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THE ROLE OF MYCORRHIZAL FUNGI AND MICROSITES IN PRIMARY SUCCESSION ON MOUNT ST. HELENS[1]

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This study was designed to examine the role of vesicular-arbuscular mycorrhizae (VAM) and microsites on the growth of pioneer species. Flat, rill, near-rock, and dead lupine microsites were created in plots in barren areas of the Pumice Plain of Mount St. Helens. VAM propagules were added to the soil in half of the plots. Six pioneer species were planted into both VAM and non-VAM inoculated microsites. Plants in dead lupine microsites were greater in biomass than those in flat, rill, and near-rock microsites. Significant effects of VAM on plant biomass did not occur. Microsites continue to be important to plant colonization on the Pumice Plain, but VAM do not yet appear to play an important role. This may be due to limited nutrient availability and the facultatively mycotrophic nature of the colonizing plant species. It is unlikely that VAM play an important role in successional processes in newly emplaced nutrient-poor surfaces.

Key words: lupine; microsites; Mount St. Helens; pioneer species; vesicular-arbuscular mycorrhizae; volcanoes.

In the stressful environments on Mount St. Helens it is known that microsite patterns play a crucial role in plant colonization (del Moral and Bliss, 1993). However, little is known about how vesicular-arbuscular mycorrhizae (VAM) affect primary successional processes on volcanic surfaces. This study was conducted to determine the role of VAM in plant growth on Mount St. Helens and how they may interact with microsites prevalent on barren surfaces.

During primary succession on new volcanic substrates, pioneer species are expected to be nonmycorrhizal (Allen 1991). Only nonmycotrophic and facultatively mycorrhizal species usually inhabit these sites. Obligately mycotrophic species would be prevented from establishing in a site until a population of VAM fungi had built up. Thus, the seral sequence could reflect the mycorrhizal dependencies of the colonizing species, and the rate of succession may be related to the increase of mycorrhizal inoculum over time. Species of early-successional stages are nonmycotrophic, followed by facultatively mycotrophic species in the intermediate stages of succession, and obligately mycotrophic species dominate later seral communities (Doerr, Redente, and Reeves 1984; Gange, Brown, and Farmer, 1990; Allen, 1991; Boerner, 1992).

Although mycorrhizae are considered to be important determinants of plant successional sequences, our knowledge of their role during early primary succession is scant. Also, the dispersal patterns of mycorrhizal fungi onto barren, new landscapes and the influence these patterns have on initial establishment have received little study (Allen, 1987). The nutrient-poor conditions of volcanic primary successional sites may preclude an active role by mycorrhizae in early primary succession. The mycorrhizal asssociation has been found to be neutral or even detrimental to the host plant in nutrient-poor environments (Fitter, 1986; Anderson and Liberta, 1989; Allen, 1991).

On Mount St. Helens microsite patterns play an important role in plant colonization processes (del Moral and Wood, 1993). Pioneers do not establish randomly on new barren sites. Favorable microsites clearly are the loci of invasion and colonizing species establish significantly more often on some microsite types than on others. The harshness of conditions on exposed posteruption surfaces is emphasized by the fact that while most seedlings are strongly associated with specific microsites, most microsites are devoid of seedlings (del Moral and Bliss, 1993). Microclimatic features may be moderated in microsites. For example, rills may be moister due to longer snow retention and rocks are shadier on their north side. These patterns are becoming less apparent on the Pumice Plain as plants spread out from initial loci and amelioration of harsh sites proceeds. Amelioration gradually improves all sites and obviates the need for certain microsites by certain species. Seedling establishment is enhanced by any factor that reduces drought stress and increases nutrient uptake (del Moral and Bliss, 1993).

Field tests of VAM benefits are rare due to the difficulty of obtaining appropriate nonmycorrhizal controls. Mine spoils are an environment analogous to Mount St. Helens because VAM fungal propagules are infrequent or nonexistent (Medve, 1984; Jasper, Robson, and Abbott, 1988). However, plants that colonize these wastes are often found to have normal VAM colonization levels (Stahl, Williams, and Christensen, 1988; Diaz and Honrubia, 1994). This suggests that VAM colonization is beneficial for plants that colonize these sites. VAM colonization of plants on spoils has been found to improve plant survival and growth (Lambert and Cole, 1980; Call and Davies, 1988). In areas that have lost their mycorrhizal inoculum due to disturbance such as strip mining, the addition of stored topsoil is a common way to restore

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mycorrhizal inoculum (Zak and Parkinson, 1983; Gardner and Malajczuk, 1988). In this study the addition of topsoil was the approach used to add inoculum into a VAM-free environment.

