experiment), plants were greater in biomass in the nutrient addition experiment than in the competition experiment. Why this occurred is unknown since the greater length of the nutrient addition experiment was insufficient to provide for such a difference.

In a field experiment conducted on the Pumice Plain using these same species, biomass trends between mycorrhizal and non-mycorrhizal treatments were towards greater biomass plants in the non-mycorrhizal treatment, the opposite of this greenhouse experiment (Titus and del Moral 1998). A negative or parasitic response to mycorrhizal colonization in the field and not in the greenhouse by facultatively mycotrophic species may be due to several environmental factors (e.g., Hattingh et

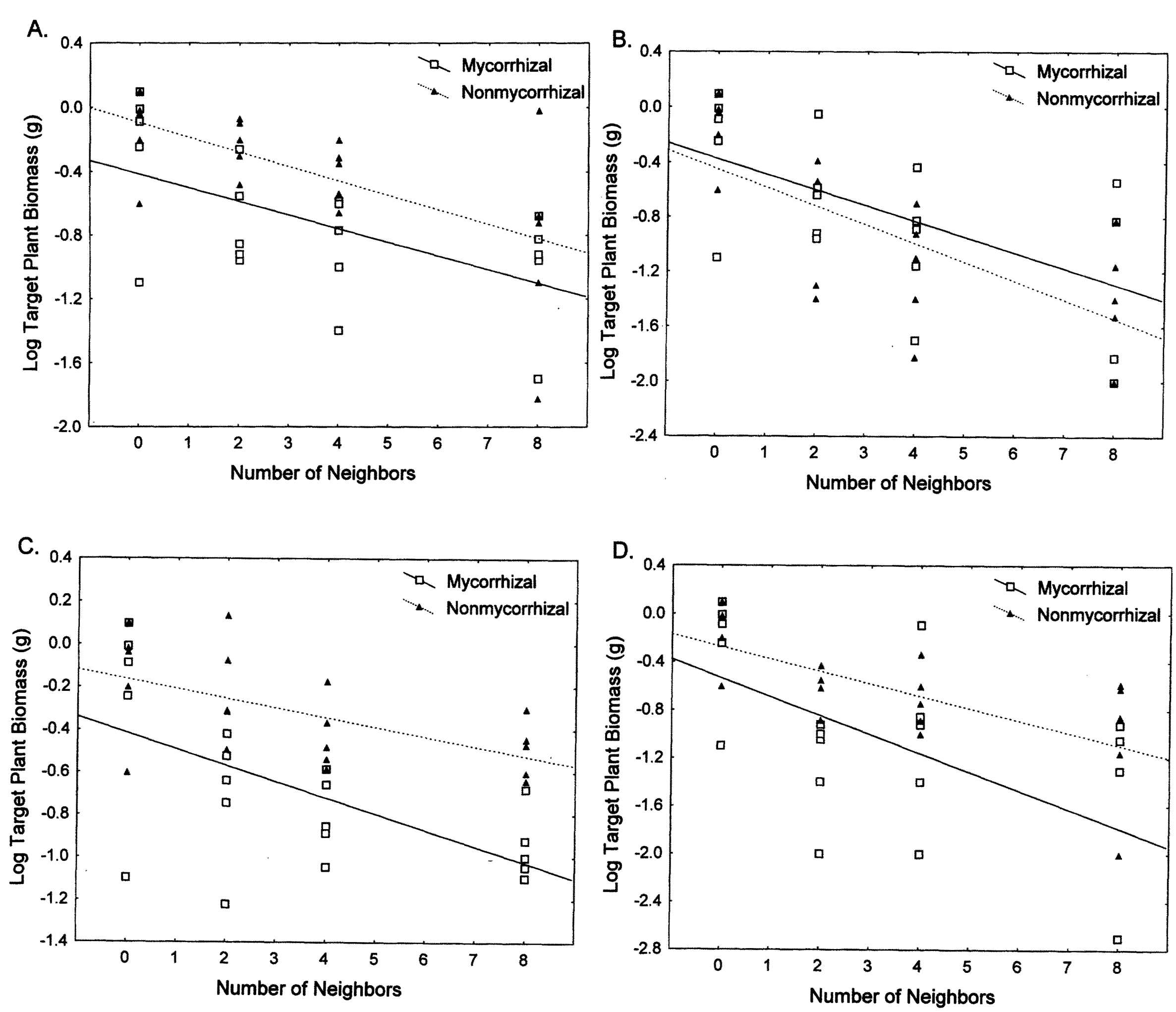


Fig. 4. The relationship between log target plant biomass and number of neighbors. Open squares and solid lines indicate the inoculated with mycorrhizae (+myc) treatments. Closed triangles and dashed lines indicate the not inoculated with mycorrhizae (−myc) treatments. Equations of the lines are in braces. A. *Epilobium angustifolium* in competition with *Anaphalis margaritacea.* +myc $r^2=0.33$, $P=0.0083$ $\{Y= -0.42+ -0.086X\}$; *+myc* $r^2=0.37$, $P=0.0043$ $\{Y= -0.94+ -0.91X\}$. B. *Epilobium angustifolium* in competition with *Carex mertensii.* +myc $r^2=0.35$, $P=0.0061$ $\{Y= -0.37+ -0.12X\}$; −myc $r^2=0.46$, $P=0.001$ $\{Y= -0.45+ -0.14X\}$. C. *Epilobium angustifolium* in competition with *Epilobium angustifolium.