Edaphic limitations to growth and photosynthesis in Sierran and Great Basin vegetation

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Summary. Soils derived from hydrothermally altered andesite support unique communities of Sierran conifers (*Pinus ponderosa* Laws. and *P. jeffreyi* Grev. and Balf.) amongst sagebrush (*Artemisia tridentata* Nutt.) vegetation in the western Great Basin. Plants grown in soil derived from hydrothermally altered bedrock had lower growth rates, total biomass, and net photosynthetic rates than plants grown in soil derived from unaltered andesite of the same formation. Total dry mass was 10 to 28% lower for conifers grown in altered soil whereas dry mass of *Artemisia tridentata* and *Bromus tectorum* L. was reduced by over 90%. Results from a nutrient amendment experiment indicated that low phosphorus was the dominant limitation in altered soil, and phosphorus-deficiency affected growth primarily by limiting leaf area development rather than direct inhibition of photosynthesis. The proportionately greater reduction of biomass for *Artemisia* and *Bromus* grown in altered soil supports our hypothesis that Great Basin vegetation is excluded from altered soil by intolerance to nutrient deficiency. The Sierran conifers growing on this rock type are therefore free of competition for water with Great Basin vegetation and are able to persist in an exceptionally dry climate.

Key words: *Artemisia tridentata* – *Bromus tectorum* – *Pinus jeffreyi* – *Pinus monophylla* – *Pinus ponderosa*

Soils derived from hydrothermally altered bedrock support unique "edaphic" communities with striking differences in physiognomy and composition (Billings 1950; Goldberg 1982). In the western Great Basin soils derived from hydrothermally altered andesites support open woodland communities of Sierran conifers, primarily *Pinus ponderosa* Laws. and *P. jeffreyi* Grev. and Balf., in the midst of sagebrush vegetation (*Artemisia tridentata* Nutt.) (Billings 1950). Isolated stands of Sierran conifers on hydrothermally altered rock are located in the desert as much as 60 km east of the continuous Sierran montane forests. Few Great Basin species occur on soil derived from altered rock, and Sierran conifers are completely excluded from the matrix of Great Basin vegetation. Goldberg (1982, 1985), studying a similar situation in the Sierra Madre of Mexico, observed that evergreen oaks were restricted to altered parent materi-

al, whereas deciduous oaks were dominant on surrounding native soils.

Soils derived from altered rock are acidic and in many cases have low concentrations of cations, nitrogen, and phosphorus (Billings 1950; Salisbury 1954, 1964; Schlesinger et al. 1988). As a result of lower vegetation cover, higher soil water availability is maintained on altered rock during the growing season (DeLucia et al. 1988). We hypothesize that Great Basin species are excluded from soils derived from altered rock by intolerance to nutrient deficiency, whereas competition for water prevents the establishment of Sierran conifers in the adjacent Great Basin vegetation. Implicit in this hypothesis is that native Great Basin vegetation is more drought tolerant but less tolerant of nutrient deficiency than adjacent Sierran vegetation. In late summer Great Basin shrubs maintain higher stomatal conductances and photosynthetic rates at substantially lower water potentials than Sierran conifers growing nearby (DeLucia et al. 1988 and unpublished data).

The low phosphorus of soils derived from hydrothermally altered andesite are a convenient medium to examine the response of dominant Great Basin and Sierran species to nutrient deficiency. In this paper we examine the effect of soils derived from hydrothermally altered and unaltered andesite on growth, biomass allocation, and photosynthesis in several Great Basin and Sierran species. Experiments were conducted with potted plants in growth chambers using field-collected soils.

Materials and methods

Pinus ponderosa and *P. jeffreyi* were selected as representative Sierran species. These species occur in the western Great Basin but are restricted to soil derived from hydrothermally altered rock. *Pinus monophylla* Torr. and Frem. grows on altered soil, although at considerably lower basal area and density than on soils derived from unaltered andesite (DeLucia et al. 1988) and was chosen as a representative Great Basin conifer. *Artemisia tridentata* and *Bromus tectorum* L. were selected as a Great Basin shrub and herbaceous annual, respectively. *Artemisia* and *Bromus* are widely distributed in the Great Basin but are largely excluded from altered soils.

Seeds from *Pinus ponderosa* and *P. jeffreyi* were collected near Reno, Nevada, from trees growing in altered soil on the southeast shoulder of Peavine Mountain and from *P. monophylla* growing in unaltered soil at a comparable

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elevation in the Virginia Mountains south of Reno. Seeds from *Artemisia* and *Bromus* were collected from plants growing in unaltered soil near the Desert Research Institute in Reno. Collections were made from open-pollinated plants in the fall of 1985.

