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THE ROLE OF LUPINE IN SUCCESSION ON MOUNT ST. HELENS: FACILITATION OR INHIBITION?[1]

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Abstract. The barren landscape created on the north side of Mount St. Helens (Washington State, USA) by the 1980 eruption provides an excellent setting in which to examine the role of pioneer species in facilitating or inhibiting subsequent invaders in primary succession. We investigated the influence of *Lupinus lepidus,* a nitrogen-fixing pioneer species, on two invading species, *Anaphalis margaritacea* and *Epilobium angustifolium.* Seedlings of both invaders were initiated in the greenhouse and transplanted to four field treatments: (1) control (plots devoid of lupine), (2) live (plots with vigorous lupine), (3) mulch (lupines herbicided but left in place), and (4) no-mulch (lupines herbicided and dead aboveground biomass removed).

Patches of *L. lepidus* exerted both facilitative and inhibitory effects on the other species. First season survivorship of seedlings planted into lupine patches was generally lower than that of seedlings planted into barren control plots. However, for both *A. margaritacea* and *E. angustifolium,* surviving seedlings within lupine patches grew larger than did controls. In addition, *A. margaritacea* seedlings had a much higher probability of flowering when planted within lupine patches. Comparisons among treatments indicated that both substrate alteration and the mulching effect of lupine litter mediated the effects of lupine patches on transplant performance.

Our results show that both facilitation and inhibition occurred, but at different stages in the life cycle of invading species. Consequently, a complete demographic model may be needed in order to assess the net effect of a pioneer on its successors.

Key words: Anaphalis margaritacea; *colonization;* Epilobium angustifolium; *facilitation; inhibition; invasion;* Lupinus lepidus; *Mount St. Helens; pioneer species; primary succession.*

INTRODUCTION

The past decade has witnessed a flourishing of experimental studies designed to determine whether early successional species facilitate, inhibit, or have no effect upon their successors (Sousa 1979, Dean and Hurd 1980, Hils and Vankat 1982, Gallagher et al. 1983, Lubchenco 1983, Turner 1983, Burton and Mueller-Dombois 1984, Harris et al. 1984, Monk and Gabrielson 1985, Armesto and Pickett 1986, Walker and Chapin 1986). Most of the recent studies have emphasized secondary succession, which is more commonly encountered than primary succession in the anthropogenic landscapes accessible to most ecologists. However, studies of secondary succession may not provide an accurate portrayal of mechanisms operating in primary succession, where facilitation may be of greater importance (Connell and Slatyer 1977, Tilman 1988). Since experimental studies of facilitation and inhibi-

tion in primary succession are relatively scarce, we took advantage of the disturbance caused by the 1980 eruption of Mount St. Helens (Washington State, USA) to perform such an investigation.

We performed our experiments in the region most severely damaged by the eruption, the 20-km² barren landscape immediately north of the volcano known as the Pumice Plains. This region was initially buried by avalanche debris from the collapsed north side of the volcano and then blanketed by pyroclastic flows (mixtures of hot volcanic ash and pumice). Thus, in contrast with less devastated areas farther from the volcano where vegetation has reestablished rapidly from surviving seeds and root fragments (del Moral 1983), the Pumice Plains represents a true primary successional substrate.

We focussed on the effects of the perennial lupine *Lupinus lepidus* Dougl. on two other perennial species, pearly everlasting (*Anaphalis margaritacea* (L.) B. & H.) and fireweed (*Epilobium angustifolium* L.), which are the most common colonists on the Pumice Plains

(Wood and del Moral 1988). Lupine plants (which are nonclonal and attain a maximum height and diameter of ≈ 10 and 25 cm, respectively) are presently growing in dense, island-like patches which contrast sharply with the surrounding sea of mostly uncolonized pumice (Wood and del Moral 1988).

