

COMPETITION AND FACILITATION: CONTRASTING EFFECTS OF *ARTEMISIA TRIDENTATA* ON DESERT VS. MONTANE PINES¹

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Abstract. Circumstantial evidence suggests that *Artemisia tridentata* may out-compete *Pinus ponderosa* and *P. jefferyi* for water at ecotones between shrub steppe and montane forest vegetation in the Great Basin. Other studies indicate that within the shrub steppe *Artemisia* may act as a nurse plant for a third species of pine, *P. monophylla*. We used field experiments to study these contrasting effects of *Artemisia* on *P. ponderosa* and *P. monophylla* within the context of the distributional patterns in western Nevada of all three species on andesite, and on sites where hydrothermal activity has altered the andesite. At intermediate elevations in the Great Basin *Artemisia* and *P. monophylla* are restricted to unaltered desert soils, whereas *P. ponderosa* is restricted to acidic, nutrient-poor altered andesite. Although mature *P. monophylla* were virtually absent in our study plots on altered andesite, first- and second-year seedlings were common. On adjacent unaltered andesite, all size classes of *P. monophylla* occurred, and *P. monophylla* seedlings were associated with *Artemisia* shrubs. *Pinus ponderosa* and *P. jefferyi* adults and seedlings were rare on unaltered andesite, but a wide range of size classes was found on altered andesite. In experiments, all *P. ponderosa* seedlings on unaltered andesite were consumed by predators regardless of positive or negative spatial association with shrubs. Of the *P. monophylla* seedlings that germinated on unaltered andesite, all that were under shrubs survived, but only 6% of those that germinated in the intershrub spaces survived. On the open altered andesite the mortality of *P. monophylla* seedlings due to abiotic stress was high, with a final survival of only 3%, whereas 28% of *P. ponderosa* seedlings survived the first growing season on altered andesite. On unaltered andesite, survival and conductance of *P. ponderosa* saplings was enhanced by shrub removal, but *P. monophylla* survival was significantly higher under shrubs than in shrub-removal plots or in intershrub spaces. In *Artemisia*-removal experiments, we found that *Artemisia* competed with *P. ponderosa* seedlings and saplings for water. Removal of *Artemisia* decreased water use efficiency (WUE) of *P. monophylla* seedlings. The absence of *Artemisia* may restrict *Pinus monophylla* from outcrops of altered andesite in the Great Basin, but provide refuges for *P. ponderosa*.

Key words: altered andesite; *Artemisia tridentata*; competition; facilitation; field experiments; gas exchange; Great Basin Desert; interference; *Pinus ponderosa*; *Pinus monophylla*; plant interactions.

INTRODUCTION

The relative importance of interference vs. facilitation within a plant community appears to be species-specific as individuals may compete with some neighbors and facilitate others (Silander and Antonovics 1982, Callaway et al. 1991, 1994, Bertness and Shumway 1993, Bertness and Callaway 1994). By studying the mechanisms that regulate differences in interactions among similar species, and that might control shifts between facilitation and competition, we may gain a

better understanding of how complex interactions affect plant community structure and dynamics.

In the Great Basin and eastern Sierra Nevada, *Artemisia tridentata* Nutt. (Great Basin sagebrush) appears to differ in its effects on two associated pine species, *Pinus ponderosa* Laws. (ponderosa pine) and *P. monophylla* Torr. & Frém. (single-needled pinyon pine), which have similar leaf-level physiological characteristics, water relations, and nutrient requirements (DeLucia et al. 1988, 1989, DeLucia and Heckathorn 1989, Schlesinger et al. 1989). This system provides a unique opportunity to study complex interactions and the mechanisms behind them because the communities are simple, and a single dominant species (*A. triden-*

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tata) appears to have contrasting effects on two congeners.

Evidence for competition between *Artemisia* and *P. ponderosa* comes from ecophysiological studies on adjacent but distinctly different soil types. DeLucia et al. (1988) compared daily and seasonal patterns of water use of *Artemisia* and *P. ponderosa* and hypothesized that profligate use of soil water by *Artemisia* at low soil water potentials competitively excluded the more water-conservative *P. ponderosa* from the nutrient-rich soils on which *Artemisia* could grow, and restricted the distribution of *P. ponderosa* to nutrient-poor outcrops in the Great Basin. In contrast, positive spatial associations between *Artemisia* and *P. monophylla* have been documented, which suggests that *Artemisia* may act as nurse plants for *P. monophylla* (Phillips 1909, Everett et al. 1983) as well as the related *P. edulis* Engelm. (two-needled pinyon [Weldon et al. 1990]). Neither competition nor facilitation between *Artemisia* and associated pines has been studied with manipulative field experiments. The geographic distributions of *Artemisia tridentata*, *P. ponderosa*, and *P. monophylla* overlap in the northeastern Great Basin, which provides an opportunity to experimentally investigate the effects of *Artemisia* on these pines and the importance of facilitation and competition as determinants of community structure. "Islands" of Sierran pines, including *P. ponderosa*, occur on outcrops of nutrient-poor sites created by local hydrothermal activity thought to have commenced during the Miocene (Gianella 1936, Hutschiniller 1988). These islands are virtually devoid of *Artemisia* and rarely occupied by *P. monophylla* (Billings 1950, DeLucia et al. 1988, Schlesinger et al. 1989). Outcrops of altered andesite are surrounded by typical desert soils with Great Basin shrub communities dominated by *Artemisia* and often including *P. monophylla*. The ecotone between these two communities is sharp, with complete turnover of these species occurring within ≈ 5 m. Greenhouse experiments show that *Artemisia* cannot grow on altered andesite because of nutrient limitations; however, contrasting with its field distributions, *P. monophylla* grows as well on soils derived from altered andesite as on typical desert soils (DeLucia et al. 1989). Considered together, this information suggests that the absence of *Artemisia* on altered andesite may create refuges for *P. ponderosa* because of reduced competition, but create unfavorable habitat lacking the biotic safe-sites required by *P. monophylla*.

We hypothesized that (1) *Artemisia* affects the community structure of these Great Basin habitats by limiting the distribution of *P. ponderosa* to altered andesite via competitive interactions, (2) *Artemisia* promotes *P. monophylla* on typical desert soils via facilitative interactions, and (3) the absence of *Artemisia* prevents *P. monophylla* from occupying altered andesite. We investigated these general hypotheses by quantifying natural spatial patterns of pine seedlings and adults and

by comparing survival, growth, and gas exchange of pine seedlings in shrub-removal experiments.