Soils derived from altered and unaltered andesite were collected from adjacent sites on the southeast shoulder of Peavine Mountain. Soil was collected to a depth of 10 cm and was passed through a screen with 0.6-cm mesh. The typical brown desert soils of the Great Basin are Xerollic Haplargids derived from andesites. Soils developed from hydrothermally altered andesites are shallow Lithic Entisols (Billings 1950; Schlesinger et al. 1988). The two soil types were subsampled and sieved to 2-mm mesh for chemical and physical analyses as described by Schlesinger et al. (1988). The altered and unaltered soil used in the following experiments are classified as a sandy-clay-loam and clay, respectively. Total nitrogen is the same in both soils (0.05%) but in 1:5 water extracts pH and calcium in altered soil are 5.37 and 0.40 µg/l, respectively, compared to 7.25 and 7.80 µg/l, respectively, in unaltered soil. Available phosphorus (Olsen's HCO_3^- P) in altered and unaltered soil is 8.8 and 27.6 µg/g, respectively (Schlesinger et al. 1988).

In the first experiment *Pinus ponderosa*, *P. jeffreyi*, and *P. monophylla* were grown in 500-ml pots containing field-collected soils derived from hydrothermally altered or unaltered andesite. The bottom of each pot was filled with 3 cm of washed river gravel to facilitate drainage. After stratification at 5° C for 6 weeks, five seeds were planted per pot, and seedlings were thinned to one per pot soon after emergence. Following 89 days in a greenhouse plants were randomly sorted into two groups for an initial and final harvest. Plants comprising the final harvest were then moved into a growth chamber and grown for an additional 79 days. Environmental conditions in the chamber were: irradiance, 700 µmol s^{-1} m^{-2} (PAR) at pot height; day temperature, 25° C; night temperature, 15° C; relative humidity, 70% day and night; photoperiod, 16 h. At each harvest the dry mass (60° C until constant mass) of roots, stems, and needles was determined, and total needle area was estimated by the bead method (Thompson and Leyton 1971). Before the final harvest, gas exchange measurements were made on five randomly selected seedlings of each species growing in altered or unaltered soil.

The effects of nutrient additions on *Pinus ponderosa* and *P. monophylla* grown in altered soil were examined in a second experiment. Seedlings were grown for 54 days in a greenhouse and then randomly sorted into seven groups. One group was harvested and the other six were transferred to a growth chamber and grown for an additional 80 days with various nutrient amendments. The nutrient treatments were: ALL, 1/2 strength modified Hoagland's solution; NP, nitrogen and phosphorus only; N, nitrogen only; P, phosphorus only; CAT, Mg, Ca, and K; NONE, distilled water (DW). Nutrient concentrations were equivalent to the concentrations in 1/2 strength modified Hoagland's, and N, P, and CAT were added as NO_3NH_4 (9.5 mol N m^{-3}), $NaPO_4$ (1 mol P m^{-3}), and chloride salts, respectively. Nutrient solution (50 mL) was added to each pot in the morning and the same amount of DW was added in the late afternoon. The "NONE" treatment received DW at both times. Gas exchange measurements were made on randomly selected seedlings prior to the final harvest.

In a third experiment the effect of soil type on growth of *Artemisia* and *Bromus* was examined. Plants were grown from seeds under the same environmental conditions as in the previous experiments, except that relative humidity was maintained at 50% (24 h). Seeds were planted in 1000-ml pots filled with mixtures of altered and unaltered soil or a standard greenhouse potting mix (2 loam:1 perlite:1 peat moss, v/v). Altered (A) and unaltered (U) soil were mixed by volume in the following ratios: OA/3U, 1A/2U, 2A/1U, and 3A/OU. In each case perlite (33%, v/v) was added to field-collected soils to facilitate aeration. Seeds of both species were planted at the same time but because *Artemisia* had a slower growth rate, the initial harvest was 14 days later than for *Bromus*. Plants were randomly assigned to two groups for an initial and final harvest, and the initial harvest was done after 23 and 37 days for *Bromus* and *Artemisia*, respectively. The final harvest was done after 15 days for both species. *Bromus* shoots were divided into leaves and stems at the base of the leaf blades, and leaf areas for both species were determined with a leaf-area meter (LICOR 3000). Plants were watered daily and those growing in the greenhouse soil were fertilized once per week with 12N:31P:14K. Gas exchange measurements were not made in this experiment.

