NUTRIENT-USE EFFICIENCY OF WOODY PLANTS ON CONTRASTING SOILS IN THE WESTERN GREAT BASIN, NEVADA[1]

WILLIAM H. SCHLESINGER
Department of Botany, Duke University, Durham, North Carolina 27706 USA

EVAN H. DELUCIA
Department of Plant Biology, University of Illinois, Urbana, Illinois 61801 USA

AND

W. D. BILLINGS
Department of Botany, Duke University, Durham, North Carolina 27706 USA

Abstract. Soils that develop on areas of hydrothermally altered rock in the western Great Basin of Nevada support Sierran conifers, such as *Pinus ponderosa*, in a desert climate. These soils have low pH (≈ 3.7) and low concentrations of HCO_3^--extractable P (5.6 µg/g), compared to adjacent brown desert soils supporting sagebrush (*Artemisia tridentata*) vegetation. The occurrence of Sierran conifers appears to be related to their tolerance of the unusual soil chemistry, high nutrient-use efficiency in growth, high reabsorption of foliar nutrients before leaf abscission, and slow growth rates. Most of these traits appear to be inherent characteristics of evergreen vegetation, and show little acclimation to the nutrient-poor conditions on hydrothermally altered rock. In contrast, plants of the Great Basin sagebrush vegetation are physiologically intolerant of the unusual soils that develop from hydrothermally altered rock and are excluded from such sites.

Key words: andesite; Artemisia tridentata; Great Basin; hydrothermal alteration; Nevada; nitrogen; nutrient-use efficiency; phosphorus; Pinus ponderosa; Sierra Nevada; soil chemistry.

INTRODUCTION

Abrupt discontinuities in plant distribution across soil types have always intrigued plant ecologists. Such edaphic control is often seen in soil contrasts that include limestone, serpentine, or hydrothermally altered rock. Billings (1950) described the occurrence of Sierran flora and vegetation on outcrops of soil derived from hydrothermally altered rock in the Great Basin Desert of Nevada. In this dry climate, islands of *Pinus ponderosa* Laws. and *P. jeffreyi* Grev. and Balf. surrounded by a regional matrix of sagebrush vegetation (*Artemisia tridentata* Nutt.) provide a striking contrast in physiognomy (Fig. 1). Billings (1950) found that Great Basin species could grow on altered soils only if they received amendments of P and N. Conversely, it appears that conifers are excluded from typical desert soils by competition for water with desert vegetation (DeLucia et al. 1988). Studying an analogous situation in the Sierra Madre of Mexico, Goldberg (1982, 1985) linked the occurrence of evergreen oaks to tolerance of low pH in the soils that develop from altered rock.

Andesite is the dominant rock in much of western Nevada, and localized hydrothermal alteration of these andesites is thought to have commenced during the Miocene (Gianella 1936, Hutsinpiller 1988). Several

hydrothermal springs are still active at low elevations near Reno. In the Great Basin, soils derived from andesites form Xerollic Haplargids that are typical brown desert soils. Soils on altered bedrock are shallow Lithic Entisols, which are light colored and very acid (Billings 1950). Acidity is derived from the weathering of pyrite deposited during the original alteration.

Pinus ponderosa, P. jeffreyi, P. lambertiana Dougl., and other conifers occur on soils derived from both altered and unaltered rock in the Sierra Nevada, but in the western Great Basin Desert, these and other Sierran species are restricted to soils derived from altered parent material. Shrubs, particularly *Artemisia tridentata,* are strongly dominant on the adjacent brown desert soils. *Pinus monophylla* Torr. and Frem. also occurs on soils derived from unaltered rock on mountain slopes southeast of Reno, Nevada.

The occurrence of Sierran species on soils derived from hydrothermally altered rock extends eastward to the western shoreline of Pleistocene Lake Lahontan at ≈ 1340 m elevation (Fig. 2). One of these sites (site 5) is near the abandoned mining town of Ramsey, 60 km east of the eastern slopes of the Sierra Nevada. We link the occurrence of Sierran species such as *P. ponderosa* at these sites to a probable widespread distribution of this forest type during the pluvial periods of the Pleistocene (Martin and Mehringer 1965, Spaulding et al. 1983, Wells 1983). As the climate dried during the

FIG. 1. Open woodland dominated by *Pinus ponderosa*, *P. jeffreyi*, and *P. lambertiana* on soil derived from hydrothermally altered andesite at 1700 m elevation on the south slope of Peavine Mountain, northwest of Reno, Nevada. The surrounding vegetation is typical Great Basin sagebrush and associated species, dominated by *Artemisia tridentata*.

Holocene, the Sierran species were left in relict communities on the hydrothermally altered soils (Billings 1950).

In this paper we characterize the soil conditions for pairs of adjacent sites occupying soils derived from hydrothermally altered and country rock near Reno, Nevada. Then, we examine the mechanisms that allow Sierran species to persist on nutrient-poor soils derived from altered rock. At least one mechanism may include an efficient use of nutrients during growth on nutrient-deficient soils. High nutrient-use efficiency (NUE) is seen in species that achieve high growth rates per unit nutrient uptake (Chapin 1980). We hypothesized that Sierran conifers would show greater NUE in growth than species of Great Basin shrubs. High NUE is also found in species that show greater retranslocation of foliar nutrients before leaf abscision (Vitousek 1982). We hypothesize that such reabsorption would be greater in species of Sierran conifers than in Great Basin shrubs.