MATERIALS AND METHODS

Study site—The Pumice Plain was formed by the 18 May 1980 eruption of Mount St. Helens (46°12′N, 122°11′W). The Pumice Plain covers 20 km^2 immediately north of the crater between 1150 and 1300 m elevation. It was formed by deposits of material from a debris avalanche, subsequent pyroclastic flows, and air-fall pumice, and was repeatedly impacted by later mud flows. The Pumice Plain is blanketed by pumice that ranges in depth from 10 to 200 m. The surface is flat or gently sloping, with numerous gullies created by erosion dissecting the surface. Surface pumice particles range in size from 1 mm to 10 cm (del Moral and Bliss, 1993). This study was conducted on a portion of the Pumice Plain that escaped the debris avalanche but was affected by the blast, later pyroclastic flows and air-fall pumice deposits (del Moral and Bliss, 1993).

The climate is maritime, with cool, wet winters and warm, dry summers. Periods of drought often occur in July and August. Annual precipitation averages 237 cm, yet usually <5% of this falls between June and August. The growing season begins by June and ends by early September. Air temperatures range from mean monthly minima of −4.2°C in January and 7.3°C in August to maxima of 0.5°C in January and 22.2°C in July (Spirit Lake Ranger Station [987 m above sea level], Pacific Northwest River Basins Commission 1969). Summer temperatures range from 0° to 35°C with a mean of ~12°C. Surface soil temperatures are often very high in the summer, approaching 50°C on tephra surfaces (Reynolds and Bliss, 1986).

Pumice Plain soil is immature and extremely nutrient poor, with very low concentrations of C, N, and microbial biomass (del Moral and Bliss, 1993). Considerable variation in soil moisture values has been recorded between and within microsites. Substrates with fine particles contain more moisture than areas with coarse particles and erosion rills are more moist than other microsites (del Moral and Bliss, 1993). In summer the surface tephra dries quickly between rains, thus most Pumice Plain habitats do not remain moist for periods sufficient to allow seedling establishment. However, the surface layer of tephra acts as a mulch to impede evaporation and is capable of holding considerable moisture at lower depths so that adult plants rarely suffer from drought (Reynolds and Bliss, 1986).

Design—Fifteen plots were established in particularly barren areas on the Pumice Plain in order to reduce the risk that VAM propagules were present. Each plot consisted of two 13 by 7 m treatment subplots. One subplot was the inoculated mycorrhizal subplot and the other was the uninoculated nonmycorrhizal subplot. A buffer of at least 5 m separated subplots in order to avoid contamination of uninoculated quadrats (Allen and Allen, 1988). Each subplot consisted of 28 1-m^2 quadrats separated by 1 m, for a total of 56 quadrats per plot. Quadrats in inoculated subplots received soil containing mycorrhizal propagules and quadrats in uninoculated subplots received the same type and quantity of soil but after sterilization.

The mycorrhizal treatment was established by the addition of 1000 g of soil from Bear Meadow (located 10 km northeast of the Pumice Plain, outside the blast zone, at a similar elevation as the Pumice Plain) to each quadrat to provide VAM inoculum. The soil in each quadrat was removed to a depth of 1 cm and a 0.5-cm thick layer of Bear Meadow soil was spread over the center 0.25 m^2 of each quadrat. The original 1 cm layer of soil was then replaced. For the nonmycorrhizal treatment Bear Meadow soil was steamed for 15 min, cooled, transported to the field and added to the quadrats in the uninoculated subplots. Steaming effectively eliminated mycorrhizal inoculum potential (Titus, 1995). The soil additions represent a slight nutrient input into all the quadrats. Only one morphological spore type was found in Bear Meadow soil (14.6 ± 13.9 spores per 100 mL soil, determined to be *Glomus macrocarpum* (Tul. & Tul) (Titus, 1995). Mycotrophic species collected at Bear Meadow were VAM colonized, and in the greenhouse plants were readily VAM colonized when grown in Bear Meadow soil. The addition of this soil to the quadrats added organisms other than mycorrhizal fungi. Thus the plants in the inoculated quadrats had access to the full range of symbionts available in a native soil.