The harvest data were used to calculate relative growth rate (RGR) and net assimilation rate (NAR) by the equations of Evans (1972). Plants from each harvest were ranked by total dry mass and growth analysis parameters were calculated using similarly ranked pairs of plants from the initial and final harvests. NAR was calculated on a total leaf area basis for the conifers and a projected leaf area basis for *Artemisia* and *Bromus* and is therefore not directly comparable. The data were analyzed with either a 2-way or 1-way ANOVA ($P \leq 0.05$), depending on the experiment, and the HSD multiple range test (SAS Institute).

Net photosynthesis and transpiration were measured on conifer seedlings with an open IR gas analysis system. The shoot was sealed in a well-mixed, temperature- and humidity-controlled cuvette. Foliage temperatures inside the cuvette were measured by looping fine-wire thermocouples around individual needles. The CO_2 and H_2O concentrations before and after the cuvette were measured with an ADC 225 IRGA and General Eastern dew point hygrometers, respectively. The air was mixed to 21% O_2 and 0.035% CO_2 from bottled gas using mass flow valves (Tylan). Gas exchange was measured under conditions of saturating irradiance (1200 µmol s^{-1} m^{-2}, PAR) and at an air temperature and VPD of 25° C and 1kPa, respectively. Net photosynthesis, stomatal conductance, and intercellular CO_2 concentration (c_i) were calculated on a total leaf surface area and dry mass basis using the equations of von Caemmerer and Farquhar (1981).

Nitrogen and phosphorus analyses of foliage were performed by the Agronomy Analytical Laboratory at Cornell University. Tissue was dried to 90° C before analysis of total N using a Perkin Elmer CHN Analyzer, and P was determined in dry ash following Greweling (1976). Replicate samples often were combined to obtain enough foliage for analysis. Nutrient data therefore were not treated statistically.

Results

Plants grown in soil from altered rocks generally accumulated less total dry mass and leaf area over the growth

Table 1. The effect of soil type on biomass and growth parameters for *Pinus monophylla*, *P. ponderosa*, and *P. jeffreyi*. Species and soil effects were tested with a 2-way ANOVA and are designated by SP and SO, respectively. The probability level for all statistical tests was $P \leq 0.05$. Interspecific differences within a soil type were determined with the HSD multiple range test. A *t*-test was used to compare means within a species but for different soil types and an asterick designates that means are significantly different. $N = 13$ to 16 ± 1 SD

Species/soil	Biomass and growth analysis				
	Total DW (g)	RGR (g g⁻¹ d⁻¹)	NAR (g m⁻² d⁻¹)	Root/shoot (g g⁻¹)	Leaf area (cm²)
Pinus monophylla					
altered soil	0.3724 ± 0.1239[a]*	0.0074 ± 0.0020[a]*	1.794 ± 0.529*	0.56 ± 0.29[a]	16.2 ± 5.1[a]*
unaltered soil	0.4585 ± 0.1022[a]	0.0108 ± 0.0016[a]	2.861 ± 0.620[a]	0.57 ± 0.25[a]	20.5 ± 3.5[a]
Pinus ponderosa					
altered soil	0.8137 ± 0.1753[b]*	0.0138 ± 0.0015[b]*	1.872 ± 0.219*	0.84 ± 0.17[b]	62.9 ± 15.6[b]*
unaltered soil	1.1313 ± 0.2312[b]	0.0240 ± 0.0009[b]	3.137 ± 0.270[b]	0.95 ± 0.11[b]	80.0 ± 17.3[b]
Pinus jeffreyi					
altered soil	0.9411 ± 0.1568[b]	0.0131 ± 0.0009[b]*	1.740 ± 0.162*	0.96 ± 0.13[b]	65.2 ± 12.4[b]
unaltered soil	1.0473 ± 0.2774[b]	0.0173 ± 0.0012[c]	2.281 ± 0.278[b]	1.06 ± 0.17[b]	67.3 ± 19.8[b]
	SP, SO	SP, SO SP × SO	SP, SO SP × SO	SP	SP, SO

Table 2. The effect of soil type on biomass and growth analysis parameters for *Artemisia tridentata* and *Bromus tectorum*. Plants were grown in greenhouse (GH), altered (A), or unaltered (U) soil, or a mixture of A and U. Soil effects within a species were analyzed by a 1-way ANOVA and HSD multiple range test. Means designated with different letters are different at $P \leq 0.05$. $N = 9$ to 10 ± 1 SD