METHODS

Fourteen sites near Reno, Nevada were chosen for study (Fig. 2). These range from five sites at elevations of 1750–2100 m in the Sierra Nevada, to nine sites of 1400–2000 m elevation on Great Basin mountain slopes. Mean annual precipitation ranges from ≈950 mm near the upper Sierra Nevada sites (e.g., sites 2, 4, and 7) to ≈250 mm at Great Basin sites.

Each site consisted of a pair of adjacent soil types: one derived from country rock and one derived from hydrothermally altered parent materials. At each site, a homogeneous 0.1-ha area on each parent material was chosen for vegetation and soil studies. Three sites, representative of vegetation in the Sierra Nevada, and in the pinyon and sagebrush zones of the Great Basin,

were designated as intensive study sites (DeLucia et al. 1988, Fig. 2). During vegetation sampling, a composite sample of surface soil was gathered from 0–5-cm depth from five subsamples taken along a 50-m transect at each site. At the three intensive sites, these five subsamples were analyzed individually to offer some measure of intrasite variability. All soils were dried at 80°C for 24 h and sieved to pass 2-mm mesh.

Soils were analyzed for organic carbon and total nitrogen using a CHN analyzer (Perkin-Elmer Model 240C). Particle size distribution (% sand, silt, and clay) was determined following the hygrometer method (Day 1965). A 1:5 extract was prepared to determine soluble ions by shaking 30 g of soil with 150 mL of distilled water for 24 h. This was filtered through a 0.45-μm Millipore HA filter. A Ross Combination Electrode (Orion 83-02-00) was used to measure the pH of this solution with an Orion pH Meter (Model 701), and alkalinity, expressed as HCO_3^- concentration in millimoles per litre, was determined by titration with 0.01 mol/L H_2SO_4 to pH 4.5. Concentrations of soluble F^-, Cl^-, PO_4^{3-}, NO_3^-, and SO_4^- were determined on a Dionex 2010i ion chromatograph, and Ca^{2+}, Mg^{2+}, Na^+, and K^+ were determined on a Perkin-Elmer Model 370 atomic absorption spectrophotometer. On separate samples of dry soil, HCO_3^--extractable phosphorus (Olson et al. 1954) and soil pH in 0.01 mol/L $CaCl_2$ were determined for a further soil characterization. Although the HCO_3^--extractable P method was developed for use on soils of alkaline pH, it is often a useful index of available P in acid soils (Bowman et al. 1978, Muriuki and Barber 1983, Sharpley et al. 1987) and provided a convenient comparative measure in our study where adjacent soils contrast so strongly in pH.

Foliage collections were made in the field during September 1986. Foliage was collected from all dominant species at the intensive study sites. Foliage of *Pinus ponderosa*, *P. monophylla*, and *Artemisia tridentata* was also collected where these occurred at the remaining 11 sites. In every case, we collected ≈10 g of fully mature leaves from all points around the basal perimeter of the crown of five individuals of each species. We also made similar collections of attached senescent leaves that were ready to abscise. We considered leaves ready to abscise if they fell off the branch when touched or when the branch was shaken lightly. Except at the intensive study sites, the foliage collections from the five individuals were composited, resulting in one sample of mature and one sample of senescent foliage for each species at each site.

Specific leaf mass (SLM; mg/cm²) was calculated for mature and abscised leaves of species at the intensive study sites. For broad-leaf species, one-sided leaf area was measured with a LI-COR Model LI-3000 leaf area meter, and for needle-leaf species leaf dimensions were measured with calipers and total leaf area was calculated by assuming simple geometric shapes. All foliage was dried at 90° before further analysis for N, using the Perkin-Elmer CHN analyzer, and P and Ca in dry

ash, following Greweling (1976). These analyses were performed by the Agronomy Analytical Laboratory at Cornell University and cross-checked with standard samples traceable to the National Bureau of Standards.

When there were no differences in SLM between fresh and abscising foliage for a species, we used differences in nutrient concentration to calculate an index of nutrient-use efficiency that is the result of the reabsorption of nutrients before leaf abscision (NUER), viz. (Concentration in Mature Foliage − Concentration in Senescent Leaves) ÷ (Concentration in Mature Foliage).

We calculated nutrient-use efficiency during growth (NUEG) of seedlings in several experiments in the Duke University Phytotron. Seed collections were made in autumn 1985 from several sites near Reno. Seeds of *Pinus ponderosa* were collected from the foothills of Peavine Mountain, near the Desert Research Institute north of Reno. Those of *P. monophylla* were collected from the Virginia Mountains southeast of Reno, and *Artemisia tridentata* seeds were collected near the Desert Research Institute. Soils derived from altered and unaltered andesite were collected from adjacent sites on Peavine Mountain near the abandoned Nevada Central Mine. The soils were sieved to pass 6-mm mesh.

After stratification seeds of each species were planted in 350-mL, 7 cm diameter pots containing field-collected soils. In a first experiment, seedlings of *P. ponderosa* and *P. monophylla* were grown in each soil type. Five seeds were planted per pot, and seedlings were thinned to one per pot soon after emergence. To facilitate drainage, the bottom of each pot was filled with 3 cm of washed river gravel. Following 89 d in a greenhouse, plants were randomly sorted into two groups for an initial and a final harvest. Plants comprising the final harvest were then moved into a growth chamber in the Duke University Phytotron and grown for an additional 79 d. We maintained the growth chamber at 700 μmol·s^{-1}·m^{-2} irradiance (PAR) at the soil surface, 25° day : 15° night temperature, 70% relative humidity, and 16-h day : 8 h night photoperiod/thermoperiod. For the initial and final harvest, biomass was determined for roots, stems, and needles after drying at 60°. Plant tissues were analyzed for N, P, and Ca as described above for field-collected tissues.