For several reasons, lupine might be expected to facilitate the establishment of other colonists. Pyroclastic substrate from the Pumice Plains has been shown to contain exceptionally low levels of nitrate (del Moral and Clampitt 1985). However, *L. lepidus* is a nitrogen-fixing legume, and the concentrations of ammonium and nitrate ions in the soil solution are an order of magnitude higher within lupine patches than at barren sites on the Pumice Plains (Nuhn 1987). Thus, lupines may facilitate other species by ameliorating edaphic conditions. In addition, shading or mulching by *L. lepidus* might facilitate colonization by ameliorating conditions of high surface temperature and low moisture availability which typically prevail in July and August (Reynolds and Bliss 1986). That is, lupine might exert "nurse plant" effects (Niering et al. 1963) that have been shown to promote colonization elsewhere on Mount St. Helens (Wood and del Moral 1987).

On the other hand, two observations suggest possible inhibitory effects of lupines: (1) several large lupine patches have persisted as virtual monocultures for >2 yr, and (2) the spatial distributions of *A. margaritacea* and *E. angustifolium* in a large region of the Pumice Plains were not correlated with the distribution of *L. lepidus* (Wood and del Moral 1988).

To clarify the role *L. lepidus* will play in the ongoing colonization of the Pumice Plains, we conducted seedling transplant experiments to determine whether colonization within lupine patches is enhanced, unaffected, or reduced relative to colonization of barren substrate.

METHODS

General methods

We performed two seedling transplant experiments at Mount St. Helens in 1986 through 1988. *Anaphalis margaritacea* and *Epilobium angustifolium* seedlings were grown from seeds collected in the autumn prior to the initiation of each experiment (i.e., at the time of natural dispersal) from sites adjacent to the Pumice Plains. All seedlings were initiated in a greenhouse on the University of Washington campus (30° day/22°C night, 12 h photoperiod) in 135-cm³ pots filled with a mixture of 25% peat and 75% pyroclastic substrate collected from the Pumice Plains. After 3 or 5 wk (Experiment 1 and 2, respectively), when seedlings had $\approx$ two or eight true leaves, they were moved outside for 1 wk for hardening off. Seedlings were then transplanted with the potting soil to randomly assigned treatment plots on the Pumice Plains and watered only on the day of planting.

Experiment 1: lupine effects on transplant survival

In late spring 1986, before lupines had fully leafed out, we randomly selected three distinct lupine patches 5–10 m in diameter which were located within a 2-ha region. Each block in our experiment consisted of a 2 × 3 m plot within one of the three lupine patches (lupine treatment) and an equal-sized plot centered within a 5 m radius of the patch in an uncolonized area (control treatment). During the 1st wk of June, 300 seedlings of each species were planted alternately into a square grid within each plot, with 10-cm spacing between adjacent seedlings. A total of 3600 seedlings was used in the experiment. Survival of seedlings was determined by monthly censuses.

At the initiation of the experiment, lupine patches varied both in the amount of invasion and vigor of the lupines. To quantify aboveground characteristics of the experimental lupine patches, two transects of 10 20 × 50 cm quadrats were laid through the section of each patch containing our experimental plots. Adjacent quadrats were 50 cm apart. For each quadrat, we recorded: (1) the percent cover of live lupines and of lupine litter, and (2) the percent cover of each invading species encountered in the quadrat (excluding experimental transplants).

Seedling survival at the end of one growing season was analyzed by one-way analysis of variance with treatment as the main effect. Four lupine patch characteristics (cover of live lupine, of lupine litter, and of all invading species combined, and species richness of invaders) were analyzed using one-way analysis of variance with patch as the main effect. Proportional survival and percent cover data were arcsine transformed prior to analysis to improve normality.

Experiment 2: effect of live vs. dead lupine

Seedling survival in Experiment 1 was lower in the two lupine patches dominated by live lupines than in the patch where a large fraction of the lupines had died (see Results). We hypothesized that live lupines would inhibit survival and growth of invaders but that dead lupines would improve invader performance. In addition, we wished to determine whether dead lupines facilitated colonizer success through belowground effects alone (e.g., by nitrogen addition), through the mulching effects of lupine litter (e.g., increased subsurface moisture), or both.