The following four microsites were incorporated into the study: (1) Flat included microsites that have homogeneous gravel, sand, or silt substrates and within which the topography is nearly flat. Pumice particles within this microsite are <5 cm in diameter. (2) Rills were small gullies formed by water erosion. These are linear habitats that offer marginal protection for seedlings from wind, collect more snow, and receive less solar radiation (del Moral and Bliss, 1993). Rill edges, where the seeds were planted, are more stable than rill bottoms and drainages. (3) Near-rock are microsites adjacent to rocks that are >20 cm in diameter. On exposed surfaces these rocks have the potential to protect seedlings from direct solar exposure, reduce wind and surface temperatures, and are more likely to trap seeds than are flat microsites. (4) Dead lupine patches are microsites located inside patches of dead *Lupinus lepidus* Douglas plants. Lupine patches are described in Morris and Wood (1989), del Moral and Bliss (1993), and del Moral, Titus, and Cook (1995).

The four microsites were incorporated into the study as follows: (1) excavation of small gullies to simulate rill microsites; (2) placement of two rocks in the quadrat to simulate near-rock microsites; and (3) placement of *Lupinus lepidus* into the quadrat to simulate adjacent-to-*Lupinus lepidus* microsites. *Lupinus lepidus* plants were washed and microwaved in order to prevent inocula transfer (Ferris, 1988; Clapperton and Reid, 1992). Flat microsites needed no modification.

Seeds of seven pioneer species were collected on the Pumice Plain during the summer of 1991. The seven species used were the facultatively mycotrophic *Anaphalis margaritacea* (L.) Benth & Hook., *Epilobium angustifolium* L., *Hieracium albiflorum* (L.) Benth & Hook., *Hypochaeris radicata* L., *Juncus parryi* Engelm., and *Penstemon cardwellii* Howell, and the nonmycotrophic *Carex mertensii* Prescott (Chapin, 1995; Titus, 1995).

Seeds were planted in the four microsites of the inoculated and uninoculated subplots for each treatment. They were planted in monocultures in the sampling quadrats at high densities in September 1991 to allow for natural stratification. To prevent density-dependent mortality, seedlings of *Penstemon* were thinned during the summer of 1992. Because seed establishment was poor for all other species, greenhouse-grown seedlings were planted in the quadrats. Seeds were planted in the University of Washington Botany Greenhouse in May 1992, and subsequently outplanted on 14 and 15 June 1992. Seedlings were watered at the time of outplanting. Each treatment quadrat contained four individual conspecific plants.

Survival and growth for each plant were recorded at the end of June, end of July, and end of August over two growing seasons. However, results of the growth data were similar to biomass and therefore are not discussed here.

At the end of the first growing season (11–12 September 1992) six plants of each species were harvested randomly from each treatment across the 15 plots. Roots were washed, cleared, and stained with trypan blue (Brundrett, Melville, and Peterson, 1994). Percentage VAM colonization was estimated by placing a grid of 1-cm squares below a petri plate that contained the root sample under a dissecting microscope. One hundred locations where 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 being colonized. The number of mycorrhizal "hits" is an estimate of percentage roots colonized (Brundrett, Melville, and Peterson, 1994).

After the second growing season, 11–13 September 1993, plants were

TABLE 1. Percentage VAM colonization in plots on the Pumice Plain. Inoculated = plots with soil containing mycorrhizal propagules added. Uninoculated = plots with sterilized soil added. Percentage plants colonized shows the percentage of plants that were VAM. Comparisons between microsites were conducted by the nonparametric Kruskal-Wallis test and comparisons between years were made by the nonparametric Wilcoxon paired-sample test. Values within each year with different superscripts were different at $\alpha = 0.05$. Asterisks indicate microsites that were different between years at $\alpha = 0.05$ (mean ± standard deviation, 1992 $N = 6$, 1993 $N = 15$).