METHODS

Species distributions on and off altered andesite

We used two approaches to measure species distributions. For this part of the study *Pinus ponderosa* and *P. jefferyi* were recorded as "yellow pines" because seedlings of the two species were indistinguishable in the field. Only *P. ponderosa* was used throughout the rest of the study. First, we analyzed data collected in May 1986 at five sites near Reno, Nevada, described by Billings (1950) and DeLucia et al. (1988) where *P. monophylla* was a major component of the vegetation. Pine seedling and shrub densities were measured, at each of the sites, in 50.2×2 m plots on altered andesite and 50.2×2 m plots on unaltered andesite. Adult pine densities were measured at each site in one 0.1-ha plot on altered andesite and one 0.1-ha plot on unaltered andesite. We used separate two-way contingency analyses ($df = 1$; SYSTAT, Wilkinson 1990) for each species to test for differences in seedling and adult ratios between altered and unaltered andesite. Yellow pines were tested as a group and sites were pooled.

For our second approach, we measured densities of *Artemisia*, *P. monophylla*, and the yellow pines (*P. ponderosa* + *P. jefferyi*); size classes of the pines; and spatial associations between pine seedlings and *Artemisia* at the Virginia Mountains site, 20 km southwest of Reno, Nevada, in August 1993. We measured species distributions and interspecific associations along 50-m transects on north- and south-facing slopes. On each aspect, 10 transects were located on altered andesite and 10 on unaltered andesite. Point-centered quarter sampling (Cottam and Curtis 1956) was used at 10 random points on each transect. Densities were calculated for shrubs and pine seedlings (< 0.5 cm stem diameter at ground level), saplings (0.5–5.0 cm stem diameter at ground level), and mature individuals (> 5 cm stem diameter at ground level) of *P. ponderosa* and *P. monophylla*. All pine seedlings were recorded as either under the canopy of a shrub or in the open. Projected ground areas covered by each individual shrub and *P. monophylla* were estimated from two measurements of canopy diameter for each shrub and tree recorded on the transect and used to estimate total shrub cover on altered and unaltered andesite. Observed shrub—seedling association was tested against expected with chi-square tests.

Germination and seedling survival of planted seeds

To study the fate of *P. ponderosa* and *P. monophylla* seeds and seedlings on altered and unaltered andesite, we buried 510 seeds of each species in each soil type. Single seeds were planted 2–3 cm deep at 1-m intervals on permanent transects in November 1992 at the Desert Research Institute (DRI) and Peavine sites (see site

TABLE 1. Densities (individuals/ha) of pines and dominant shrubs on hydrothermally altered and unaltered andesite in five sites in the eastern Sierra Nevada and adjacent Great Basin. Two-way contingency analysis showed no significant difference between substrates in the ratios of seedlings and adults of yellow pines pooled across sites ($G = 3.5$, $df = 12$, $P = 0.06$).

Site	Alt. (m)	Yellow pines†				<i>Pinus monophylla</i>	
		Altered andesite		Unaltered andesite		Altered andesite	
		Adult	Seedling	Adult	Seedling	Adult	Seedling
Virginia Mts.	1540	100	750	0	0	10	400
Virginia Mts.	1645	60	50	0	0	0	250
Alpine County	1830	20	50	30	0	20	0
Virginia Mts.	1830	90	1000	0	0	10	2750
Alpine County	1920	70	1150	0	100	0	400
Mean and 1 SE		82 ± 18	817 ± 289	5 ± 5	17 ± 17	12 ± 5	658 ± 423

† *Pinus ponderosa* and *P. jefferyi*.

‡ *Ribes velutinum* dominant.

|| *Purshia tridentata* dominant, otherwise *Artemisia tridentata* is only species recorded.

descriptions in DeLucia et al. 1988, Schlesinger et al. 1989, Callaway et al. 1994). The transects were randomly located and equal numbers of seeds were planted at each site. Because these sites are close to each other and similar topographically we analyzed the pooled results with a chi-square test using one degree of freedom. Seeds were recorded as either under shrubs or in the open. To facilitate the relocation of the seeds they were buried directly on top of 1 × 1 cm steel markers. Transects were surveyed in May, June, and September 1993 for seedlings, and in September all planting sites were excavated. If markers were present without seeds, we presumed the seed to have been removed by predators. If no seedling, seed, or marker could be found at a particular planting location, that replicate was not included in the analyses of seed fates because we were uncertain of relocating the position accurately. Analysis of seedling germination (presence of shoot in May) was based on all 510 sites where seeds had been planted. For each census period, pine seedlings were recorded as living, present but dead, or missing. We often found chewed stems or cut shoots at sites where seedlings had disappeared, which suggested that missing seedlings were removed by predators.

Survival and growth of planted seedlings in shrub-removal experiments on unaltered andesite

To examine the effects of shrubs on soil moisture availability and the survival and growth of pine seedlings, we transplanted 40 four-month-old seedlings of each pine species into each of three treatments in *Artemisia*-dominated vegetation on unaltered andesite on 10 May 1992 at the DRI site. *Pinus ponderosa* and *P. monophylla* seeds were collected in northwestern Nevada, and seedlings were grown in greenhouses for 3 mo. Before planting in the field the seedlings were left outside to acclimate to the natural climate. Seedlings were planted in the following experimental treatments: (1) under *Artemisia* shrubs; (2) in intershrub spaces; (3) plots from which all shrubs had been removed by hand between 5 and 8 May 1992. Seedlings were plant-

ed in holes 20 cm deep and initially given 1 L of water each. Three days after planting all seedlings received another 1 L of water. Treatments were established within 10 randomly located blocks at the DRI site. Each block consisted of a 10 × 20 m shrub-removal plot, a contiguous 10 × 20 m plot in which pine seedlings were planted under *Artemisia*, and a third contiguous 10 × 20 m plot in which pine seedlings were planted in the intershrub spaces. Treatment plots were located randomly within a block and four seedlings of each species were alternately planted at 2-m intervals on a transect through the middle of each plot. Seedling survival was censused periodically from May through September 1992, after which surviving seedlings were harvested, measured for leaf area, dried at 60°C, and weighed. Block, treatment, and species differences in survival, leaf area, and shoot mass were tested with three-way ANOVA (Wilkinson 1990).

Soil moisture was measured every 3 d between 11 May and 23 May with a Campbell-Pacific Model 503 neutron moisture probe that was fitted with an adapter for surface sampling (≈0–20 cm depth) and calibrated with gravimetric soil samples. Neutron probe measurements were taken for 30 s at three locations in each plot that were ≥1 m from the watered seedlings and that represented the treatments in each plot. Samples in the shrub-removal treatment were randomly located. Only trace amounts of rainfall were recorded during our sample period. The three measurements taken on each day were averaged and differences in soil moisture over time were tested with two-way (day × treatment) repeated-measures ANOVA, and with one-way ANOVA at each date (Systat 1990).