Four treatments (which we will refer to as control, live, mulch, and no-mulch) were used. Control treatment plots were again located on barren ground, within a 2 m radius of lupine patches. In live treatment plots, seedlings were planted into vigorous regions of lupine patches. In mulch treatment plots, lupines were sprayed with a nonpersistent herbicide (Ortho Kleenup, at 3 mL active ingredient [glyphosate] per litre) 3 wk before

seedling transplantation, and the resulting lupine litter was left in place. In no-mulch treatment plots, lupines were sprayed as in the mulch treatment, but all aboveground biomass was carefully removed using clippers.

The same three lupine patches were used in Experiment 2, although plots were located in regions of each patch not utilized in Experiment 1. In each patch, two plots were assigned to the live treatment and one plot to each of the remaining treatments (the unbalanced design resulted when an additional treatment was abandoned due to logistical difficulties). On 9 June 1987, 25 seedlings of each species were interplanted in each plot. In live treatment plots, each seedling was located within a 5 cm radius of a live lupine individual, but the 50 seedlings in each plot were confined to a 2 × 2 m area. In the remaining plots, seedlings were transplanted into a 9 × 6 grid centered within a 1 × 1 m plot, with 10-cm spacing between adjacent seedlings. Seedling survival was censused on 29 July and 10 October 1987 and on 22 September 1988. Three measures of transplant size (height, longest leaf length, and number of shoots at the base) and flowering stage (flowers present or absent) were quantified for all surviving seedlings at the end of each growing season.

We chose three response variables to analyze for treatment effects on transplant performance: (1) proportional survival per plot (from transplantation to the end of the first growing season and from the end of the first to the end of the second growing season); (2) the size of transplants at the end of each growing season; and (3) the proportion of the initial cohort in each plot that flowered by the end of each season. Since preliminary analysis indicated species differences in survival, growth, and flowering, the two species were analyzed separately.

The effects of treatments on survival and flowering were analyzed by one-way analysis of variance. To control for differences in plant size at the end of the first growing season, proportional survival during the second season was analyzed using one-way analysis of covariance with mean values of height, longest leaf length, and number of shoots (*A. margaritacea* only) in each plot at the end of the first season as covariates (number of shoots was not sufficiently variable in *E. angustifolium* to use as a covariate). Proportional survival and flowering were arcsine transformed prior to analysis to improve normality. To control for correlations among our measures of transplant size, size data were analyzed using one-way multivariate analysis of variance with height, leaf length, and shoot number as dependent variables.

In analyzing differences among treatment means, we limited the number of tests we performed by conducting three orthogonal planned comparisons using the survival, size, and flowering data. A comparison of control vs. combined lupine treatments was intended to detect an overall effect of lupines (live or dead) on the performance of invaders. A comparison of the

live treatment vs. the combined mulch and no-mulch treatments was performed to determine whether live lupines had a different effect on performance than dead lupines. Finally, a comparison between mulch and no-mulch treatments was intended to provide information about the cause of any dead lupine effects.

Because the data were unbalanced due to differential mortality (size data) and unequal number of replicates (survival, size, and flowering data), all analyses were performed using the SAS GLM Procedure. Reported *P* values were calculated using Type III sums of squares (SAS 1985).

RESULTS

Experiment 1: lupine effects on transplant survival

Seedling survival. — The effect of lupines on the survival of transplanted seedlings varied among lupine patches (Fig. 1). On average, only 0.33% of *Anaphalis margaritacea* seedlings and 0.17% of *Epilobium angustifolium* seedlings remained alive at the end of the season in lupine treatments in blocks 1 and 2, compared with 30% of *A. margaritacea* seedlings and 1.5% of *E. angustifolium* seedlings in the respective control plots. In block 3, however, the relationship between survival and treatment was reversed (Fig. 1): seedling survival was higher for both species in the lupine treatment than in the control. Because block 3 behaved differently than blocks 1 and 2, there was no overall treatment effect on first-season survival for either species.

By July of the following year, the apparent inhibitory effect of lupine patches on *A. margaritacea* was amplified in blocks 1 and 2. While an average of 12.5% of the initial cohort remained alive in the respective control plots, no seedlings survived in the lupine treatments. For *E. angustifolium,* all transplants in blocks 1 and 2 had died by July 1987, regardless of treatment. Thus, the initially higher survival of *E. angustifolium* seedlings in control vs. lupine plots from blocks 1 and 2 was a transient effect. Unfortunately, we were unable to quantify 1987 survival for either species in the lupine plot from block 3, since the surviving seedlings grew so large that we could not distinguish them from other large, nonexperimental plants that had invaded the third lupine patch in abundance (see below).