Species/soil	Biomass and growth analysis				
	Total DW (g)	RGR (g g⁻¹ d⁻¹)	NAR (g m⁻² d⁻¹)	Root/shoot (g g⁻¹)	Leaf area (cm²)
Artemisia tridentata					
greenhouse soil	0.7290 ± 0.2311[a]	0.0841 ± 0.0154[a]	20.404 ± 4.583[a]	0.39 ± 0.09[a]	24.1 ± 7.2[a]
altered soil (A)	0.0103 ± 0.0018[b]	0.0539 ± 0.0193[b]	26.553 ± 1.467[ac]	0.63 ± 0.10[ab]	0.3 ± 0.04[b]
2(A):1(U)	0.1160 ± 0.0664[bc]	0.0650 ± 0.0216[ab]	36.501 ± 11.833[bc]	0.72 ± 0.28[ab]	2.4 ± 1.4[bc]
1(A):2(U)	0.2636 ± 0.0809[c]	0.0639 ± 0.0154[ab]	39.429 ± 12.815[b]	1.11 ± 0.97[b]	4.9 ± 2.3[c]
unaltered soil (U)	0.2708 ± 0.0746[c]	0.0642 ± 0.0084[ab]	44.787 ± 5.367[b]	0.94 ± 0.21[ab]	4.1 ± 1.2[bc]
Bromus tectorum					
greenhouse soil	1.3899 ± 0.1339[a]	0.1543 ± 0.0110[a]	13.378 ± 1.201[a]	0.63 ± 0.15[a]	70.1 ± 11.6[a]
altered soil (A)	0.0213 ± 0.0094[b]	0.0407 ± 0.0217[c]	29.074 ± 25.427[b]	0.87 ± 0.32[a]	0.7 ± 0.4[b]
2(A):1(U)	0.1659 ± 0.0253[c]	0.1008 ± 0.0109[b]	21.361 ± 3.221[ab]	1.35 ± 0.19[b]	5.3 ± 1.1[bc]
1(A):2(U)	0.2677 ± 0.0570[d]	0.0936 ± 0.0047[b]	24.119 ± 6.636[ab]	1.34 ± 0.21[b]	7.7 ± 2.2[c]
unaltered soil (U)	0.2150 ± 0.0436[cd]	0.0903 ± 0.0061[b]	22.955 ± 4.704[ab]	1.33 ± 0.18[b]	6.3 ± 1.2[bc]

interval and pines grown in altered soil had lower relative growth rates (RGR) and net assimilation rates (NAR) than those grown in unaltered soil (Tables 1 and 2). The magnitude of the response, however, was different for each species. Total dry mass of conifers was approximately 10 to 28% lower when grown in altered soil (Table 1), whereas dry mass of *Artemisia* and *Bromus* grown in altered soil was reduced by 90% (Table 2). Similarly, leaf area for *Artemisia* and *Bromus* was lower when grown in altered soil and the percentage difference was substantially greater than for the conifers. The largest difference in biomass and leaf area for *Artemisia* and *Bromus* grown in mixtures of field-collected soils occurred between the 1A/2U and 3A/OU treatments (Table 2). Because of the high clay content in unaltered soil, the addition of up to 33% (v/v) altered soil may have improved the texture of the mix resulting in slightly greater biomass accumulation for *Bromus*.

Interspecific differences in the allocation of carbon to root and shoot growth were observed for the conifers, but soil type had no effect. A lower root:shoot ratio was measured for *Pinus monophylla* than for the Sierran pines (Table 2). For *Bromus* root growth was more strongly inhibited than shoot growth in altered soil causing a decrease in root:shoot ratio (Table 2). A similar trend was observed for *Artemisia*.