Unfortunately, seeds of *Artemisia tridentata* failed to germinate during the first experiment. Seedlings of this species were grown in a second experiment under identical conditions except that relative humidity was 50%, field-collected soils were mixed with perlite to facilitate aeration, and the initial and final harvests were made after 37 and 52 d, respectively.

The harvest data were used to calculate relative growth rate (RGR; Evans 1972, Hunt 1978), for which significant differences were determined by analysis of variance, followed by Tukey's Range Test ($P < .05$). Root specific absorption rate (SAR; Williams 1948, Hackett 1969) was calculated from the final nutrient
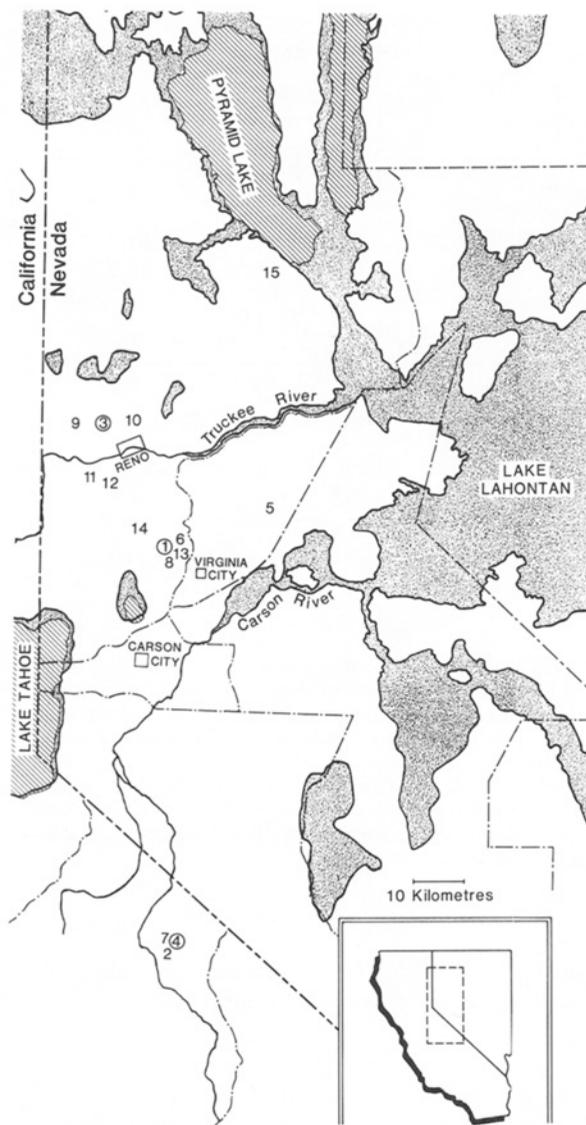

FIG. 2. Western Nevada and eastern California, showing the western shoreline of the Pleistocene Lake Lahontan (stippled), the extent of present-day lakes (hatched), and location of the study sites. Intensive study sites, as described in the text and by DeLucia et al. (1988), are circled. Base map is taken from Synder et al. (1964). Sierran vegetation is found on altered rock at site 15, but that site was not sampled in the present study.

content divided by the final root biomass. Nutrient-use efficiency in growth (NUEG) was calculated as final biomass divided by final nutrient content (Chapin 1980). This index is the inverse of tissue concentration for experiments such as this, in which there is no senescence and loss of tissues. An alternative index of nutrient-use efficiency in growth (E), which gives added weight to the mass of plant growth during the experiment, was calculated following Siddiqi and Glass (1981). Small amounts of some tissues precluded the analysis of all constitutents in some samples. In these cases
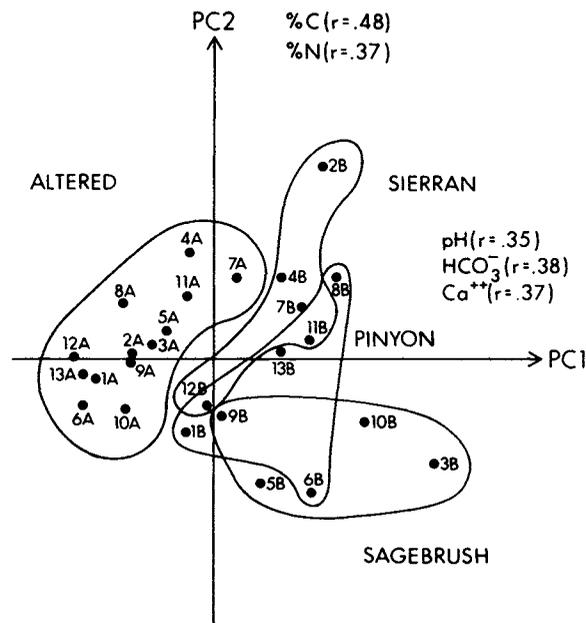
FIG. 3. Principal component analysis of the soil data, in which each site is represented by a sample from altered (A) and unaltered (B) parent materials. All samples from altered sites form one cluster, while adjacent B sites are grouped according to vegetation (Sierran conifer, pinyon–juniper, or sagebrush). The first two axes explain 48% of the variance and are most strongly correlated with the 5 variables indicated, out of a possible total of 18 soil properties that were measured in each sample.

indices of SAR, NUEG, and E were not subjected to statistical analyses because of missing data.