Gas exchange of planted seedlings in shrub-removal experiments on unaltered andesite

We measured daily patterns of photosynthesis and conductance of five randomly chosen seedlings of each species in each of the three treatments in two adjacent blocks on 27 and 28 May 1992 with a LI-COR 6200 infrared gas-analysis system. Gas exchange was mea-

In contrast, ratios of seedlings to adults differed significantly between sites for *Pinus monophylla* ($G = 363.9$, $df = 12$, $P < 0.0001$).

<i>Pinus monophylla</i>		<i>Artemisia tridentata</i>	
Unaltered andesite		Altered andesite	Unaltered andesite
Adult	Seedling	Adult	Adult
20	0	0	4200
30	0	0	2300
20	50	0	5600
860	450	0	1400
100	200	0	3650§
313 ± 169	483 ± 350	0	3791 ± 699

sured on whole-seedling shoots in a custom-designed 1.2-L cuvette. Fan speed in the cuvette was adjusted to create a boundary-layer resistance of ≈ 20.0 s/m (see Smith 1980). Measurements of ambient humidity and leaf temperature were taken prior to each measurement of gas exchange on leaves immediately prior to enclosure in the cuvette and subsequently used to estimate transpiration (Percy et al. 1992). Water-use efficiency (WUE) was calculated as CO_2 uptake (in moles) divided by H_2O transpired (in moles). Both days were cloudless and similar in temperature and humidity; thus, we combined measurements from both days for a given species and treatment to increase sample sizes. To compare daily patterns of gas exchange among species and treatments, the 10–12 diurnal measurements for each individual seedling were fitted to a fourth-order regression curve and the areas under the curve were integrated. These integrated daily gas-exchange rates were statistically analyzed with two-way (species by treatment) ANOVA. Because our sample sizes were limited, we did not include block effects in the ANOVA; however, we expected the block effects to be small because the blocks were within 20 m of each other on the same north-facing slope.

Survival and leaf conductance of P. ponderosa in shrub-removal experiments

Because of high losses of 4-mo-old *P. ponderosa* seedlings in the 1992 experiment, apparently due to predation, we could not compare physiological responses or growth in treatments over the whole growing season. To redress this problem, in May 1993 we planted 40 two-year-old *P. ponderosa* saplings in each of the three treatments in the same 10 blocks used for the 1992 experiment. Shrub regrowth was removed. These saplings were planted and initially watered as were the seedlings, then censused every week during the summer. Conductance was measured with a LICOR 1600 steady-state porometer every 2 wk, between 0800 and 1030, from 16 June to 7 September, on all living saplings in each treatment in three of the blocks. Different saplings were measured during each sampling period, but because of mortality, less than five saplings

remained for open and under-shrub treatments in the later weeks.

Young *P. ponderosa* were rare on unaltered andesite; however, we located 14 saplings, ranging from 3.2 to 11.7 cm stem diameter at ground level, intermixed with *Artemisia* on unaltered andesite at the Peavine site. These saplings were grouped into seven pairs of similar-sized plants and used in a third shrub-removal experiment. All shrubs were removed within a radius of 1 m around one randomly chosen member of each pair in September 1992. Beginning the following spring, conductance was measured between 0900 and 1100 on three different fascicles on the east-facing side of each sapling, and recorded as the mean of the three fascicles. Measurements were made every 2 wk from 20 May to 9 September 1993.

Survival of naturally occurring P. monophylla seedlings with imitation nurse plants on altered andesite

To test the potential importance of *Artemisia* nurse plants in the survival of *P. monophylla* seedlings on altered andesite, we conducted field experiments with “imitation” nurse shrubs in the Virginia Mountains. In August 1993, we sheltered 25 natural first-year *P. monophylla* seedlings on a north-facing slope and 20 first-year seedlings on a south-facing slope with imitation nurse plants and compared their survival to paired first-year seedlings without imitation nurse plants. To imitate nurse plants, we cut branches from *Artemisia* shrubs, sprayed the leaves with lacquer to promote leaf retention, and staked the branches into the soil so that they sheltered the *P. monophylla* seedlings. Mimic nurse plants were located so that small branches sheltered *P. monophylla* seedlings from above and on three sides. Seedlings were censused between August 1993 and September 1994.

RESULTS

Species distributions on unaltered and altered andesite

Artemisia tridentata and other shrubs were absent from all plots located on altered andesite in all five study sites in the Sierra Nevada and the adjacent Great Basin that were sampled in 1986 (Table 1). For the five sites combined, yellow pine seedlings and adults were 48 times and 16 times more common, respectively, on altered andesite than on unaltered andesite. The ratios of seedlings to adults for yellow pines were 10:1 on altered andesite and 3.4:1 on unaltered andesite, but these ratios did not differ significantly ($G = 3.5$, $df = 1$, $P = 0.061$) suggesting that seedlings had similar probabilities of becoming adults on either substrate.

Relative distributions of *P. monophylla* seedlings and adults between substrates were different than for yellow pines and indicated that *P. monophylla* ger-

TABLE 2. Densities (individuals/ha) of dominant perennials on hydrothermally altered and unaltered andesite in the Virginia Mountains.

	Altered andesite	Unaltered andesite
North-facing slope		
<i>Artemisia tridentata</i> †	1	765
<i>P. monophylla</i> seedlings	167	82
<i>P. monophylla</i> saplings	0	48
Mature <i>P. monophylla</i>	0	426
Yellow pine seedlings	36	0
Yellow pine saplings	17	0
Mature yellow pines	209	2
South-facing slope		
<i>Artemisia tridentata</i>	4	522
<i>P. monophylla</i> seedlings	104	71
<i>P. monophylla</i> saplings	0	50
Mature <i>P. monophylla</i>	1	258
Yellow pine seedlings	24	0
Yellow pine saplings	9	0
Mature yellow pines	158	1

† *Artemisia tridentata* constituted >95% of the shrub density of the transects.

minated readily on altered andesite, but few seedlings survived to maturity (Table 1). Seedlings were abundant on both altered and unaltered andesite, but adults were virtually absent on soils derived from altered andesite. The ratio of seedlings to adults was 55:1 on altered andesite vs. 1.5:1 on unaltered andesite. Expected proportions of adult density, as predicted from seedling density, differed from the observed ($G = 363.9$, $df = 1$, $P < 0.001$).