Characteristics of lupine patches. — Since survival in lupine patch 3 was strikingly different from the other two patches, we quantified several patch characteristics which, we hypothesized, could account for the observed difference. Transect data revealed that the third lupine patch differed significantly from the others both in the amount of invasion by nonexperimental plants and in the relative cover of dead vs. live lupines. Both the species richness and the combined percent cover of invading species were significantly higher in the third lupine patch than in the other two patches (Table 1).
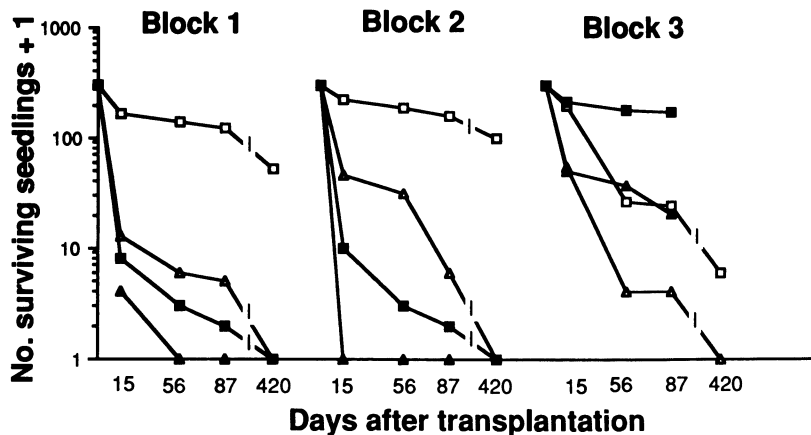
FIG. 1. Survivorship of transplanted seedlings in Experiment 1. Each experimental block consisted of a plot within a lupine patch and a plot in adjacent barren ground. □ = *Anaphalis margaritacea* in control plots; ■ = *A. margaritacea* in lupine plots; △ = *Epilobium angustifolium* in control plots; ▲ = *E. angustifolium* in lupine plots.

Thus, it appeared that survival and/or growth of natural colonists, like that of experimental seedlings, was enhanced in the third lupine patch. In addition, quadrats from the third patch had a significantly higher cover of dead lupine and a significantly lower cover of live lupine ($P < .0001$, Table 1).

Experiment 2: effect of live vs. dead lupine

Survival. — Contrary to our hypothesis that dead lupine would be facilitative but live lupine inhibitory, seedling survival through the first growing season was lower in all lupine treatments than in control plots (Fig. 2a). This difference was significant for *E. angustifolium* ($P = .017$). Although the difference was not quite significant for *A. margaritacea* ($P = .075$), the mean survivorship of *A. margaritacea* among treatments followed a pattern similar to *E. angustifolium* (Fig. 2a). Mean survival was lower in live than in dead lupine (mulch + no-mulch) treatments, but this difference was not significant, nor was the difference between mulch and no-mulch treatments for either species. Overall seedling survival was higher than in Experiment 1, probably because seedlings were larger at transplantation.

During the second growing season, the pattern of survival was reversed: control transplants survived less well than transplants in lupine treatments (Fig. 2b). For *A. margaritacea*, differences among treatments in transplant size after the first growing season (see below) explained differences in survival during the second season. Treatments had no significant effect on survival when the effects of plant size were factored out (ANCOVA treatment effect: $P = .59$). Treatments continued to contribute to second season survival of *E. angustifolium* even after their effects on transplant size were accounted for (ANCOVA treatment effect: $P = .033$).

Transplant size. — In contrast with the pattern ob-

served for seedling survivorship, surviving transplants grew more vigorously in lupine treatments than in controls. The means of all three measures of transplant size for *A. margaritacea* and of plant height and longest leaf length for *E. angustifolium* were consistently lower in control plots than in any of the lupine treatment plots (Fig. 3).