RESULTS

Soils

To avoid a priori bias in favor of certain soil variables, we used principal components analysis (PCA) to indicate which of the 18 measured soil parameters were most important in the contrast of soils from hydrothermally altered and unaltered bedrock. Soils from Site 14, the area of current active hydrothermal venting at Steamboat springs south of Reno, were unusual in many respects, yielding a skewed distribution of sites in preliminary multivariate analyses of the data. We omitted those samples from the final PCA that uses the correlation matrix algorithm of the Statistical Analysis System (SAS Institute 1982). PCA of all measured soil parameters in the remaining samples suggests that pH, alkalinity, and soluble calcium form the major contrast between soils derived from altered and unaltered bedrock (Fig. 3).

The PCA suggests that all altered soils share basic similarities, but adjacent soils derived from unaltered parent materials differ depending upon whether they are found under forest vegetation in the Sierra Nevada

or under pinyon–juniper woodland or sagebrush in the Great Basin. The secondary axis is correlated with %C ($r = 0.48$) and %N ($r = 0.37$), reflecting a greater accumulation of these constitutents under forest vegetation on both altered and unaltered sites than under sagebrush in the desert. Together these axes explain 48% of the variance. Soil parameters that were not correlated with any of the first three axes (% sand, % silt, % clay, F, Cl, NO_3, Mg, K, and Na) are not discussed further.

Although it was not strongly associated with the first two principal components, SO_4 was significantly correlated with pH in the 1:5 extract ($r = -0.53$; $n = 26$ from 13 sites) and in 0.01 mol/L $CaCl_2$ ($r = -0.44$). Similarly, water-soluble P was significantly correlated to pH ($r = 0.61$) and Ca ($r = 0.59$), and HCO_3-P was significantly correlated to pH ($r = 0.33$), %C ($r = 0.40$), %N ($r = 0.37$), and water-soluble P ($r = 0.35$).

Mean values for the soil properties of greatest interest are given in Table 1, in which Great Basin sites are differentiated according to whether the surrounding vegetation is dominated by pinyon–juniper woodland or sagebrush. For most parameters, differences between adjacent paired samples are greater in sites from the Great Basin desert than in sites in the Sierra Nevada. Soils derived from unaltered rock showed a mean concentration of available P of 26.5 μg/g in bicarbonate extractions at pH 8.5. This value, which is typical of desert soils (Lajtha and Schlesinger 1988), may be suboptimal for the growth of many agricultural species (Stevenson 1986). It is less than the mean for 168 USDA benchmark soils (Tiessen et al. 1984), although the USDA samples are ground before analysis, a process which tends to increase extractable P (Lajtha and Schlesinger 1988). Soils derived from altered andesite in the desert are very acid (pH 3.7) and have exceptionally low levels of phosphorus. Soils from altered and country rock in the Sierra Nevada are similar in organic C and total N and show higher mean contents of these elements than in any soils from the Great Basin. Surprisingly, soils on altered rock in the Great Basin have higher concentrations of C and N than adjacent desert soils supporting sagebrush. While these differences are not significant, they confirm the separation of these sites along the second axis of the PCA.

Foliar analysis

In nearly all cases in which the same species occurred across soil types, mean foliar concentrations of N, P, and Ca were slightly lower for plants growing on soil derived from altered rock. Although few of these differences are significant, this trend is seen for all dominant species that occur on both soil types at the intensive study sites (Table 2), as well as in comparisons of species that occur more broadly (Table 3). For species occurring at a large number of sites, there were few significant correlations between the nutrient content of mature foliage and soil parameters. In *Pinus ponderosa*

TABLE 1. Soil chemical properties on altered and unaltered parent materials in the Sierra Nevada and Great Basin. All data are means with 1 SE in parentheses. Analysis of variance was used to distinguish main effects due to location and soil type; t tests were used to distinguish differences between soil types within a location. Asterisks indicate significance at $P < .05$.

Location	n	pH in 0.01 mol/L CaCl$_2$	Measured on 1:5 soil extract					HCO$_3^-$-P† (μg/g)	C (mg/g)	N (mg/g)
			pH	HCO$_3^-$ (mg/L)	SO$_4^=$ (mg/L)	Ca^{2+} (mg/L)	P (μg/g)			
Sierra Nevada										
Unaltered	5	5.72 (0.19) *	6.23 (0.19) *	0.30 (0.06) *	1.01 (0.12) *	6.38 (1.03) *	0.54 (0.23)	22.6 (5.2)	0.234 (0.044)	0.011 (0.002)
Altered	5	3.99 (0.22)	5.06 (0.17)	0.07 (0.03)	5.54 (1.46)	2.24 (0.70)	0.27 (0.22)	32.0 (19.0)	0.224 (0.031)	0.008 (0.002)
Great Basin										
Pinyon Zone										
Unaltered	4	6.19 (0.24) *	6.70 (0.13) *	0.56 (0.21) *	1.21 (0.23)	4.06 (1.10) *	1.14 (0.33) *	23.3 (6.1) *	0.142 (0.043)	0.008 (0.002)
Altered	4	3.66 (0.12)	4.81 (0.18)	0.04 (0.02)	6.46 (2.61)	0.98 (0.43)	0.02 (0.02)	2.9 (1.7)	0.107 (0.042)	0.005 (0.002)
Sagebrush zone										
Unaltered	4	6.55 (0.17) *	7.00 (0.13) *	0.45 (0.11) *	0.84 (0.22)	6.07 (2.15)	2.81 (1.25)	31.4 (4.4) *	0.078 (0.012)	0.006 (0.001)
Altered	4	3.74 (0.15)	4.69 (0.23)	0.03 (0.02)	19.86 (12.81)	2.64 (1.55)	0.16 (0.16)	5.6 (2.9)	0.115 (0.015)	0.009 (0.002)
ANOVA for main effects										
Location		NS	NS	NS	NS	NS	NS	NS	*	NS
Soil		*	*	*	*	*	*	NS	NS	NS