Nutrient amendments had no statistically significant ($P \leq 0.05$) effect on biomass or other growth parameters for *Pinus monophylla* (Table 3). *Pinus ponderosa*, however, responded strongly. The addition of nitrogen and phosphorus together resulted in greater total dry mass and RGR relative to the controls (NONE). When added separately phosphorus caused greater biomass and growth rate than nitrogen (Table 3). The stimulation of growth for *P. ponderosa* by phosphorus appeared to operate primarily through enhanced leaf area development rather than by direct stimulation of photosynthetic capacity. Phosphorus amendment caused approximately 38% greater leaf area in *P. ponderosa*, but no significant change in NAR or net photosynthe-

Table 3. The effect of nutrient amendments on biomass and growth parameters for *Pinus monophylla* and *P. ponderosa* grown in altered soil. See Methods for explanation of nutrient additions. Species (SP) and nutrient (NU) effects were tested with a 2-way ANOVA and significant differences are designated by the abbreviations at the bottom of each column. Nutrient effects within a species were tested with a 1-way ANOVA and HSD multiple range test. Means designated by a different letter are different at $P \leq 0.05$. $N = 8$ to 9 ± 1 SD

	Biomass and growth analysis				
	Total DW (g)	RGR (g g^{-1} d^{-1})	NAR (g m^{-2} d^{-1})	Root/shoot (g g^{-1})	Leaf area (cm^2)
Pinus monophylla					
Altered Soil$^+$					
ALL	0.5363 ± 0.1930^a	0.0144 ± 0.0013^a	2.921 ± 0.125^a	0.57 ± 0.09^a	23.3 ± 8.6^a
NP	0.5123 ± 0.1303^a	0.0142 ± 0.0009^a	3.102 ± 0.261^a	0.62 ± 0.10^a	21.1 ± 6.1^a
N	0.4895 ± 0.1148^a	0.0137 ± 0.0014^a	3.040 ± 0.285^a	0.63 ± 0.11^a	20.4 ± 4.4^a
P	0.5041 ± 0.1328^a	0.0140 ± 0.0020^a	3.150 ± 0.291^a	0.65 ± 0.12^a	20.3 ± 5.1^a
CAT	0.4260 ± 0.0489^a	0.0122 ± 0.0028^a	2.975 ± 0.197^a	0.57 ± 0.08^a	18.2 ± 2.0^a
NONE	0.4983 ± 0.1096^a	0.0140 ± 0.0016^a	3.165 ± 0.389^a	0.67 ± 0.21^a	20.0 ± 4.2^a
Pinus ponderosa					
Altered Soil$^+$					
ALL	1.3543 ± 0.2073^b	0.0356 ± 0.0024^b	1.575 ± 0.178^b	0.77 ± 0.17^b	109.6 ± 17.9^b
NP	1.7601 ± 0.3672^a	0.0388 ± 0.0015^a	1.543 ± 0.174^b	0.73 ± 0.12^b	144.2 ± 26.2^a
N	0.8762 ± 0.1521^c	0.0300 ± 0.0021^c	1.806 ± 0.143^{ab}	0.97 ± 0.17^{ab}	61.6 ± 10.9^c
P	1.3747 ± 0.2863^b	0.0356 ± 0.0011^b	1.700 ± 0.186^{ab}	0.96 ± 0.20^{ab}	104.6 ± 27.4^b
CAT	0.7728 ± 0.0906^c	0.0285 ± 0.0022^c	1.734 ± 0.258^{ab}	0.96 ± 0.26^{ab}	56.9 ± 6.0^c
NONE	0.9510 ± 0.1533^c	0.0311 ± 0.0023^c	1.893 ± 0.171^a	1.12 ± 0.18^a	64.3 ± 14.1^c
	SP, NU (SP)	SP, NU (SP)	SP, NU (SP)	SP, NU (SP)	SP, NU (SP)

Table 4. The effect of soil type on gas-exchange characteristics of *Pinus monophylla*, *P. ponderosa*, and *P. jeffreyi*. The ratio of intercellular to ambient CO_2 concentration is designated c_i/c_a. Data were analyzed as in Table 2. $N = 5 \pm 1$ SD

| Species/soil	Gas-exchange				
	Net photosynthesis (μmol m^{-2} s^{-1})	Transpiration (mmol m^{-2} s^{-1})	Conductance (mmol m^{-2} s^{-1})	WUE (mmol CO_2 mol H_2O^{-1})	c_i/c_a
Pinus monophylla					
altered soil	1.3 ± 0.3^a	$0.2 \pm 0.1^{a*}$	$19 \pm 3^{a*}$	$0.0062 \pm 0.0012^{a*}$	$0.66 \pm 0.05^{a*}$
unaltered soil	1.8 ± 0.3^b	0.5 ± 0.1^b	53 ± 11^a	0.0036 ± 0.0001^b	0.81 ± 0.01^a
Pinus ponderosa					
altered soil	$1.5 \pm 0.2^{a*}$	0.6 ± 0.1^b	80 ± 10^b	$0.0023 \pm 0.0002^{b*}$	$0.87 \pm 0.01^{b*}$
unaltered soil	1.9 ± 0.2^b	0.6 ± 0.1^b	81 ± 4^b	0.0031 ± 0.0003^b	0.84 ± 0.01^b
Pinus jeffreyi					
altered soil	1.8 ± 0.3^a	$0.4 \pm 0.1^{c*}$	$45 \pm 8^{c*}$	$0.0044 \pm 0.0008^{c*}$	$0.77 \pm 0.05^{c*}$
unaltered soil	2.0 ± 0.3^b	0.6 ± 0.1^b	71 ± 10^b	0.0034 ± 0.0003^b	0.83 ± 0.02^b
	SP, SO	SP, SO, SP $\times$ SO	SP, SO, SP $\times$ SO	SP, SP $\times$ SO	SP, SO, SP $\times$ SO