On transects in the Virginia Mountains, *P. monophylla* seedlings were also much more abundant on altered andesite than on unaltered andesite (Table 2). In contrast, mature *P. monophylla* were virtually absent on altered andesite, but were numerous on unaltered andesite. Yellow pine seedlings were less common than those of *P. monophylla* on altered andesite, but adult *P. ponderosa* and *P. jefferyi* were abundant (Table 2). No yellow pine seedlings were found on transects on unaltered andesite and adult yellow pines were rare.

Both approaches showed corresponding patterns of plant distributions on altered and unaltered andesite. First, seedlings of yellow pines and *P. monophylla* were common on altered andesite, but seedlings of the latter rarely reached maturity. Second, seedlings and adults of yellow pines were virtually absent on unaltered andesite where *P. monophylla* in all size classes were abundant.

As expected from the low proportion of shrub cover, all *P. monophylla* seedlings on altered andesite were in the open. On unaltered andesite, however, *P. monophylla* seedlings had positive spatial associations with *Artemisia* shrubs (Table 3). On north slopes 71% of *P. monophylla* seedlings were under shrubs even though shrubs covered only 32% of the area sampled ($\chi^2 = 57.9$, $df = 2$, $P < 0.001$). On south-facing slopes 86% of *P. monophylla* seedlings were under shrubs which covered only 23% of the area sampled ($\chi^2 = 187$, $df = 2$, $P < 0.001$).

Germination and seedling survival of planted seeds

Pinus ponderosa experienced high seed predation and low germination rates on both soil types, but seedlings in the shrub matrix on unaltered andesite had a much lower probability of surviving than those on altered andesite. Because we missed events occurring prior to May, actual germination was likely to have been higher. In August, we were able to locate 211 of the 463 *P. ponderosa* seed markers not associated with seedlings in May, and 110 of these were found with ungerminated seeds (Table 4). Thus we estimated seed predation for *P. ponderosa* on altered andesite at 48%. Estimated seed predation rates were significantly higher on unaltered andesite than altered andesite ($\chi^2 = 18.79$, $df = 2$, $P < 0.001$) and tended to be higher under shrubs (77%) than in intershrub spaces (68%) on the unaltered andesite. Of the 510 *P. ponderosa* seeds planted on altered andesite in November 1992, only 9% produced seedlings that were alive in May 1993 (Table 4). Six percent of *P. ponderosa* seeds germinated on unaltered andesite ($\chi^2_{\text{substrate}} = 4.0$, $df = 2$, $P > 0.05$).

TABLE 3. Goodness-of-fit tests for spatial associations between *Pinus monophylla* seedlings and *Artemisia tridentata* shrubs on unaltered andesite in the Virginia Mountains.

Site aspect	Cover type	Relative frequency	Number of associated <i>Pinus monophylla</i> seedlings	
			Observed	Expected
North	Open	0.46	18	38
	<i>Pinus monophylla</i>	0.22	6	18
	<i>Artemisia tridentata</i>	0.32	58	26
	$n = 82$ seedlings $\chi^2 = 57.9$, $P < 0.001$			
South	Open	0.57	2	41
	<i>Pinus monophylla</i>	0.20	5	14
	<i>Artemisia tridentata</i>	0.23	64	16
	$n = 71$ seedlings $\chi^2 = 187.0$, $P < 0.001$			

TABLE 4. Germination and survival of *Pinus ponderosa* and *P. monophylla* from seeds planted in November on hydrothermally altered andesite and on unaltered andesite at Desert Research Institute and Peavine Mountain.

	<i>Pinus ponderosa</i>			<i>Pinus monophylla</i>		
	Unaltered andesite			Unaltered andesite		
	Altered andesite	Under shrub	Open	Altered andesite	Under shrub	Open
No. seeds planted	510	271	239	510	278	232
Markers located	211	130	81	244	91	104
Seeds present	110	30	26	125	7	13
Seed predation (%)†	48	77	68	49	92	87
Seedlings						
May	47	14	13	66	12	16
July	30	5	0	56	12	16
August	13	0	0	2	12	1
Initial germination (%)	9	6	5	13	5	6
Final survival (%)	28	0	0	3	100	6
Seedling predation (%)†	29	100	100	6	0	27

† Predation of either seedlings or seeds was assumed if a previously located seedling disappeared or if a marker was located without the seed.

with similar numbers recorded under shrubs versus intershrub spaces. Twenty-eight percent of *P. ponderosa* seedlings that germinated on altered andesite in May survived until August 1993 and only 29% of the mortality was attributed to predation; the rest dried in place. In contrast, all *P. ponderosa* seedling mortality on unaltered andesite (in *Artemisia*-dominated shrubland) appeared to be the result of predation.

Pinus monophylla experienced much higher seed predation and lower germination rates on unaltered andesite than on altered andesite (Table 4). However, in contrast with *P. ponderosa*, seedling survival directly under shrub canopies was higher than on the open al-

tered andesite or in the open intershrub spaces. On altered andesite, *P. monophylla* seed predation was estimated at 49%, whereas on unaltered andesite seed predation was estimated at 92% and 87% under shrubs and in the intershrub spaces, respectively ($\chi^2_{\text{microsite}} = 56.39$, $df = 2$, $P < 0.001$). Thirteen percent of *P. monophylla* seeds planted on altered andesite were located as seedlings in May. Of these, only 3% survived until August on altered andesite. In contrast to *P. ponderosa*, a much higher proportion of the mortality on altered andesite ($\chi^2_{\text{species}} = 9.78$, $df = 1$, $P < 0.01$) occurred by seedlings drying in place, which suggests that seedling success for *P. monophylla* was strongly limited by abiotic stress. On unaltered andesite, the percentage of *P. monophylla* seeds that produced seedlings on the unaltered andesite was similar to that of *P. ponderosa*, with 5% germinating under shrubs and 6% germinating in the spaces between shrubs. All *P. monophylla* seedlings under shrubs survived until August, in comparison to only 6% of seedlings in the intershrub spaces.

Survival, growth, and gas exchange of planted seedlings in shrub-removal experiments on unaltered andesite

Removal of shrubs resulted in significantly higher soil moisture content near the soil surface (Fig. 1, repeated-measures ANOVA, $F_{\text{treat}} = 4.79$, $df = 2$, $P = 0.017$). Soil moisture in intershrub spaces was not significantly different than under shrubs.