† HCO$_3^-$-P is a determination of available P from extraction at pH 8.5 (Olson et al. 1954).

needle P was positively correlated with soil C ($r = 0.59$), soil N ($r = 0.61$), water-soluble P ($r = 0.57$), and pH in CaCl$_2$ ($r = 0.60$), all at $P < .05$. Among Great Basin species, foliar P was *negatively* correlated to soil P in *P. monophylla* ($r = -0.63$ for HCO$_3$-P) and foliar Ca was positively correlated to water-soluble P ($r = 0.77$) in *Artemisia tridentata*.

There was little difference in specific leaf mass (SLM) between fully mature (11.74 mg/cm^2) and abscising (11.65 mg/cm^2) needles of *P. ponderosa*, indicating little accumulation or withdrawal of carbon compounds after needle elongation. Similar patterns were found for the other coniferous species. SLM increased with leaf age in *Arctostaphylos patula*, but the means were not significantly different. The pattern in *A. tridentata* was complicated by changes in the morphology of leaves that are produced throughout the growing season (Miller and Shultz 1987). Most of the autumn litterfall is composed of large, tridentate leaves produced in the spring; these leaves show little change in SLM before abscission (17.37 mg/cm^2 vs. 16.35 mg/cm^2). Fully mature leaves on these shrubs during September are small leaves with high SLM (30.84 mg/cm^2) that are produced late in the growing season and retained during the winter.

Among species that occurred on both soil types at the intensive study sites, there were no significant differences across soil type in the fraction of N and P reabsorbed before leaf abscission (Table 2). *Pinus jef-*

freyi showed greater reabsorption of foliar N on soils derived from unaltered rock in the Sierra Nevada, but this difference is not significant due to a large standard error for the value from altered soil. Abscised leaves of *Arctostaphylos patula* had higher concentrations of P than fresh leaves, indicating transport of P to leaf tissue before abscission. This is particularly surprising since this species also shows higher SLM in abscised leaves. In all species, Ca concentrations in abscised tissues were higher than in fresh tissue, yielding a negative reabsorption fraction. Thus, nutrient reabsorption efficiency for Ca is not discussed further.

Nutrient reabsorption efficiencies for N and P were always higher in *Pinus ponderosa* than in *Artemisia tridentata* (Table 4). For *P. ponderosa* there was no tendency for greater mean reabsorption of foliar P among collections made on the low-phosphorus soils derived from altered rock in the Great Basin. Phosphorus reabsorption efficiency of *P. ponderosa* was negatively correlated with soil HCO$_3^-$-extractable P ($r = -0.54$), but the correlation is not significant when a single outlier datum is omitted. Nitrogen reabsorption efficiency showed a significant ($P < .05$) negative correlation to soil organic C ($r = -0.64$) and total N ($r = -0.57$) in *Artemisia tridentata*. *Pinus ponderosa*, *P. monophylla*, and *A. tridentata* showed no significant correlations between the concentrations in mature foliage and nutrient reabsorption efficiency for any nutrient.

WILLIAM H. SCHLESINGER ET AL.

TABLE 2. Comparisons of foliar nutrient concentrations and nutrient reabsorption in species that occurred on soils over both altered and unaltered parent materials at the intensive study sites. All data are means ± 1 SE, with $n = 5$, and t tests ($P <$ .05) are used to distinguish differences between soils within species and nutrients. Significant differences between means are indicated by an asterisk.

	Concentration (mg/g)		Fractional reabsorption	
Location	Altered	Unaltered	Altered	Unaltered
Sierra Nevada				
Pinus jeffreyi				
N	0.094 ± 0.003	0.102 ± 0.005	0.14 ± 0.34	0.55 ± 0.07
P	0.012 ± 0.001	0.011 ± 0.001	0.48 ± 0.04	0.44 ± 0.07
Ca	0.021 ± 0.002 *	0.040 ± 0.004	−1.20 ± 0.24 *	−0.50 ± 0.11
Arctostaphylos patula				
N	0.093 ± 0.005	0.111 ± 0.012	0.66 ± 0.06	0.71 ± 0.06
P	0.018 ± 0.002	0.019 ± 0.002	−0.75 ± 0.42	−0.27 ± 0.15
Ca	0.079 ± 0.016	0.106 ± 0.009	−1.11 ± 0.33	−0.82 ± 0.21
Great Basin				
Pinyon zone				
Pinus monophylla				
N	0.091 ± 0.005	0.096 ± 0.004	0.45 ± 0.04	0.40 ± 0.05
P	0.020 ± 0.001	0.020 ± 0.001	0.65 ± 0.12	0.62 ± 0.08
Ca	0.028 ± 0.002	0.021 ± 0.003	−2.56 ± 0.31	−2.69 ± 0.26
Juniperus osteosperma				
N	0.083 ± 0.008	0.090 ± 0.003	0.42 ± 0.07	0.44 ± 0.07
P	0.009 ± 0.001 *	0.012 ± 0.001	0.64 ± 0.07	0.66 ± 0.04
Ca	0.082 ± 0.006 *	0.108 ± 0.006	−0.33 ± 0.10	−0.59 ± 0.16
Amelanchier alnifolia				
N	0.126 ± 0.010	0.128 ± 0.008	0.60 ± 0.03	0.56 ± 0.07
P	0.010 ± 0.001 *	0.016 ± 0.000	0.29 ± 0.17	0.19 ± 0.09
Ca	0.121 ± 0.007	0.131 ± 0.011	−0.17 ± 0.04	−0.11 ± 0.06
Sagebrush zone				
No dominant species in common with those on altered rocks				