sis (Tables 3 and 5). The addition of cations to altered soil, either as a group or as part of the "ALL" treatment, had a detrimental effect and may have accumulated to inhibitory levels in the soil.

Photosynthesis and stomatal conductance were consistently lower in pines grown in altered soil, but the magnitude of the response depended on the species and differences were not always statistically significant (Table 4). A 20% to 30% reduction in photosynthesis was observed for *Pinus monophylla* and *P. ponderosa* grown in altered soil, but a less than 10% reduction was observed for *P. jeffreyi*. The intercellular CO_2 concentration, indicated by the ratio c_i/c_a,

was lower for *P. monophylla* and *P. jeffreyi* grown in altered soil indicating that the reduction in photosynthesis may be due in part to a stomatal limitation. No consistent trend was observed for the effect of altered soil on water-use efficiency (WUE); however, *P. monophylla*, a Great Basin conifer, maintained a higher WUE than the two Sierran conifers, *P. ponderosa* and *P. jeffreyi*. As with the growth data nutrient amendments had no significant effect on net photosynthesis, conductance, or transpiration for *P. monophylla* (Table 5). Net photosynthesis was stimulated in *P. ponderosa* by the addition of nitrogen and phosphorus together. The addition of nitrogen and phosphorus caused

Table 5. The effect of nutrient amendment on gas exchange characteristics of *Pinus monophylla* and *P. ponderosa*. Data were analyzed as in Table 4. $N = 5 \pm 1$ SD

Species/nutrient	Gas-exchange Net photosynthesis $(\mu mol\ m^{-2}\ s^{-1})$	Transpiration $(mmol\ m^{-2}\ s^{-1})$	Conductance $(mmol\ m^{-2}\ s^{-1})$	WUE $(mmol\ CO_2\ mol\ H_2O^{-1})$	C_i/C_a
Pinus monophylla					
Altered soil[+]					
ALL	2.5 ± 0.7^a	0.3 ± 0.1^a	34 ± 9^a	0.0072 ± 0.0013^{ab}	0.62 ± 0.06^{ab}
NP	2.5 ± 0.4^a	0.3 ± 0.1^a	32 ± 7^a	0.0077 ± 0.0006^{ab}	0.60 ± 0.03^{ab}
N	2.7 ± 0.7^a	0.3 ± 0.1^a	32 ± 13^a	0.0082 ± 0.0017^b	0.55 ± 0.12^b
P	1.7 ± 1.0^a	0.3 ± 0.2^a	30 ± 20^a	0.0056 ± 0.0025^{ab}	0.66 ± 0.13^{ab}
CAT	1.8 ± 0.4^a	0.3 ± 0.1^a	31 ± 13^a	0.0060 ± 0.0017^{ab}	0.67 ± 0.11^{ab}
NONE	2.1 ± 0.3^a	0.4 ± 0.1^a	45 ± 10^a	0.0048 ± 0.0007^a	0.75 ± 0.04^a
Pinus ponderosa					
Altered soil[+]					
ALL	3.2 ± 0.4^{ab}	0.5 ± 0.1^{ab}	82 ± 7^{ab}	0.0058 ± 0.0016^{ab}	0.75 ± 0.02^{ab}
NP	3.3 ± 0.6^a	0.3 ± 0.1^c	46 ± 6^c	0.0097 ± 0.0023^b	0.57 ± 0.09^c
N	2.4 ± 0.6^{ab}	0.7 ± 0.1^{ab}	92 ± 11^a	0.0034 ± 0.0010^{ab}	0.82 ± 0.05^{ab}
P	2.4 ± 0.3^{ab}	0.5 ± 0.1^b	70 ± 18^b	0.0046 ± 0.0030^{ab}	0.72 ± 0.07^b
CAT	2.0 ± 0.7^b	0.7 ± 0.0^a	89 ± 9^{ab}	0.0033 ± 0.0004^a	0.86 ± 0.04^a
NONE	2.0 ± 0.9^b	0.6 ± 0.1^{ab}	85 ± 7^{ab}	0.0026 ± 0.0016^a	0.84 ± 0.07^{ab}
	SP, NU	SP, NU, SP × NU	SP, NU, SP × NU	SP, NU, SP × NU	SP, NU, SP × NU
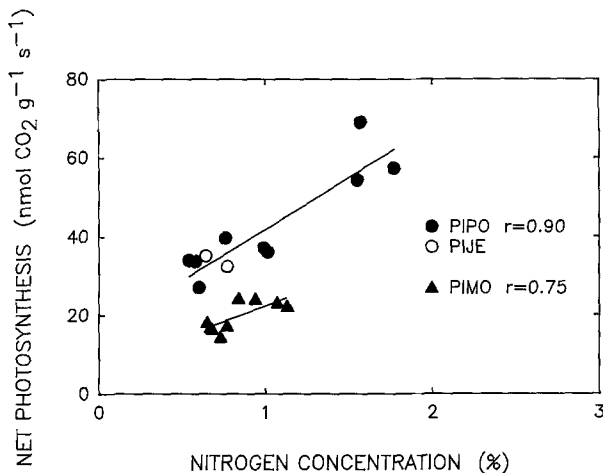
Fig. 1. Net photosynthesis versus foliage nitrogen concentration for *Pinus ponderosa* (PIPO, ●), *P. jeffreyi* (PIJE, o), and *P. monophylla* (PIMO, ▲). Photosynthesis and nitrogen content are expressed on a dry mass basis. The photosynthetic data were recalculated from Tables 4 and 5. Some data were omitted because insufficient tissue was available for N determination. The slopes of the regression lines are significantly different from 0 at $P \le 0.05$