Of the 40 four-month-old *P. ponderosa* seedlings planted in each treatment in May 1992 on unaltered andesite at DRI, two survived where shrubs had been cut, one survived under *Artemisia* shrubs, and one survived in the intershrub spaces (Fig. 2). Ninety-two percent and 77% of *P. ponderosa* seedling mortality appeared to be due to predation in the shrub-removal treatment and intershrub spaces, respectively; however,

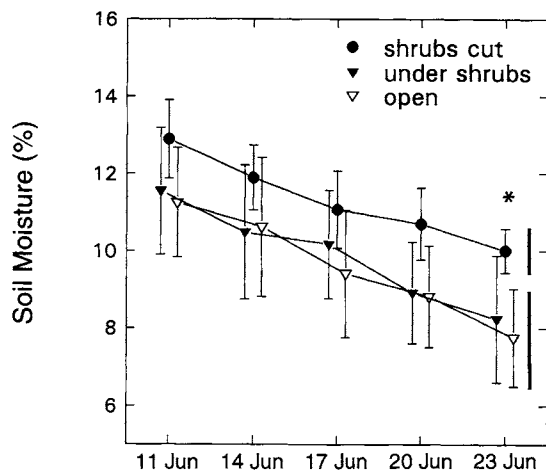


FIG. 1. Percent soil moisture in the upper 20 cm under shrubs, in intershrub spaces, and in shrub-removal treatments, on unaltered andesite at the Desert Research Institute. Data show means ± 1 SE; * indicates higher soil moisture in shrub-removal plots based on a pairwise (within block) Student's *t* test. Treatments whose final means do not share a solid vertical bar (at right of data field) were significantly different as determined by repeated-measures ANOVA, $P < 0.005$.

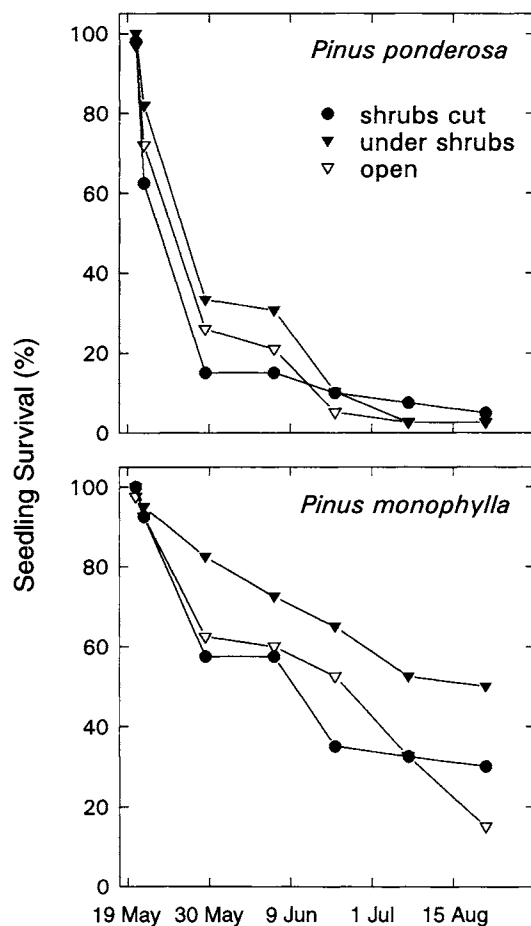


FIG. 2. Survival of 4-mo-old, planted *Pinus ponderosa* and *Pinus monophylla* seedlings on unaltered andesite under *Artemisia tridentata* shrubs, in the intershrub spaces, and in shrub-removal treatments. For all species and treatments, initial $n = 40$ seedlings.

predation appeared to account for only 50% of mortality under shrubs (Table 5). As in the seed-planting experiment, we often observed chewed stems and cut shoots at locations where seedlings disappeared. Very low survivorship of *P. ponderosa* precluded growth analyses at the end of the growing season.

Of the *P. monophylla* seedlings planted in May, 50%

survived under shrubs, 30% survived in the shrub-removal treatment, and 15% survived in the intershrub spaces (Fig. 2, two-way block \times treatment ANOVA, $F_{\text{treat}} = 13.73$, $df = 2, 9$, $P < 0.001$). Predation estimates, which were much lower than for *P. ponderosa* seedlings, accounted for 68% in the shrub-removal treatment, 47% in the intershrub spaces, and 20% under shrubs (Table 5). As in the seed-planting experiment, low predation on *P. monophylla* seedlings in comparison to *P. ponderosa* seedlings suggests the former were generally less palatable. In contrast to survival, mass of seedlings that survived was highest in the cut treatment and lowest under shrubs (Table 5, two-way block \times treatment ANOVA, $F_{\text{treat}} = 3.806$, $df = 2, 8$, $P = 0.035$). Total leaf area was 16% higher in the shrub-removal treatment than under shrubs, but treatment effects were only marginally significant ($F_{\text{treat}} = 3.302$, $df = 2, 8$, $P = 0.052$). Specific leaf mass did not differ among treatments ($F_{\text{treat}} = 2.937$, $df = 2, 8$, $P = 0.070$).

Integrated daily transpiration rates of *P. ponderosa* in shrub-removal plots were 41% higher than rates under shrubs and 49% higher than for seedlings in intershrub spaces (two-way ANOVA, $F_{\text{treat}} = 15.0$, $df = 2, 24$, $P < 0.001$, Table 6). Transpiration rates of *P. monophylla* seedlings were not significantly different among the three treatments (Table 6). Across all treatments, *P. ponderosa* seedlings transpired at greater rates than *P. monophylla* seedlings (two-way ANOVA, $F_{\text{species}} = 119.6$, $df = 1, 24$, $P < 0.001$).

Whole-shoot photosynthetic rates of *P. ponderosa* were higher than for *P. monophylla* (two-way ANOVA, $F_{\text{species}} = 58.0$, $df = 1, 24$, $P < 0.001$, Table 6). As found for transpiration, shrub removal elicited stronger responses from *P. ponderosa* than *P. monophylla*, the former increasing daily integrated rates of photosynthesis from 14.8 ± 1.7 and 12.4 ± 1.0 $\text{mmol} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (means ± 1 SE) in intershrub spaces and under shrubs, respectively, to 24.2 ± 1.3 $\text{mmol} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ where shrubs were removed (two-way ANOVA, $F_{\text{treat}} = 19.8$, $df = 2, 34$, $P < 0.001$). Integrated daily PAR was 53% less under shrubs than in the open, but net carbon assimilation were similar for seedlings in these microhabitats.