		1992				1993			
		Inoculated		Uninoculated		Inoculated		Uninoculated	
Species	Microsite	% VAM colonization	% Plants colonized	% VAM colonization	% Plants colonized	% VAM colonization	% Plants colonized	% VAM colonization	% Plants colonized
Anaphalis margaritacea	Flat	10.4 ± 13.7[a]	100	0	0	6.5 ± 6.3[a]	79	0	0
	Rill	14.2 ± 16.7[a]	100	0	0	3.0 ± 5.9[a]	71	1.9 ± 6.9	7
	Near rock	14.3 ± 12.7[a]*	100	0	0	5.2 ± 6.3[a]*	71	2.5 ± 8.7	7
	Dead lupine	15.5 ± 14.7[a]	100	0	0	10.6 ± 14.4[a]	50	0.2 ± 0.8	7
Epilobium angustifolium	Flat	0.7 ± 1.2[a]	33	0	0	1.5 ± 2.5[a]	50	1.3 ± 3.6	14
	Rill	2.2 ± 2.4[a]	67	0	0	2.0 ± 4.3[a]	71	0	0
	Near rock	0.5 ± 0.8[a]	33	0	0	5.2 ± 6.7[a]	50	0	0
	Dead lupine	1.5 ± 2.0[a]	50	0	0	6.4 ± 11.5[a]	57	2.0 ± 4.8	21
Hieracium albiflorum	Flat	1.2 ± 0.4[a]	100	0	0	4.9 ± 7.8[a]	71	1.1 ± 2.9	14
	Rill	16.2 ± 23.1[b]	100	0	0	15.9 ± 21.9[a]	64	0.3 ± 0.8	14
	Near rock	1.5 ± 0.8[a]	100	0	0	16.0 ± 22.2[a]	71	1.5 ± 3.3	29
	Dead lupine	2.0 ± 0.9[a]	100	0	0	10.6 ± 14.4[a]	79	4.7 ± 8.5	36
Hypochaeris radicata	Flat	6.3 ± 7.2[a]	83	0	0	11.1 ± 11.9[a]	79	2.8 ± 4.9	29
	Rill	2.5 ± 2.9[a]*	67	0	0	18.7 ± 22.2[a]*	57	0.8 ± 2.8	14
	Near rock	6.3 ± 8.0[a]	67	0	0	9.9 ± 13.6[a]	50	2.3 ± 5.5	29
	Dead lupine	5.0 ± 8.4[a]	33	0	0	8.9 ± 9.8[a]	50	5.4 ± 13.4	29
Penstemon cardwellii	Flat	0.3 ± 0.5[a]	33	0	0	2.6 ± 4.2[a]	36	0	0
	Near rock	0.3 ± 0.5[a]	33	0	0	3.3 ± 6.2[a]	36	1.0 ± 3.7	7
	Dead lupine	8.5 ± 11.5[a]	50	0	0	9.5 ± 11.9[a]	71	0.4 ± 1.3	7

harvested, returned to the University of Washington, and frozen until processing. Plants were dried for 3 d at 80°C and root, shoot, and reproductive dry masses measured to the nearest 0.01 g. Prior to drying a uniform 0.10-g root sample was excised from one plant of each quadrat. For root systems that were <0.20 g, 20–50% of the root were removed for examination and the quantity recorded. VAM colonization was determined as above.

Data analysis—Mycorrhizal colonization levels for each species were contrasted across microsites in the mycorrhizal treatment subplots by the nonparametric Kruskal-Wallis test with chi-square correction for ties (Zar, 1984; Norusis, 1993). Post hoc tests were conducted by the nonparametric variant of Tukey's honestly significant difference test (Zar, 1984, p. 199). Mycorrhizal colonization levels between 1992 and 1993 were compared by the nonparametric Wilcoxon paired-sample test (Zar, 1984; Norusis, 1993). This test was used because plants collected from the same plots were compared between 1992 and 1993. This test calculates and ranks the raw differences between the two years.

Biomass was log transformed to improve normality and homoscedasticity. Data were analyzed by two-way ANOVA to analyze mycorrhizal and microsite treatments for each species, blocking for plot to remove differences between plots (Zar, 1984; Norusis, 1993). Post hoc tests were conducted with Tukey's honestly significant difference test.

RESULTS

Plant survival—Survival of the outplanted seedlings was >95% for the first growing season (summer of 1992) and >99% of those survived through the second growing season (summer of 1993). The exceptions were *Juncus,* which had very low survival in all microsites (4%) and in the greenhouse (5%), and *Penstemon,* which had very low survival in rills (9%). *Juncus* was removed from the analysis of the experiment as was the rill treatment for *Penstemon.* Insect herbivory was common on the study plants, but no sign of mammal herbivory was observed.