* +myc $r^2=0.36$, $P=0.0054$ $\{Y= -0.42+ -0.076X\}$; −myc $r^2=0.32$, $P=0.010$ $\{Y= -0.16+ -0.045X\}$. D. *Epilobium angustifolium* in competition with *Hypochaeris radicata.* +myc $r^2=0.34$, $P=0.0067$ $\{Y=-0.53+ -0.16X\}$; −myc $r^2=0.45$, $P=0.0012$ $\{Y= -0.27+ -0.10X\}$.

al. 1973, Allen and Allen 1986, Fitter 1986, Smith et al. 1986, Anderson and Liberta 1989).

Experiment II

The presence or absence of mycorrhizae can alter the competitive outcome between plants and influence competitive hierarchies (Grime et al. 1987, Hetrick et al. 1989, Hartnett et al. 1993). Unlike other studies on mycorrhizal-mediated competition, which involve a facultative mycotrophic species versus an obligately mycotrophic species (Fitter 1977, Hetrick et al. 1989, Hartnett et al. 1993) or between obligately mycotrophic species (Allen and Allen 1990), this study utilized three facultatively mycotrophic species and one non-mycotrophic species. The facultative nature is evidenced by the lack of a significant biomass response to the mycorrhizal condition when grown alone or with conspecifics, and by the absence of significant differences in competitive intensity between mycorrhizal and non-mycorrhizal treatments. However, species vary in their degree of facultativeness. Some species may be slightly more dependent or better able to take advantage of the VAM