Phytotron experiments

Seedlings of *Artemisia tridentata* showed a higher RGR than those of *Pinus ponderosa* or *P. monophylla* when each was grown in soils derived from either altered or unaltered andesite (Table 5). However, these data are somewhat deceptive. The high RGR for *A. tridentata* in altered soil was due to a relatively large percentage change from a very small initial biomass; these plants were nearly dead at the second harvest.

For each species, RGR was not significantly higher when plants were grown on unaltered soil. Similarly, SAR for N and P showed no consistent tendency for higher values when the various species were grown in the richer soil derived from unaltered rock. There was no indication that *P. ponderosa* is specifically adapted to the lower availability of nutrients on altered soils by virtue of high rates of root uptake. Nutrient-use efficiency of N in growth showed higher values for both *P. ponderosa* and *P. monophylla* than for *A. tridentata*, whether these indices were calculated as NUEG following Chapin (1980) or E following Siddiqi and Glass (1981). Nutrient-use efficiency of N and P in growth of *P. ponderosa* was higher on soil derived from unaltered rock, but this pattern was not seen for *P. monophylla*.

DISCUSSION

Our soil data confirm earlier papers (Billings 1950, Salisbury 1954, Goldberg 1982, 1985) that report low concentrations of cations and phosphorus in acidic soils derived from hydrothermally altered rock. Soil differences between parent materials show the strongest contrast in desert regions, where climate (i.e., low precipitation) has had the least modifying effect (Jenny 1980). Higher contents of organic carbon and total nitrogen in the Sierra Nevada presumably reflect the higher net primary production and input to soil organic pools under forest vegetation in mesic, montane conditions. This trend appears to extend to the occurrence of forest vegetation on altered soils in the Great Basin; these have higher concentrations of organic carbon and total nitrogen than adjacent desert soils supporting sagebrush.

The very low availability of P in soils derived from altered rock is probably due to precipitation with Fe and Al minerals in acid conditions (cf. Salisbury 1954). Among the soil samples, water-soluble P was correlated to pH ($r = 0.61$), and extraction with HCO_3^- at pH 8.5 yielded much higher P concentrations (Table 1). Although the principal component analysis found that pH, alkalinity, and Ca explained the most variance

TABLE 3. Nutrient concentrations in mature foliage for species occurring in many of the field sites. All data are means with 1 SE in parentheses. *t* tests showed no differences in mean concentrations in the two instances when a species occurred on soils over both parent materials at a site ($P > .05$); thus data within location were combined and analysis of variance was used to distinguish effects due to location. Dashes indicate that the species did not occur at that site.

Location Vegetation zone	Pinus ponderosa				Pinus monophylla				Artemisia tridentata			
	N (mg/g)	P (mg/g)	Ca (mg/g)	Sites (*n*)	N (mg/g)	P (mg/g)	Ca (mg/g)	Sites (*n*)	N (mg/g)	P (mg/g)	Ca (mg/g)	Sites (*n*)
Sierra Nevada												
Unaltered	0.118 (0.029)	0.015 (0.003)	0.018 (0.006)	2	0.117 (0.005)	0.018 (0.000)	0.028 (0.004)	3	0.143 (0.010)	0.023 (0.004)	0.049 (0.005)	4
Altered	0.081 (0.007)	0.010 (0.001)	0.014 (0.003)	4	—	—	—		—	—	—	
Great Basin Pinyon zone												
Unaltered	—	—	—		0.097 (0.002)	0.017 (0.001)	0.027 (0.003)	4	0.139 (0.013)	0.020 (0.002)	0.052 (0.006)	4
Altered	0.101 (0.008)	0.010 (0.001)	0.018 (0.001)	4	0.097 (0.006)	0.017 (0.002)	0.031 (0.004)	2	—	—	—	
Sagebrush zone												
Unaltered	—	—	—		—	—	—		0.133 (0.008)	0.022 (0.002)	0.080 (0.024)	4
Altered	0.106 (0.006)	0.011 (0.000)	0.017 (0.002)	4	—	—	—		—	—	—	
					ANOVA for main effect							
Location	NS	NS	NS		*	NS	NS		NS	NS	NS	

among sites, we suspect that the biological effect of these differences is likely to be found through their control on phosphorus availability. Goldberg (1985) was able to grow *bodenvag* species on soils from hydrothermally altered rock with additions of $CaCO_3$, but the main effect of $CaCO_3$ may have been exerted through its effect on soil pH and phosphorus solubility, as is the case in many temperate soils.

When nutrients are reabsorbed from leaf tissue before abscission, there is the potential for these constituents to be reused in subsequent growth. High fractional reabsorptions are often associated with nutrient-poor

TABLE 4. Percent nutrient reabsorption before leaf abscission for species occurring at many of the field sites on soils derived from different types of parent material. All data are means with 1 SE in parentheses. Statistical analysis as in Table 3. Dashes indicate that the species did not occur at that site.