Planned comparisons using the multivariate growth data corroborated a higher increment of growth for seedlings within lupine patches. After one growing season, transplants were significantly larger (1) in controls than in combined lupine treatments ($P < .0001$ for both species); (2) when planted among dead lupines (mulch + no-mulch plots) than among live lupines ($P < .0001$ for *E. angustifolium* and $P < .0005$ for *A.*
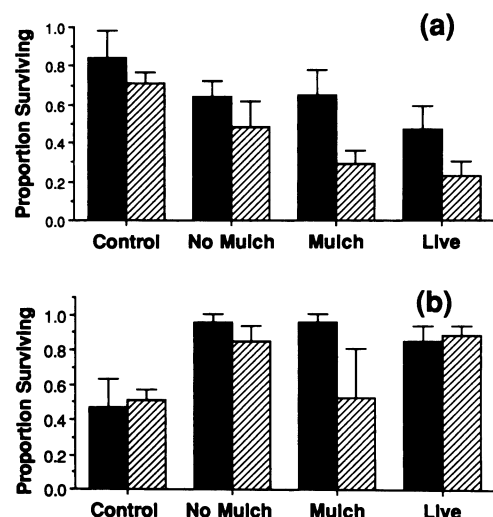

FIG. 2. Survivorship of transplanted seedlings in Experiment 2: (a) proportion of initial cohort surviving to end of first growing season; (b) proportion alive at end of first season surviving to end of second season (means + 1 SE). Dark bars = *Anaphalis margaritacea*; hatched bars = *Epilobium angustifolium*.

TABLE 1. Characteristics of lupine patches in Experiment 1. Data are means + 1 SE for 20 0.1-m² quadrats; P values for patch effects were obtained from one-way ANOVAs. Means sharing the same superscript are not significantly different (Bonferroni test, overall α = .05).

Lupine patch characteristic	Patch 1	Patch 2	Patch 3	Magnitude of patch effect
Species richness of invaders (species/0.1 m²)	0.0 + 0.0[a]	0.2 + 0.09[a]	1.6 + 0.18[b]	P < .0001
Cover of invaders (%)	0.0 + 0.0[a]	0.7 + 0.5[a]	11.5 + 2.3[b]	P < .0001
Cover of live lupine (%)	71.5 + 3.9[a]	76.4 + 4.6[a]	29.7 + 2.8[b]	P < .0001
Cover of lupine litter (%)	12.0 + 2.3[a]	8.5 + 2.4[a]	48.8 + 3.6[b]	P < .0001

margaritacea); and (3) for *A. margaritacea*, in mulched plots relative to unmulched plots (P < .001). These comparisons remained highly significant (P < .01) at the end of the second growing season, with the exception that the size of *E. angustifolium* transplants was no longer different in live vs. dead lupine plots (P = .11).

Flowering.—The proportion of *A. margaritacea* transplants flowering in the first growing season exhibited a pattern among treatments similar to transplant size but strikingly different from transplant survival (cf. Figs. 2–4). Significantly more *A. margaritacea* seedlings flowered by the end of 1987 in lupine treatments than in controls (P < .01). Transplants in dead lupine plots were more likely to flower than seedlings transplanted among live lupines (P < .01), and mulching

resulted in a significant increase in the probability of flowering compared to the no-mulch treatment (P < .01).

By the end of the second growing season, the probability of flowering for *A. margaritacea* was still significantly higher in lupine plots than in controls (Fig. 4b, P = .001), although the differences between live and dead lupine treatments, and between mulch and no-mulch treatments, were less pronounced (P = .058 and .69, respectively).