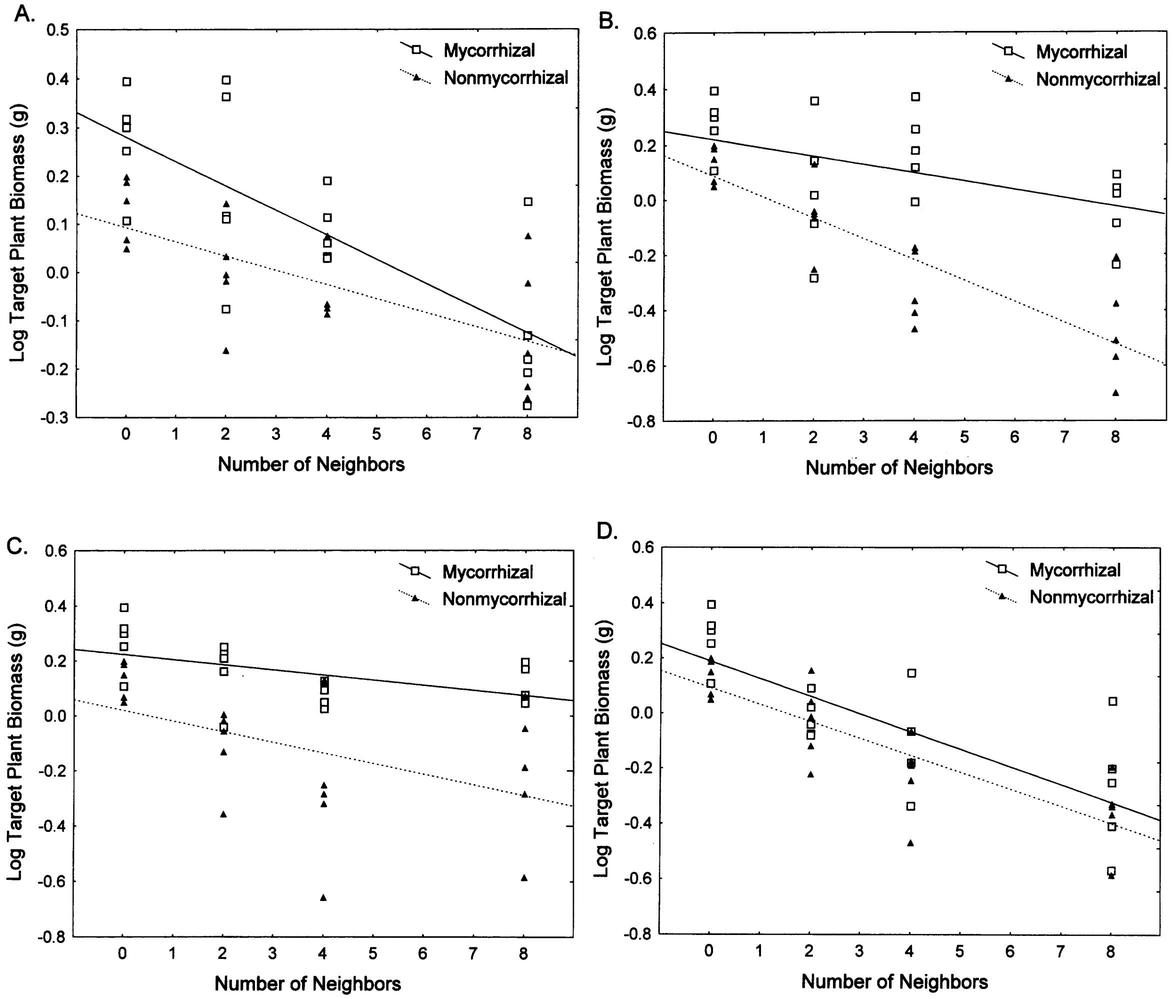


Fig. 5. The relationship between log target plant biomass and number of neighbors. Open squares and solid lines indicate the inoculated with mycorrhizae (+myc) treatments. Closed triangles and dashed lines indicate the not inoculated with mycorrhizae (−myc) treatments. Equations of the lines are in braces. A. *Hypochaeris radicata* in competition with *Anaphalis margaritacea*. +myc $r^2=0.60$, $P=0.0001$ $\{Y=0.29+-0.052X\}$; −myc $r^2=0.45$, $P=0.0013$ $\{Y=0.093+-0.029X\}$. B. *Hypochaeris radicata* in competition with *Carex mertensii*. +myc $r^2=0.0099$, $P=0.68$ $\{Y=0.097+-0.010X\}$; −myc $r^2=0.73$, $P=0.0000$ $\{Y=0.086+-0.076X\}$. C. *Hypochaeris radicata* in competition with *Epilobium angustifolium*. +myc $r^2=0.26$, $P=0.022$ $\{Y=0.22+-0.019X\}$; −myc $r^2=0.23$, $P=0.033$ $\{Y=0.020+-0.039X\}$. D. *Hypochaeris radicata* in competition with *Hypochaeris radicata*. +myc $r^2=0.58$, $P=0.0001$ $\{Y=0.18+-0.063X\}$; −myc $r^2=0.68$, $P=0.0000$ $\{Y=0.093+-0.062X\}$.

symbiosis than others. Thus, a hierarchy of increasing mycorrhizal dependence (or decrease in parasitic relationship) is seen here. *Carex* was the least mycotrophic species, as evidenced by greater biomass and greater competitiveness under non-mycorrhizal conditions. *Epilobium angustifolium* is facultatively mycotrophic and had greater biomass under non-mycorrhizal conditions. *Anaphalis* had greater biomass under mycorrhizal conditions than under non-mycorrhizal conditions. *Hypochaeris* had greater biomass and was more competitive under mycorrhizal conditions. The significant effect on competitive intensity between *Hypochaeris* and *Carex* illustrates the difference in competition between the species at opposite ends of the hierarchy. VAM, therefore, can have a significant effect on competition between facultative and non-mycotrophic species at low nutrient levels. VAM may be one of many interacting factors determining competitive dominance and species change over successional time.