Location	Nitrogen			Phosphorus		
	Pinus ponderosa	Pinus monophylla	Artemisia tridentata	Pinus ponderosa	Pinus monophylla	Artemisia tridentata
Sierra Nevada						
Unaltered	0.68 (0.06)	0.35 (0.10)	0.40 (0.04)	0.62 (0.08)	0.50 (0.09)	0.37 (0.08)
Altered	0.63 (0.03)	—	—	0.54 (0.07)	—	—
Great Basin Pinyon Zone						
Unaltered	—	0.48 (0.04)	0.56 (0.03)	—	0.60 (0.02)	0.44 (0.06)
Altered	0.58 (0.07)	0.49 (0.04)	—	0.57 (0.05)	0.64 (0.03)	—
Sagebrush Zone						
Unaltered	—	—	0.53 (0.05)	—	—	0.26 (0.08)
Altered	0.61 (0.03)	—	—	0.62 (0.05)	—	—
		ANOVA for main effect				
Location	NS	NS	*	NS	NS	NS

TABLE 5. Relative growth rate, specific absorption rate, and nutrient-use efficiency for seedlings grown in the Duke University Phytotron. Data followed by the same superscript are not significantly different in ANOVA followed by Tukey's range test ($P < .05$). Dashes indicate insufficient material for nutrient analysis.

Species Soil	Relative growth rate ($mg \cdot g^{-1} \cdot d^{-1}$)	Final biomass (g)	Specific absorption rate (mg/g)			Indices of nutrient use efficiency during growth*					
						NUEG (mg/mg)			E (g^2/mg)		
			N	P	Ca	N	P	Ca	N	P	Ca
Pinus ponderosa											
Altered	13.8[a]	0.81[a]	19.0	2.0	2.0	114.2	1092	1082	0.093	0.889	0.880
Unaltered	24.0[a]	1.13[a]	11.7	1.7	6.1	175.5	1239	336	0.198	1.402	0.380
P. monophylla											
Altered	7.4[b]	0.37[b]	20.8	5.6	—	139.2	516	—	0.052	0.192	—
Unaltered	10.8[b]	0.46[b]	46.4	3.8	8.5	60.1	135	328	0.027	0.337	0.150
Artemisia tridentata											
Altered	53.9[c]	0.01[c]	46.6	—	—	55.7	—	—	0.00057	—	—
Unaltered	64.2[c]	0.27[d]	21.1	—	—	99.6	—	—	0.0270	—	—

* See last paragraph of Methods.

sites, conferring a greater efficiency of nutrient use in these species (Waring and Schlesinger 1985). In species in which SLM increases as a result of the accumulation of carbon compounds with tissue age, the initial nutrient concentrations are diluted. This dilution suggests an apparent reabsorption of foliar nutrients when, in fact, there is no change in the content per unit of leaf area. In such cases, absolute reabsorptions of nutrients are indicated only when indices of nutrient reabsorption efficiency exceed changes in SLM, when both are expressed on a fractional basis. In the absence of strong changes in SLM with leaf age, our comparisons of nutrient concentrations in fresh and abscised foliage are directly indicative of nutrient reabsorption efficiency (Tables 2 and 4).

Conifers generally show higher reabsorption efficiency than broad-leaf species (Vitousek 1982, Waring and Schlesinger 1985). As we hypothesized, high reabsorption efficiency in species of Sierran conifers may allow their occurrence on soils derived from hydrothermally altered parent materials, but it is unclear that this process is enhanced in the exceptionally low P soils derived from altered rocks in the desert. Birk and Vitousek (1986) also found no tendency for greater reabsorption of N per fascicle in Pinus taeda across a nitrogen fertility gradient in the southeastern United States, and Pastor et al. (1984) found little change in the concentrations of N and P in the litter of several species along a nitrogen mineralization gradient in Wisconsin. Reabsorption of N and P in Pinus ponderosa is relatively high compared to mean fractional reabsorption of 0.52 N and 0.43 P calculated in a literature review by Chapin and Kedrowski (1983); nutrient reabsorption efficiency for Artemisia tridentata is lower. We suggest that long-term evolution in soils with relatively high availability of P has not selected for high nutrient reabsorption efficiency in desert species of the Great Basin, although these species show spe-

cialized mechanisms to enhance P uptake in calcareous conditions (Jurinak et al. 1986). Great Basin species are excluded from acid, nutrient-poor soils unless P is added (Billings 1950).

As we hypothesized, NUEG of Pinus ponderosa, a representative Sierran conifer, was greater than that of Artemisia tridentata, a representative Great Basin shrub. High NUEG was associated with low RGR. Many species that occupy nutrient-poor sites show little change in RGR when grown in nutrient-rich conditions (Chapin et al. 1986). The growth of P. ponderosa was slightly, but not significantly, greater in soil derived from unaltered rock in the Phytotron experiments. None of the species studied showed a tendency for higher SAR when grown in soil derived from unaltered rock, unlike the response of chaparral shrubs (Gray and Schlesinger 1983) and P. taeda (Birk and Vitousek 1986) to high N conditions. Sierran species survive on altered soil by slow growth and high nutrient-use efficiency during growth (Table 5) and in the reabsorption of nutrients before leaf abscision (Table 4). This suite of characters is typical of plants that are successful in a wide variety of nutrient-poor habitats (Grime 1979).

LITERATURE CITED

Billings, W. D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. Ecology 31:62–74.

Birk, E. M., and P. M. Vitousek. 1986. Nitrogen availability and nitrogen use efficiency in loblolly pine stands. Ecology 67:69–79.

Bowman, R. A., S. R. Olson, and F. S. Watanabe. 1978.