Mycorrhizal colonization—At the end of the first growing season (1992), mycorrhizal colonization was nonexistent in the nonmycorrhizal treatment subplots (Table 1). Except for *Carex,* all species in the mycorrhizal treatment subplots were mycorrhizal. The predominant VAM structure observed was hyphae; arbuscles and vesicles were infrequent. There were no significant differences in VAM colonization levels between microsites for any species except for *Hieracium* where plants in rill microsites were significantly more colonized than in the other microsites (Table 1).

By the end of the second growing season (1993), mycorrhizal colonization was low but present in the nonmycorrhizal treatment subplots (Table 1). About 13% of the nonmycorrhizal quadrats had become colonized after 2 yr. In the mycorrhizal treatment subplots, *Carex* remained the only uncolonized species. Mycorrhizal colonization levels were not significantly different between microsites for any species in 1993.

Overall colonization levels decreased significantly from 1992 to 1993 for *Anaphalis* and increased significantly for *Hypochaeris.* The changes in VAM colonization were not significant for the other species. There were significant changes at the microsite level from 1992 to 1993 in two cases. Mycorrhizal colonization decreased significantly for *Anaphalis* at near-rock microsites and increased significantly for *Hypochaeris* at rill microsites.

Biomass—Results for root and shoot biomass were not different from total biomass in any meaningful way and root:shoot ratio results were not significant. Therefore only total biomass is discussed here.

All species had significantly greater biomass in dead lupine microsites (Table 2). Near-rock and rill microsites

TABLE 2. ANOVA tables for log biomass under four microsite and two mycorrhizal treatments. Post hoc shows the results of a Tukey's honestly significant difference test at $\alpha = 0.05$ ($N = 15$).

Species	Source	df	F	P	Post hoc[a]
Anaphalis margaritacea	Microsite	3	12.25	0.000	2 = 1 = 3 < 4
	Mycorrhizae	1	1.32	0.254	
	Interaction	3	1.40	0.248	
	Plot	14	2.20	0.031	
Carex mertensii	Microsite	3	30.03	0.000	1 = 3 < 2 < 4
	Mycorrhizae	1	0.12	0.735	
	Interaction	3	0.64	0.590	
	Plot	14	2.34	0.012	
Epilobium angustifolium	Microsite	3	44.88	0.000	1 < 3 = 2 < 4
	Mycorrhizae	1	0.42	0.520	
	Interaction	3	0.68	0.566	
	Plot	14	0.56	0.879	
Hieracium albiflorum	Microsite	3	10.44	0.000	1 = 3 = 2 < 4
	Mycorrhizae	1	1.57	0.214	
	Interaction	3	0.22	0.884	
	Plot	14	1.12	0.370	
Hypochaeris radicata	Microsite	3	12.93	0.000	1 = 2 < 4, 3 < 2, 1 = 3
	Mycorrhizae	1	3.12	0.080	
	Interaction	3	0.40	0.757	
	Plot	14	3.64	0.000	
Penstemon cardwellii	Microsite	2	57.07	0.000	1 < 3 < 4
	Mycorrhizae	1	0.77	0.384	
	Interaction	2	0.30	0.739	
	Plot	14	1.44	0.197	

[a] Codes for post hoc analysis. Microsite treatment: 1 = flat microsite, 2 = rill microsite, 3 = near-rock microsite, 4 = dead lupine microsite. Mycorrhizae treatment: 1 = soil containing VAM propagules added, 2 = sterilized soil added.

were either second or third in biomass, and plants were smallest in flat microsites.

Significant differences in biomass between mycorrhizal and nonmycorrhizal treatments did not occur, although trends were for nonmycorrhizal treatment plants to be greater in biomass than mycorrhizal treatment plants.

Plot effects—The biomass tests had the plot effect removed as a treatment. Therefore, whether or not there was a significant plot effect on plant biomass was assessed. Plot effects were significant for *Anaphalis, Carex,* and *Hypochaeris.* That is, the plot in which the plant was located had a significant influence on plant biomass. This means that there were most likely significant environmental differences between plots.