a decrease in the c_i/c_a ratio suggesting a shift from biochemical to stomatal limitation of CO_2 uptake. Nutrient amendment generally caused an increase in WUE.

Photosynthetic rates for the pines were significantly correlated with foliage nitrogen content but not with phosphorus (Fig. 1). The Sierran pines, *Pinus ponderosa* and *P. jeffreyi*, had higher leaf nitrogen contents, photosynthetic rates, and photosynthetic nitrogen-use efficiencies than *P. monophylla*. The average photosynthetic nitrogen-use efficiency (PNUE defined as the rate of net photosynthesis per unit foliage N) for *P. ponderosa* and *P. jeffreyi* was

$63.6 \pm 14.3\ \mu mol\ CO_2\ mol\ N^{-1}\ s^{-1}$ compared to 33.6 ± 4.6 for *P. monophylla*.

Discussion

Plants grown in soil derived from hydrothermally altered bedrock had lower relative growth rates, net photosynthetic rates, and total biomass than plants grown in unaltered soil. The percentage decrease in growth, however, was substantially greater for *Artemisia* and *Bromus* than for the conifers. Our results are consistent with Billings' (1950) observations of lower growth rates and higher mortality for *Artemisia* grown in altered soil, which supports our hypothesis that typical Great Basin species are excluded from altered soil by intolerance to nutrient deficiency. Similarly, Goldberg (1985) found that deciduous *Quercus* species do not become established on acidic altered soils in northwest Mexico unless soil pH is increased.

The primary limitation in altered soil may be the availability of phosphorus. The concentration of extractable phosphorus in soil derived from altered rock from several widely located sites in the Great Basin and adjacent Sierra Nevada is uniformly low, which is probably a result of complexation with iron and aluminum minerals under acidic conditions (Schlesinger et al. 1988; Salisbury 1964). Billings (1950) reported phosphorus deficiency symptoms in crop species growing in altered soil. Although phosphorus deficiency symptoms, characterized by the development of red leaf tips, did not develop in *Artemisia* during our experiment, these symptoms did appear in the Sierran pines and *Bromus*. Moreover, the addition of phosphorus caused a greater increase in total dry weight and RGR for *Pinus ponderosa* than the addition of nitrogen (Table 4).