Greenhouse evaluation of residual phosphate by four phosphorus methods in neutral and calcareous soils. Soil Science Society of America Journal 42:451–454.

Chapin, F. S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11:233–260.

Chapin, F. S., and R. A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64: 376–391.

Chapin, F. S., P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. American Naturalist 127:48–58.

Day, P. R. 1965. Particle fractionation and particle-size analysis. Pages 545–567 in C. A. Black, editor. Methods of soil analysis. American Society of Agronomy, Madison, Wisconsin, USA.

DeLucia, E. H., W. H. Schlesinger, and W. D. Billings. 1988. Soil moisture as a factor in the maintenance of Sierran conifers on hydrothermally altered rock in the western Great Basin. Ecology 69:303–311.

Evans, G. C. 1972. The quantitative analysis of plant growth. University of California Press, Berkeley, California, USA.

Gianella, V. P. 1936. Geology of the Silver City district and the southern portion of the Comstock Lode, Nevada. University of Nevada, Bulletin 30(9).

Goldberg, D. E. 1982. The distribution of evergreen and deciduous trees relative to soil type: an example from the Sierra Madre, Mexico, and a general model. Ecology 63: 942–951.

———. 1985. Effects of soil pH, competition, and seed predation on the distributions of two tree species. Ecology 66: 503–511.

Gray, J. T., and W. H. Schlesinger. 1983. Nutrient use by evergreen and deciduous shrubs in southern California. II. Experimental investigations of the relationship between growth, nitrogen uptake and nitrogen availability. Journal of Ecology 71:43–56.

Greweling, T. 1976. Chemical analysis of plant tissue. Search 6(8):1–35.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley, New York, New York, USA.

Hackett, C. 1969. A study of the root system of barley. II. Relationships between root dimensions and nutrient uptake. New Phytologist 68:1023–1030.

Hunt, R. 1978. Plant growth analysis. Edward and Arnold, London, England.

Hutsinpiller, A. 1988. Discrimination of hydrothermal alteration mineral assemblages at Virginia City, Nevada using the airborne imaging spectrometer. Remote Sensing of Environment 24:53–66.

Jenny, H. 1980. The soil resource. Ecological Studies Number 37. Springer-Verlag, New York, New York, USA.

Jurinak, J. J., L. M. Dudley, M. F. Allen, and W. G. Knight. 1986. The role of calcium oxalate in the availability of phosphorus in soils of semiarid regions: a thermodynamic study. Soil Science 142:255–261.

Lajtha, K., and W. H. Schlesinger. 1988. The biogeochemistry of phosphorus cycling and phosphorus availability along a desert soil chronosequence. Ecology 69:24–39.

Martin, P. S., and P. J. Mehringer. 1965. Pleistocene pollen analysis and biogeography of the Southwest. Pages 433–451 in H. E. Wright and D. G. Frey, editors. The Quaternary

of the United States. Princeton University Press, Princeton, New Jersey, USA.

Miller, R. F., and L. M. Shultz. 1987. Development and longevity of ephemeral and perennial leaves on Artemisia tridentata Nutt. ssp. wyomingensis. Great Basin Naturalist 47:227–230.

Muriuki, S. K., and R. G. Barber. 1983. A study on the merits of separating tropical soils into groups and using different chemical extractants for different groups in the routine measurement of available soil phosphorus. Communications in Soil Science and Plant Analysis 14:521–539.

Olson, S. R., C. V. Cole, F. S. Watanabe, and L. A. Dean. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. United States Department of Agriculture, Circular 939, Washington, D. C., USA.

Pastor, J., J. D. Aber, C. A. McClaugherty, and J. M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65:256–268.

Salisbury, F. B. 1954. Soil chemical and biological investigations of materials derived from hydrothermally altered rock in Utah. Soil Science 78:277–294.

SAS Institute. 1982. SAS (Statistical Analysis System) user's guide. Cary, North Carolina, USA.

Sharpley, A. N., H. Tiessen, and C. V. Cole. 1987. Soil phosphorus forms extracted by soil tests as a function of pedogenesis. Soil Science Society of America Journal 51: 362–365.

Siddiqi, M. Y., and A. D. M. Glass. 1981. Utilization index: a modified approach to the estimation and comparison of nutrient utilization efficiency in plants. Journal of Plant Nutrition 4:289–302.

Snyder, C. T., G. Hardman, and F. F. Zdenek. 1964. Pleistocene lakes in the Great Basin. Miscellaneous Geologic Investigations, Map 1-416. United States Geological Survey, Washington, D.C., USA.

Spaulding, W. G., E. B. Leopold, and T. R. Van Devender. 1983. Late Wisconsin paleoecology of the American Southwest. Pages 259–293 in S. C. Porter, editor. Late-Quaternary environments of the United States. Volume 1. The Late Pleistocene. University of Minnesota Press, Minneapolis, Minnesota, USA.

Stevenson, F. J. 1986. Cycles of soil. John Wiley, New York, New York, USA.

Tiessen, H., J. W. B. Stewart, and C. V. Cole. 1984. Pathways of phosphorus transformations in soils of differing pedogensis. Soil Science Society of America Journal 48: 853–858.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119:553–572.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems. Academic Press, New York, New York, USA.

Wells, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs 53:341–382.

Williams, R. F. 1948. The effects of phosphorus supply on the rates of uptake of phosphorus and nitrogen and upon certain aspects of phosphorus metabolism in gramineous plants. Australian Journal of Science, Research Series B 1: 333–361.