Target species responded differently to VAM colonization under varying competitive scenarios. *Anaphalis* had the lowest colonization when in competition with the non-mycotrophic *Carex* and highest with *Hypochaeris*. This supports the idea of greater colonization by VAM fungi when more mycotrophic hosts are available (Hartnett et al. 1993). The remaining species were influenced by density, i.e., colonization was greater without competitors. Competition may reduce VAM colonization due to reduced vigor of the host plant and reduced quantity of photosynthate to translocate (Koide 1991a, Hartnett et al. 1993). In addition, the interaction effects illustrate that the change in biomass across neighbor densities differs between the mycorrhizal and non-mycorrhizal treatments. Plant density is an important factor that influences the degree of benefit derived from mycorrhizae by the host plant (Hetrick et al. 1989, Koide 1991a, b, Carey et al. 1992). For example, Hartnett et al. (1993) found that mycorrhizae were beneficial to a mycotrophic species at low densities, but increased competitive effects of high neighbor densities overrode the mycorrhizal effect. As succession proceeds, changes in plant densities and neighbor identity will influence the effects of VAM on the host plant.

Conclusion

In general, at very low nutrient levels the role of VAM is negligible. As nutrients increase, a positive effect of VAM is observed and the difference in biomass between mycorrhizal and non-mycorrhizal plants increases. These results imply that as soil amelioration continues on the Pumice Plain, VAM will assume a more important role in plant growth for some facultatively mycotrophic species. However, as VAM fungal propagules enter the environment, pathogenic fungi are bound to increase as well making the positive effect of VAM on plant growth difficult to assess.

When *Hypochaeris* competes with *Carex*, the presence of mycorrhizae changes competitive intensity. In the field, however, it is unlikely that competitive dominance is dependent solely upon mycorrhizal associations. Mycorrhizae probably interact in important ways with other factors. As primary succession proceeds the role of VAM in the mediation of competitive outcomes is predicted to increase.

The mycorrhizal mutualism is an intensive investment for a plant. At this early stage in primary succession on Mount St. Helens with nutrients levels still low, there are no strongly evident VAM effects that can be derived from this greenhouse experiment. VAM effects are weak and contingent on at least neighbor identity and density and soil nutrient availability. As yet VAM are unlikely to alter species competitive outcomes or survival of individuals in the field.

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References

Allen, E. B. and Allen, M. F. 1986. Water relations of xeric grasses in the field: interactions of mycorrhizae and competition. – New Phytol. 104: 559–571.

– and Allen, M. F. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. – In: Grace, J. B. and Tilman, J. D. (eds.), Perspectives on plant competition. Academic Press, New York, pp. 367–389.

Allen, M. F. 1991. The ecology of mycorrhizae. – Cambridge Univ. Press, New York.

– , Allen, E. B. and Friese, C. F. 1989. Responses of the non-mycotrophic plant *Salsola kali* to invasion by vesicular-arbuscular mycorrhizal fungi. – New Phytol. 111: 45–49.

– , Crisafulli, C., Friese, C. F. and Jeakins, S. L. 1992. Re-formation of mycorrhizal symbioses on Mount St. Helens, 1980–1990: interactions of rodents and mycorrhizal fungi. – Mycol. Res. 96: 447–453.

Anderson, R. C. and Liberta, A. E. 1989. Growth of little bluestem (*Schizachyrium scoparium*) (Poaceae) in fumigated and nonfumigated soils under various inorganic nutrient conditions. – Am. J. Bot. 76: 95–104.

Boerner, R. E. J. 1992. Plant life span and response to inoculation with vesicular-arbuscular mycorrhizae. II. Species from weakly mycotrophic genera. – Mycorrhiza 1: 163–167.

Brundrett, M. C., Melville, L. and Peterson, L. 1994. Practical methods in mycorrhiza research. – Mycologue Publ., Guelph, Ontario.

Carey, P. D., Fitter, A. H. and Watkinson, A. R. 1992. A field study using the fungicide benomyl to investigate the effect of mycorrhizal fungi on plant fitness. – Oecologia 90: 550–55.

Chapin, D. M. 1995. Physiological and morphological attributes of two colonizing plant species on Mount St. Helens. – Am. Midl. Nat. 133: 76–87.

Colwell, W. E. 1943. A biological method for determining the relative boron content of soils. – Soil Sci. 56: 71–94.

del Moral, R. and Bliss, L. C. 1993. Mechanisms of primary succession: insights resulting from the eruption of Mount St. Helens. – Adv. Ecol. Res. 24: 1–66.

Fitter, A. H. 1977. Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. – New Phytol. 79: 119–125.