Few of the fireweed transplants flowered in the course of the study. Only a single fireweed individual flowered in 1987, so we could not assess the treatment effects on the proportion flowering in the first season. Treatments had no significant effect on the proportion flowering by the end of the second season (P = .62).
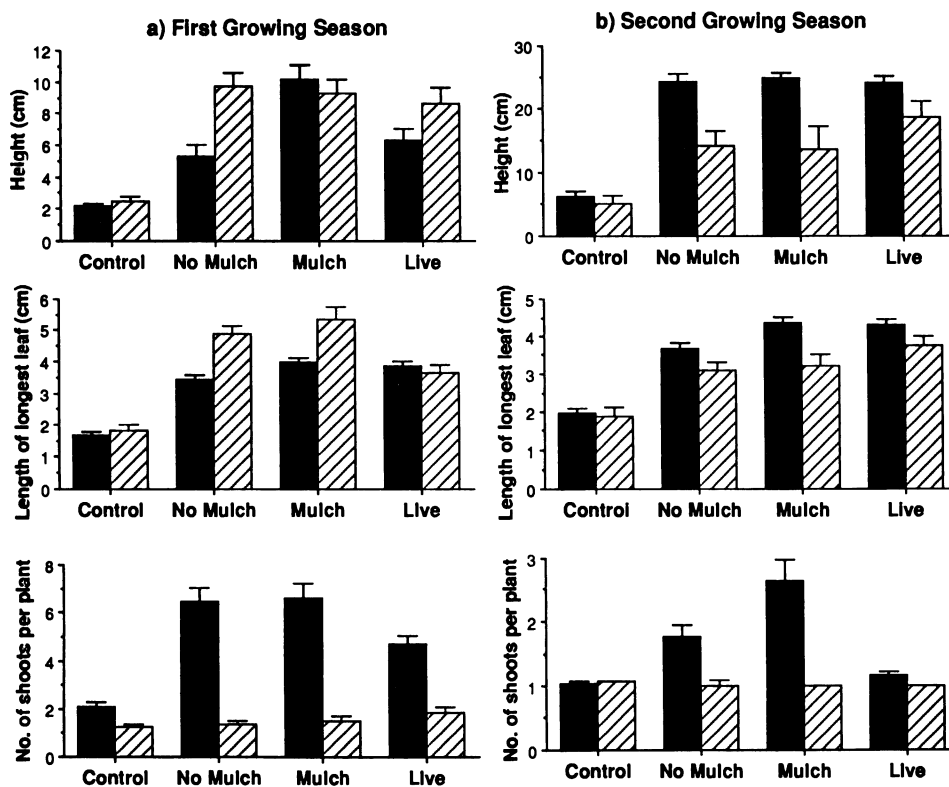

FIG. 3. Size of transplanted seedlings in Experiment 2: height, length of longest leaf, and number of shoots per plant (means + 1 SE) at (a) end of first growing season and (b) end of second growing season. Dark bars = *Anaphalis margaritacea*; hatched bars = *Epilobium angustifolium*.
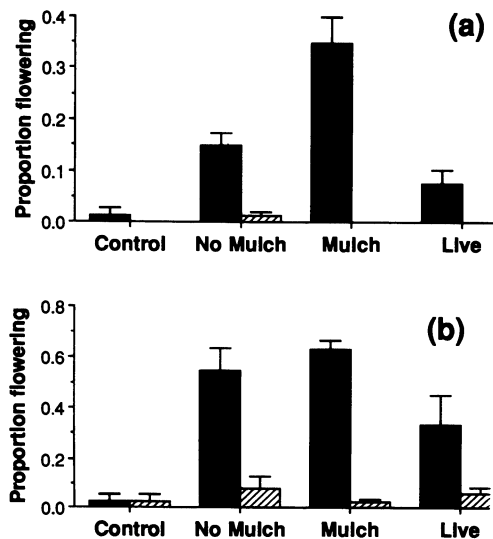
FIG. 4. Proportion of initial cohort in each plot in Experiment 2 which flowered by (a) end of first season and (b) end of second season (mean + 1 SE). Dark bars = *Anaphalis margaritacea*; hatched bars = *Epilobium angustifolium*.

DISCUSSION

This study demonstrates that patches of *Lupinus lepidus* exerted a combination of beneficial and detrimental effects on the establishment of *Anaphalis margaritacea* and *Epilobium angustifolium* at Mount St. Helens. Seedling survival after one growing season was generally lower within lupine patches than at barren control sites, yet those seedlings that survived in lupine patches grew bigger and, for *A. margaritacea*, had a higher probability of flowering. From the perspective of seedling survival, lupines appeared to inhibit subsequent colonization, while growth and flowering data suggest that lupines facilitated colonization.