DISCUSSION

Morris and Wood (1989) used transplanted seedlings to study the role of lupine mounds in succession at Mount St. Helens. The survival rates in their studies were much lower than the >95% survival of transplants in this experiment (with the exception of *Juncus*). Their low survival rates may be explained by the fact that the summers of 1986–1988 were much drier than 1992–1993 (National Climatic Data Center, 1980–1994). In addition, Mount St. Helens substrates have undergone extensive amelioration in the 5 yr between the two experiments (del Moral and Bliss, 1993). The combination of greater moisture and substrate amelioration may have yielded the high survival rates observed in this experiment.

Nonmycorrhizal subplots remained largely nonmycorrhizal throughout the experiment. However, contamination is underestimated because not all plants would be colonized by VAM fungi. VAM propagules are quite large (Schenck and Perez, 1990) and have poor dispersal abilities (Allen, 1987; Mott and Zuberer, 1987). However, propagules did immigrate to the uninoculated subplots. The most likely vectors are wind and water erosion, however animal dispersal is a possibility (Allen, 1991).

Facultative mycotrophic plants in the mycorrhizal treatments were colonized in this experiment even though conditions on Mount St. Helens are harsh and nutrient levels low. Mycorrhizal colonization was not greater in the less stressful microsites. However, this does not mean that the role of VAM in the different microsites is the same even though colonization levels were similar. Physiological interactions between VAM fungi and the plant may create different relationships at different microsites, even though VAM colonization levels for a given length of root are similar. The only significant difference in mycorrhizal colonization across microsites was observed in *Hieracium* in 1992, where plants in rill microsites were more colonized than in the other microsites. There is no apparent reason for this result.

The level of mycorrhizal colonization commonly changes over short time periods (Sanders, 1993). VAM colonization levels decreased in *Anaphalis* and increased in *Hypochaeris* from 1992 to 1993. These changes in VAM colonization levels may be only an instantaneous view of constantly changing colonization levels or parts of long-term trends.

Differences in the mycorrhizal treatment (across all microsites) reflect a trend for greater biomass in the nonmycorrhizal treatments. The presence of VAM fungal propagules and their colonization of plants had either a negligible or slightly negative effect on plant growth. VAM may be acting in a parasitic fashion on these plants

in this extremely nutrient-poor environment (Fitter, 1986; Anderson and Liberta, 1989; Allen, 1991). Thus, the nutrient-poor conditions of volcanic primary successional sites precludes an active role by mycorrhizae in early primary succession. Over successional time soil amelioration, increased plant density, and other successional processes interact to influence the role of mycorrhizae. Due to these processes the importance of mycorrhizae is expected to increase over time.

VAM fungal species vary in their potential effects on plant growth (Sanders and Fitter, 1992). Bear Meadow soil was found to contain only one morphological spore type (Titus, 1995). It is possible that if a different spore type or a more diverse assemblage of types were used in this study a more dramatic response (either positive or negative) of the plants to the VAM fungi may have been observed.

It is unlikely that the addition of sterilized soil to the nonmycorrhizal plot created the trend in greater biomass of non-VAM plants observed over the 2-yr period. However, autoclaving of soil does change soil nutrient status and a similar effect could be achieved from steaming. Therefore, altered nutrients cannot be ruled out as a cause. This experiment did not have control plots in the sense of Amaranthus and Trappe (1993), i.e., plots without sterilized soil amendments. Therefore, it is impossible to gauge the effect of the sterilized soil amendments on plant growth.

It is clear that microsites are important to colonization on the Pumice Plain. This was seen by the dramatic differences in biomass in dead lupine sites in comparison to the other microsites and also the significant differences in biomass that occurred between the other microsites.

The magnitude of the significant plot effects observed was unexpected since plots appear to be identical on the Pumice Plain. However, plots were geographically separated and environmental conditions may have varied between plots. Differences in environmental conditions may influence plant growth and the effect of microsite and VAM upon the host plant. The three species that did not show significant plot effects may be less sensitive to the environmental differences between plots or the variance was too large for a plot effect to be detected (Dutilleul, 1993; Legendre, 1993).

These results show that microsites are important to colonization on the Pumice Plain. The lack of a clear mycorrhizal effect leads to the conclusion that VAM are as yet to play an important role in the succession. This may be due to the nutrient-poor harsh environmental conditions of the Pumice Plain and the facultative nature of the invading plant species. With further substrate amelioration and the invasion of species with greater VAM dependency, VAM should assume greater importance in successional dynamics.

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