Whole-shoot WUEs of *P. ponderosa* seedlings were

TABLE 5. Growth and apparent cause of mortality for *Pinus ponderosa* and *P. monophylla* seedlings transplanted under shrubs, in spaces between shrubs (open), and where shrubs were removed (shrubs cut). For all species-treatment combinations, 40 seedlings were planted. Shared superscript letters indicate no significant differences within a row (post-ANOVA Tukey test).

	<i>Pinus ponderosa</i>			<i>Pinus monophylla</i>		
	Shrubs cut	Under shrubs	Open	Shrubs cut	Under shrubs	Open
No. seedlings surviving	2	1	1	12	20	6
Total leaf area (cm^2)	16.6 ± 0.8^a	12.8 ± 0.9^b	14.3 ± 1.4^{ab}
Aboveground mass (kg)	0.27 ± 0.02^a	0.20 ± 0.02^b	0.25 ± 0.02^{ab}
Mortality due to predation (%)†	92	50	77	68	20	47

† Predation was assumed if a previously recorded living seedling disappeared.

TABLE 6. Means and standard errors of daily integrated transpiration, photosynthesis, and water-use efficiency (WUE) of *Pinus ponderosa* and *P. monophylla* seedlings under *Artemisia tridentata* shrubs, in intershrub spaces, and in shrub-removal treatments. $n = 5$ saplings for all species-treatment combinations. Shared superscript letters indicate no significant differences within a column (post-ANOVA Tukey test).

	Transpiration ($\text{mol}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$)	Photosynthesis ($\text{mmol}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$)	WUE (mol/mol)
<i>Pinus ponderosa</i>			
Under shrubs	12.8 ± 0.9^a	14.8 ± 1.7^a	0.00114 ± 0.00005^a
Open	11.0 ± 0.8^a	12.4 ± 1.0^a	0.00112 ± 0.00002^a
Shrubs cut	21.4 ± 1.8^b	24.2 ± 1.3^b	0.00116 ± 0.00009^a
<i>Pinus monophylla</i>			
Under shrubs	5.6 ± 0.7^c	10.2 ± 0.9^a	0.00206 ± 0.00021^{ac}
Open	4.8 ± 0.3^c	9.1 ± 0.8^a	0.00196 ± 0.00026^{bc}
Shrubs cut	7.2 ± 1.1^c	10.1 ± 0.8^c	0.00147 ± 0.00011^b

also similar among treatments (Table 6, two-way ANOVA, $F_{\text{treat}} = 2.3$, $\text{df} = 2, 24$, $P = 0.126$). WUEs of *P. monophylla* were 0.001 to 0.002 mol/mol higher than for *P. ponderosa* (Table 6). Shrub removal significantly decreased daily integrated WUE for *P. monophylla* (two-way ANOVA, $F_{\text{species}} = 31.8$, $\text{df} = 1, 24$, $P < 0.001$).

Survival and conductance of *P. ponderosa* in shrub-removal experiments

We found strong differences among treatments for survival of 2-yr-old *P. ponderosa* saplings, with 28% surviving the summer when planted in plots with shrubs removed and none surviving under shrubs and in intershrub spaces (Fig. 3). In contrast to the heavy predation experienced by 4-mo-old seedlings in 1992, there was no sign of herbivory on any of the saplings, and all mortality occurred as saplings dried in place. Corresponding with the strong positive effect of shrub removal on *P. ponderosa* sapling survival was a sig-

nificant increase in conductance (Fig. 4). On 4 June, average conductances of saplings in shrub-removal treatments were ≈ 3 times greater than those in intershrub spaces or under shrubs. By the end of July, conductance of almost all saplings within the shrub matrix had ceased. Conductance of saplings in the removal plots increased substantially in late July and early August even though no rainfall occurred, suggesting that the roots of surviving saplings may have reached deeper, less transient water sources than surface moisture.

Conductances of older, naturally occurring saplings were generally three to nine times higher than conductances of saplings planted in shrub-removal plots, and, as for planted *P. ponderosa*, shrub removal had strong positive effects on conductances of naturally occurring *P. ponderosa* (Fig. 5). On 4 June, conductances of saplings around which *Artemisia* and other

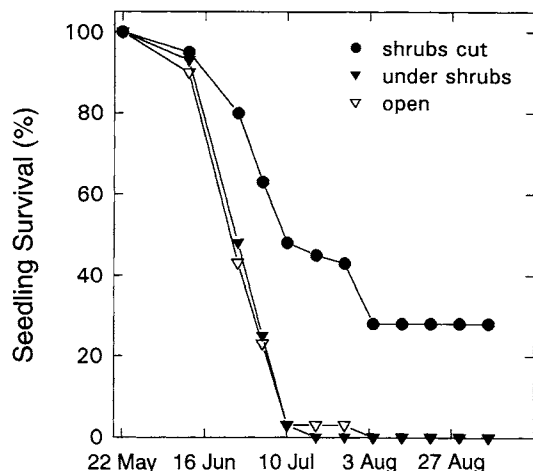


FIG. 3. Survival of 2-yr-old, planted *Pinus ponderosa* saplings on unaltered andesite under *Artemisia tridentata* shrubs (under shrubs), in the intershrub spaces (open), and in shrub-removal treatments (shrubs cut). For all treatments, initial $n = 40$ saplings.

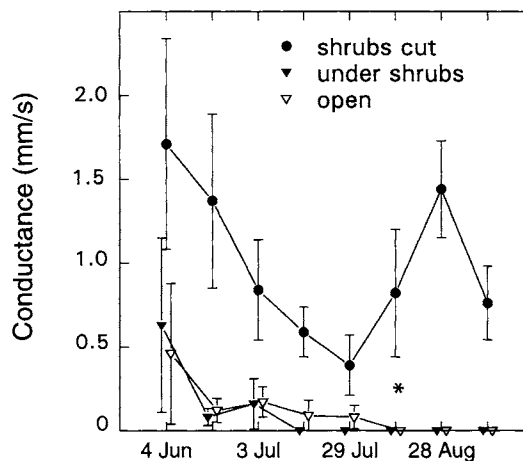


FIG. 4. Leaf conductances of 2-yr-old, planted *Pinus ponderosa* saplings on unaltered andesite under *Artemisia tridentata* shrubs (under shrubs), in the intershrub spaces (open), and in shrub-removal treatments (shrubs cut). For all treatments, initial $n = 5$ saplings; after 29 July $n < 5$ saplings in shrub matrix due to mortality. The asterisk (*) indicates the date at which saplings in the shrub matrix appeared to be dead. Means were significantly higher in the shrub-removal treatment on all dates.