At least four nonexclusive mechanisms could account for inhibition of seedling survival in lupine patches. Firstly, pathogens and/or herbivores may be more abundant within lupine patches than in nearby barren sites, and may increase the mortality of invading seedlings. Seedling inhibition within lupine patches may thus be an indirect effect mediated by other species. Secondly, live lupines may inhibit invading seedlings by competing for light, soil moisture, or nutrients. Lower initial survival in the live treatment than in the dead lupine treatments for both invaders (Fig. 2a) suggests that competitive inhibition by live lupines may supplement other inhibitory mechanisms. Thirdly, lupines may produce allelopathic substances which persist after the lupines have died, thus accounting for higher transplant mortality in both dead and live lupine treatments (Fig. 2). Finally, we cannot rule out the possibility that sites where lupine is now growing differed initially from barren sites in abiotic conditions (e.g., subsurface moisture, substrate particle size and/or nutrient availability, microtopography, etc.) which could have affected transplant performance. The differences

in transplant performance among lupine treatments suggests that the effects of lupine patches we observed were due, at least in part, to the effects of lupine itself.

One hypothesis which could explain lower first season survival in lupine patches is that transplants experienced a greater intensity of self-thinning within lupine patches due to the higher rate of growth. This hypothesis can be ruled out because the lowest survival did not occur in the treatment in which growth was highest (cf. Figs. 2a and 3a). Thus, when plots from all treatments in Experiment 2 were pooled, we found no significant correlations between first season survival and any of the three indices of mean plant size at season's end.

Lupine patches facilitated transplant growth through both belowground and aboveground effects. Substrate alteration, presumably by nitrogen addition (Nuhn 1987), benefitted both *A. margaritacea* and *E. angustifolium* seedlings (cf. no-mulch vs. control treatments in Figs. 3 and 4). The mulching effect of lupine litter provided an additional benefit to *A. margaritacea* seedlings during the first growing season (cf. mulch vs. no-mulch treatments in Figs. 3a and 4a). Mulching may compensate for the poor water retention capacity of pyroclastic substrate, provide an additional source of nitrogen, or shelter seedlings from harsh microclimatic conditions. The lack of a significant mulching effect on any aspect of *E. angustifolium* performance indicates that the mechanisms of facilitation by *L. lepidus* may operate differently for different colonizing species.

Our results suggest an important caveat to the conventional wisdom concerning the role of nitrogen fixers in primary succession: nitrogen-fixing species do not always strictly facilitate succession. Many studies have documented an increase in nitrogen availability within stands of nitrogen-fixing pioneers (Lawrence et al. 1967, Vasek and Lund 1980, Hirose and Tateno 1984, Vitousek et al. 1987). However, two experimental studies which have examined in detail the response of succeeding species (i.e., the present study and Walker and Chapin's [1986] study of alder, *Alnus tenuifolia*) have demonstrated inhibitory as well as facilitative influences of nitrogen fixers. Although Walker and Chapin report some facilitative effects of alder on growth of spruce (*Picea glauca*), which succeeds alder in primary succession on Alaska floodplains, trenching experiments demonstrated that alder competitively inhibited spruce growth.

More generally, our results support the view that the overall influence of an early colonist on later invaders will often represent a balance of facilitative and inhibitory effects (Connell et al. 1987, Huston and Smith 1987, Walker and Chapin 1987). Using probability of flowering as an index, the net effect of lupine patches appears to be facilitative (Fig. 4), at least for *A. margaritacea*. Furthermore, because invaders growing among dead lupine were likely to flower earlier than individuals invading among live lupines (Fig. 4a), fac-

tors affecting lupine mortality may modulate the rate of invasion of lupine patches.