The factors contributing to lower rates of net photosynthesis for plants grown in altered soil are complex. In many

species nitrogen and phosphorus contents can effect photosynthesis at the biochemical level (Field and Mooney 1986; Brooks 1986; Morrison and Batten 1986; Foyer and Spencer 1986). For the pines photosynthesis was positively correlated with tissue nitrogen concentration (Fig. 1). But the concentration of nitrogen and phosphorus in foliage was consistently higher for pines grown in altered soil (10–22% higher for N and 0–25% higher for P) suggesting that photosynthesis was not directly limited by these nutrients.

Low phosphorus may have induced structural and physiological changes that indirectly inhibited the rate of net photosynthesis. An increase in stomatal sensitivity to leaf water potential and a decrease in root hydraulic conductivity has been observed in phosphorus-deficient cotton (Radin 1984; Radin and Eidenbock 1984). A decrease in hydraulic conductivity in the pines could reduce stomatal conductance and thus decrease photosynthesis. The lower intercellular CO_2 concentration for *Pinus monophylla* and *P. jeffreyi* grown in altered soil indicates that photosynthesis was partially limited by stomatal conductance, consistent with these indirect effects of phosphorus on photosynthesis. A clear picture of the effect of growth in altered soil on photosynthesis requires further investigation.

The prevailing effect of phosphorus limitation on biomass accumulation appeared to be its influence on leaf area development rather than on photosynthesis. Despite a slight increase in the photosynthetic rate for *P. ponderosa* following fertilization with a combination of nitrogen and phosphorus, the net assimilation rate (NAR) was lower in fertilized plants. Fertilization with phosphorus, however, caused a substantial increase in leaf area. Although photosynthetic rates were not measured for *Artemisia* and *Bromus*, growth in altered soil caused a proportionately larger decrease in leaf area than in the growth rate parameters (Table 2); NAR was actually greater for *Bromus* grown in altered soil than in soils from unaltered rock. Phosphorus deficiency severely inhibits leaf expansion in cotton and appears to do so by reducing the hydraulic conductivity of the root system thereby decreasing turgor pressure (Radin and Eidenbock 1984).

Relative to the Sierran pines, *Pinus monophylla* displayed characteristics typically associated with stress tolerant species, including low RGR (Grime 1979) and an extremely limited response to nutrient addition (Chapin 1980). Stomatal closure for *Pinus monophylla* under field conditions occurs at approximately the same water potential as for *P. ponderosa* and *P. jeffreyi* (-1.8 MPa), however, *P. monophylla* has a higher water-use efficiency than the Sierran conifers (Drivas and Everett 1988; DeLucia et al. 1988, Table 4). Water-use efficiency (WUE) for the conifers was inversely related to photosynthetic nitrogen-use efficiency (PNUE) with *P. monophylla* having the highest WUE and the lowest PNUE. This is consistent with the hypothesis proposed by Field et al. (1983) that a physiological compromise exists between WUE and PNUE. Efficient utilization of water is thought to be an important adaptation of plants to xeric habitats (Turner and Kramer 1980). However, based on carbon isotope analysis *Artemisia* ($\delta^{13}C \sim -24.2\%_{0}$) has lower WUE than Great Basin conifers ($\delta^{13}C \sim -20.2\%_{0}$) or Sierran conifers ($\delta^{13}C \sim -21.8$ to $23.0\%_{0}$) (DeLucia et al. 1988). Where competition for water may be intense low WUE but a high degree of drought tolerance, as is seen for *Artemisia*, may be favorable.

Great Basin vegetation is characterized by low semideciduous shrubs such as *Artemisia* that possess a suite of morphological and physiological adaptations to drought (Caldwell 1985). These plants have evolved in circumneutral soils with relatively high nutrient availability and are not adapted to the nutrient-limited conditions of altered soil. In contrast conifers, including the Great Basin conifers, have a number of characteristics including evergreenness, low growth rates, and well developed mycorrihzal associations that enable them to persist in nutrient-poor soil (Chapin 1980, 1983; Chabot and Hicks 1982; Waring and Schlesinger 1985; Vitousek 1982). In addition, the Sierran pines growing on soil derived from altered rock have higher phosphorus and nitrogen retranslocation efficiencies and growth per unit nutrient uptake than *Artemisia* growing on adjacent native soil (Schlesinger et al. 1988). Intolerance of Great Basin vegetation to nutrient-poor conditions may play an important role in the maintenance of disjunct stands of Sierran conifers on altered rock. The Sierran conifers growing on this rock type do not have to compete for water with Great Basin vegetation and therefore are able to persist in a dry climate that is out of their normal range.

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