– 1986. Effect of benomyl on leaf phosphorus concentration in alpine grasslands: a test of mycorrhizal benefit. – New Phytol. 103: 767–776.

– 1989. The role and ecological significance of vesicular-arbuscular mycorrhizas in temperate ecosystems. – Agric. Ecosyst. Environ. 29: 137–151.

– and Nichols, R. 1988. The use of benomyl to control infection by vesicular-arbuscular mycorrhizal fungi. – New Phytol. 110: 201–206.

Goldberg, D. E. and Scheiner, S. M. 1993. ANOVA and ANCOVA: field competition experiments. – In: Scheiner, S. M. and Gurevitch, J. (eds), Design and analysis of ecological experiments. Chapman and Hall, New York, pp. 69–93.

Grime, J. P., Mackey, J. M. L., Hillier, S. H. and Read, D. J. 1987. Floristic diversity in a model system using experimental microcosms. – Nature 328: 420–422.

Hartnett, D. C., Hetrick, S. A. D., Wilson, G. W. T. and Gibson, D. J. 1993. Mycorrhizal influence on intra- and interspecific neighbor interactions among co-occurring prairie grasses. – J. Ecol. 81: 787–795.

Hattingh, M. J., Gray, L. E. and Gerdemann, J. W. 1973. Uptake and translocation of ^{32}P phosphate to onion roots by endomycorrhizal fungi. – Soil Sci. 116: 383–387.

Hetrick, B. A. D., Kitt, D. G. and Wilson, G. T. 1986. The influence of phosphorus fertilization, drought, fungal species, and nonsterile soil on mycorrhizal growth response in tallgrass prairie plants. – Can. J. Bot. 64: 1199–1203.

– , Wilson, G. W. T. and Hartnett, D. C. 1989. Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. – Can. J. Bot. 67: 2608–2615.

Johnson, N. C., Zak, D. R., Tilman, D. and Pfleger, F. L. 1991. Dynamics of vesicular-arbuscular mycorrhizae during old field succession. – Oecologia 86: 349–358.

Keddy, P. A. 1989. Competition. – Chapman and Hall, New York.

Koide, R. T. 1991a. Nutrient supply, nutrient demand and plant response to mycorrhizal infection. – New Phytol. 117: 365–386.

– 1991b. Density-dependent response to mycorrhizal infection in *Abutilon theophrasti* Medic. – Oecologia 85: 389–395.

– and Elliot, G. 1989. Cost, benefit and efficiency of the vesicular-arbuscular mycorrhizal symbiosis. – Funct. Ecol. 3: 252–255.

Mullen, R. B. and Schmidt, S. K. 1993. Mycorrhizal infection, phosphorus uptake, and phenology in *Ranunculus adoneus*: implications for the functioning of mycorrhizae in alpine systems. – Oecologia 94: 229–234.

Norusis, M. J. 1993. SPSS for Windows Base System User's Guide Release 6.0. – Prentice-Hall, Upper Saddle River, NJ.

Paul, N. D., Ayers, P. G. and Wyness, L. E. 1989. On the use of fungicides for experimentation in natural vegetation. – Funct. Ecol. 3: 759–769.

Schwab, S. M., Menge, J. A. and Leonard, R. T. 1983. Comparison of stages of vesicular-arbuscular mycorrhizae formation in sudangrass grown at two levels of phosphorus nutrition. – Am. J. Bot. 70: 1225–1232.

Smith, S. E, St. John, B. J., Smith, F. A. and Bromley, J. L. 1986. Effects of mycorrhizal infection on plant growth, nitrogen and phosphorus nutrition in glasshouse-grown *Allium cepa* L. – New Phytol. 103: 359–373.

Sparling, G. P. and Tinker, P. B. 1978. Mycorrhizal infection in Pennine grassland. I. Levels of infection in the field. II: effects of mycorrhizal infection on the growth of some upland grasses on gamma-irradiated soil. – J. Appl. Ecol. 15: 943–964.

Titus, J. H. and del Moral, R. 1998. The role of mycorrhizae in primary succession on Mount St. Helens. – Am. J. Bot. (in press).

Turkington, R. L. and Aarssen, L. W. 1983. The biological flora of the British Isles: *Hypochaeris radicata*. – J. Ecol. 71: 999–1022.

Zar, J. H. 1984. Biostatistical analysis. 2nd ed. – Prentice-Hall, Englewood Cliffs, NJ.