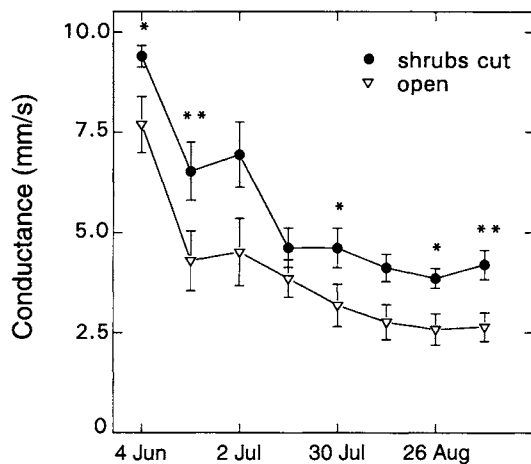


FIG. 5. Leaf conductances of paired *P. ponderosa* saplings on unaltered andesite in plots with *Artemisia tridentata* and other shrubs removed from a 3-m radius around saplings, and in control plots without shrubs removed. Data show means ± 1 SE; * indicate significantly higher conductances based on pairwise Student's *t* tests.

shrubs had been removed were 25% higher than those of the control saplings. Conductances of saplings in the removal treatment were consistently higher throughout the summer and were significantly higher (Student's *t* test, $P < 0.05$) on four of the eight sampling days. Competitive intensity did not appear to change substantially with sapling age as differences in conductances between shrub-removal and control saplings were not correlated with sapling size ($r^2 = 0.23$, $P = 0.44$).

Survival of naturally occurring *P. monophylla* seedlings on altered andesite with imitation nurse plants

On altered andesite, survival of *Pinus monophylla* seedlings was generally higher with imitation nurse plants than in the open; however, there were differences between north-facing and south-facing sites (Fig. 6). On the north-facing site 84% of naturally germinating seedlings that were provided with imitation nurse plants survived for 1 yr, whereas 68% of the seedlings in the open survived ($\chi^2 = 0.42$, $df = 1$, $P > 0.5$). On the south-facing site 35% of the seedlings under mimic nurse plants survived in comparison to only 10% in the open; however, the difference between these treatments was only marginally significant ($\chi^2 = 2.78$, $df = 1$, $P = 0.09$). All mortality observed in this experiment occurred as seedlings dried in place.

DISCUSSION

Our first hypothesis, that *Artemisia* interferes with *P. ponderosa*, was supported by field experiments, but negative effects of *Artemisia* on *P. ponderosa* appeared to be both indirect and direct. The indirect effect appeared to occur through increased predation on seeds

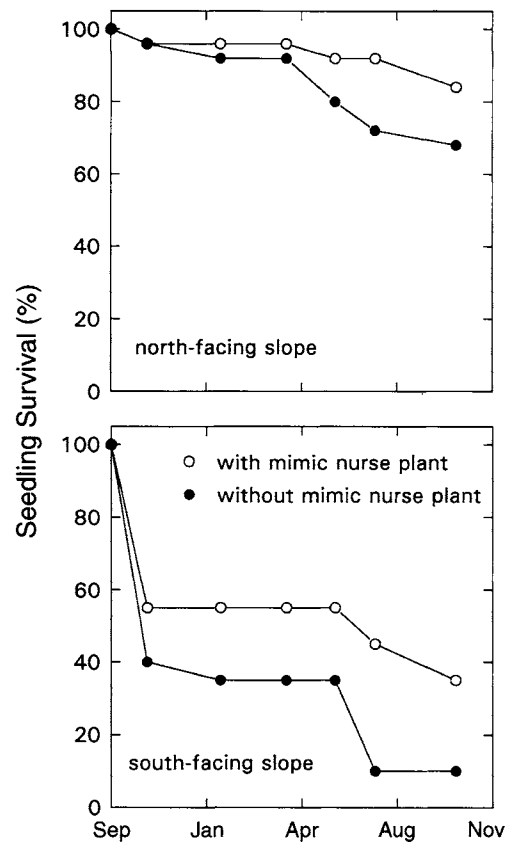


FIG. 6. Survival of naturally germinating *Pinus monophylla* seedlings on altered andesite under imitation nurse plants and in the open on north- and south-facing slopes. Initial $n = 25$ seedlings for each treatment on north-facing slopes, and $n = 20$ seedlings on south-facing slopes.

and seedlings on unaltered andesite. We suspect that seedlings were rapidly consumed by small mammals that are dependent on shrubs for cover, and that seedlings germinating on altered andesite were relatively safe because these herbivores avoid open spaces. Potential predators of seeds or seedlings of both pine species include jackrabbits (*Lepus californicus*), mule deer (*Odocoileus hemionus*), yellow pine chipmunks (*Tamias amoenus*), woodrats (*Neotoma* spp.), and deer mice (*Peromyscus maniculatus*). The importance of predation on *P. ponderosa* appeared to diminish with age as 2-yr-old saplings were virtually untouched by herbivores (D. J. Moore and R. M. Callaway, *personal observation*); however, different predation intensities on seedlings and saplings may have been confounded by the different years in which 4-mo-old and 2-yr-old *P. ponderosa* were tested. The use of greenhouse-grown, and potentially more palatable, seedlings may have overemphasized the effects of predation. Furthermore, because we did not conduct predator-exclosure experiments, the relative importance of predation in our study remains uncertain.

Artemisia shrubs also competed directly with *P. pon-*

derosa seedlings and saplings for soil water. Removal of *Artemisia* increased soil moisture and doubled the daily transpiration and photosynthetic rates of 4-month-old *P. ponderosa* seedlings and enhanced the survival and conductance of older, planted saplings. Competition for soil water from *Artemisia* also reduced the conductance of older, naturally occurring *P. ponderosa* saplings. Direct competitive and indirect predation effects may explain the absence of *P. ponderosa* seedlings and adults on unaltered andesite, and the restriction of this species to shrubless altered andesite. In a similar system in northwestern Mexico, Goldberg (1982, 1985) found that competition and high seed predation limited evergreen oaks to hydrothermally altered volcanic rock from which the otherwise dominant drought-deciduous trees were restricted by the nutrient-poor substrate.

An alternative, but not mutually exclusive, hypothesis for the restricted distribution of *P. ponderosa* is that altered andesite, because it was originally derived from hydrothermal activity, stores water differently than unaltered andesite. Curves of water potential vs. percent soil moisture differ between surface soils derived from altered and unaltered andesite (DeLucia et al. 1988). The structure of the underlying rock may also differ, as surface springs emerged on altered andesite near the DRI, Peavine Mt., and lower Virginia Mts. sites in the spring of 1993, following an exceptionally wet winter (R.M. Callaway and D. Moore, *personal observations*).