However, our experiments point to a potential difficulty in assessing the net effects of early successional species. If mechanisms of facilitation and inhibition act on different life history attributes of invaders (e.g., seedling survival vs. seedling growth rate), the net effect can no longer be computed as the sum of positive and negative effects on a single response variable. In order to integrate the potentially opposite effects of early species on different life history parameters, a complete demographic model of the invader population is needed. One approach would be to construct a transition matrix model (cf. Solbrig et al. 1988) in which the transition probabilities among life stages depend upon the local density of the early successional species. In the case of seedlings invading lupine patches, the probability of a successful transition between the seedling and adult (reproductive) stages would be the product of (1) the probability of seedling survival and (2) the probability that a surviving seedling grows to adult size, both contingent upon the local densities of live and dead lupines. At present, the data needed to construct such a model are not available for any successional system.

LITERATURE CITED

Armesto, J. J., and S. T. A. Pickett. 1986. Removal experiments to test mechanisms of plant succession in old fields. Vegetatio 66:85–93.

Burton, P. J., and D. Mueller-Dombois. 1984. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. Ecology 65:779–791.

Connell, J. H., I. R. Noble, and R. O. Slatyer. 1987. On the mechanisms producing successional change. Oikos 50:136–137.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119–1144.

Dean, T. A., and L. E. Hurd. 1980. Development in an estuarine fouling community: the influence of early colonists on later arrivals. Oecologia (Berlin) 46:295–301.

del Moral, R. 1983. Initial recovery of subalpine vegetation on Mount St. Helens, Washington. American Midland Naturalist 109:72–80.

del Moral, R., and C. A. Clampitt. 1985. Growth of native plant species on recent volcanic substrates from Mount St. Helens. American Midland Naturalist 114:72–80.

Gallagher, E. D., P. A. Jumars, and D. D. Trueblood. 1983. Facilitation of soft-bottom benthic succession by tube builders. Ecology 64:1200–1216.

Harris, L. G., A. W. Ebeling, D. R. Laur, and T. J. Rowley. 1984. Community recovery after storm damage: a case of facilitation in primary succession. Science 224:1336–1338.

Hils, M. H., and J. L. Vankat. 1982. Species removals from a first year old field plant community. Ecology 63:705–711.

Hirose, T., and M. Tateno. 1984. Soil nitrogen patterns induced by colonization of *Polygonum cuspidatum* on Mt. Fuji. Oecologia (Berlin) 61:218–223.

Huston, M., and T. Smith. 1987. Plant successsion: life history and competition. American Naturalist 130:168–198.

Lawrence, D. B., R. E. Schoenike, A. Quispel, and G. Bond. 1967. The role of *Dryas drummondii* in vegetation development following ice regression at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. Journal of Ecology 55:793–813.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivore, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123.

Monk, C. D., and F. C. Gabrielson, Jr. 1985. Effects of shade, litter, and root competition on old-field vegetation in South Carolina. Bulletin of the Torrey Botanical Club 112:383–392.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. Science 142:15–23.

Nuhn, W. 1987. Soil genesis on the 1980 pyroclastic flows of Mount St. Helens. Thesis. University of Washington, Seattle, Washington, USA.

Reynolds, G. D., and L. C. Bliss. 1986. Microenvironmental investigations of tephra covered surfaces at Mount St. Helens. Pages 147–152 *in* S. A. C. Keller, editor. Mount St. Helens: five years later. Eastern Washington University Press, Cheney, Washington, USA.

SAS. 1985. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

Solbrig, O. T., R. Sarandon, and W. Bossert. 1988. A density-dependent growth model of a perennial herb, *Viola fimbriatula*. American Naturalist 131:385–400.

Sousa, W. P. 1979. Experimental investigation of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49:227–254.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Turner, T. 1983. Facilitation as a successional mechanism in a rocky intertidal community. American Naturalist 121:729–738.

Vasek, F. C., and L. L. Lund. 1980. Soil characteristics associated with a primary succession on a Mojave Desert dry lake plant community. Ecology 61:1013–1018.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804.

Walker, L. R., and F. S. Chapin, III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67:1508–1523.

Walker, L. R., and F. S. Chapin, III. 1987. Interactions among processes controlling successional change. Oikos 50:131–135.

Wood, D. M., and R. del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. Ecology 68:780–790.

Wood, D. M., and R. del Moral. 1988. Colonizing plants on the Pumice Plains, Mount St. Helens, Washington. American Journal of Botany 75:1228–1237.