Our second hypothesis, that *Artemisia* facilitates *P. monophylla*, was also supported, and facilitative interactions also appeared to have both direct and indirect components. On unaltered andesite, a much higher proportion of naturally occurring seedlings were under shrub canopies than expected based on shrub cover. Although losses attributed to predation were significantly lower for *P. monophylla* than for *P. ponderosa* in general, shrubs provided indirect facilitation within the shrub matrix by reducing apparent predation. As for *P. ponderosa*, however, our conclusions regarding predation should be considered with caution in the absence of enclosure experiments.

Artemisia also appears to directly enhance survival of *P. monophylla* by favorably altering microclimate. Virtually all *P. monophylla* seedlings on altered andesite or in intershrub spaces eventually died from drought or temperature-related stress if they escaped predation. In contrast, none of the seedlings in the shade of shrubs died due to drought and temperature stress. Fowells (1965) reports that shade is important in the establishment of the similar pinyon species *P. edulis*. *Artemisia* also has the potential to directly facilitate neighbors via hydraulic lift (Richards and Caldwell 1987, Caldwell and Richards 1989). Shelter provided by *Artemisia* appears to have a cost: *Pinus monophylla* seedlings were smaller under shrubs than in the open or where shrubs had been cut, indicating that

while the overall effect of *Artemisia* on survival was positive, the survivors experienced reduced above-ground growth.

Facilitative interactions among other species also appeared to be mediated by a combination of direct and indirect mechanisms. In the Sonoran Desert, the beneficial effect of *Cercidium microflorum* on the saguaro, *Carnegie gigantea*, is due to both microclimate amelioration and protection from herbivores (Turner et al. 1966, 1969, Steenberg and Lowe 1969). Callaway (1992) found that positive effects of shrubs on *Quercus douglasii* were mediated by a combination of protection from predators and shade from shrub canopies. Valiente-Banuet and Ezcurra (1991) compared the relative importance of shade vs. protection from predation in the nurse-plant relationship between *Neobuxbaumia tetetzo*, a columnar cactus, and *Mimosa luisana* in the Viscaino Desert and the Gran Desierto de Altar in Mexico. They found that protection from predation improved survival, but that long-term survival occurred only when shade was provided.

Our third hypothesis, that *P. monophylla* is restricted from outcrops of altered andesite by the absence of *Artemisia* rather than by substrate characteristics, was supported by data that emphasized the general importance of nurse plants for *P. monophylla*, but not by field experiments using imitation nurse plants. *Pinus monophylla* has a high tolerance for altered andesite in the greenhouse (DeLucia et al. 1989), so if it requires the positive effects provided by *Artemisia*, the absence of *Artemisia* may explain the absence of *P. monophylla* adults on altered andesite.

Interspecific differences in our estimations of predation may have been due to dissimilar morphologies and chemical components of seeds and seedlings. The seeds of *P. monophylla* are dispersed by animals and are much larger than the wind-dispersed seeds of *P. ponderosa*. Larger seeds both are likely to be more attractive to some predators and have a higher probability of being found. Vander Wall (1992, 1993) documented the importance of chipmunk dispersal of *P. jefferyi* seeds, indicating that predation rates on yellow pines may be high. On the other hand, the leaves of the *P. monophylla* seedlings in our experiments were tougher, had sharper leaf tips, and appeared much more aromatic and resin-filled than those of *P. ponderosa*. These characteristics may have deterred predation on *P. monophylla* seedlings relative to *P. ponderosa*.

The mechanisms by which *Artemisia* directly facilitates *P. monophylla* but competes with *P. ponderosa* are not clear; however, both interactions have been attributed to the conservative water-use strategies of these pines (DeLucia et al. 1988, Drivas and Everett 1989). DeLucia et al. (1988) maintained that *Artemisia*, with relatively low WUEs and high transpiration rates, outcompeted the water-conservative *P. ponderosa* by using soil water before the latter could. *Pinus monophylla*, however, has even higher WUEs than *P. pon-*

derosa (Table 6 and DeLucia et al. 1988, 1989), yet it is facilitated by *Artemisia*. Perhaps conservative water relations conferred a disadvantage for both *P. ponderosa* and *P. monophylla* when growing with *Artemisia*, but only *P. monophylla* was conservative enough to withstand the long periods of drought induced by *Artemisia* during the seedling stage. Jaindl et al. (1993) found that *P. monophylla* did not displace another Great Basin shrub, *Cercocarpus ledifolius*, as it appears to do to many other shrubs. As for *Artemisia* and *P. ponderosa* (see DeLucia et al. 1988), rapid transpiration and depletion of soil moisture by *Cercocarpus* were cited as the factors preventing invasion by *P. monophylla*. Predawn water potentials of *Cercocarpus* (Jaindl et al. 1993) were not lower than those of *Artemisia* (DeLucia et al. 1988), so why the low growth rates and high WUE of *P. monophylla* would promote its competitive exclusion by *Cercocarpus* but also its facilitation by *Artemisia* is unclear. DeLucia et al. (1989) speculated that lower growth and respiration rates also may confer higher probabilities of *P. monophylla* surviving extended periods of low soil water availability than *P. ponderosa*. We suspect that the comparatively thick leaves and stems of *P. monophylla* were more susceptible to overheating, high respiration losses, and photoinhibition when stomata were closed and seedlings were exposed to full sun, than those of *P. ponderosa*. Differences in root architecture between *P. ponderosa* and *P. monophylla* may also have played an important role in their interactions with *Artemisia*.

Our experimental results support a number of studies in which spatial associations or species variation with plot age have been cited as evidence for the facilitative effect of *Artemisia* on *P. monophylla* or *P. edulis* (Phillips 1909, Drivas and Everett 1989, Weldon et al. 1990). Shrub facilitation of pinyon pine appears to affect patterns of invasion and replacement in the Great Basin (Woodbury 1947, Blackburn and Tueller 1970, Barney and Frischknecht 1974, Tausch et al. 1981, Eddleman and Jaindl 1991).

Considered together, our results suggest that the absence of *Artemisia* on altered andesite created refuges for *P. ponderosa* because of reduced competition from *Artemisia*, but created unfavorable habitat without the biotic safe-sites required by *P. monophylla*. Whether *Artemisia* competed with or facilitated neighboring pine species appeared to depend on subtle differences in palatability to predators, gas exchange, thermal tolerances, and responses to light.

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