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WATER RELATIONS AND THE MAINTENANCE OF SIERRAN CONIFERS ON HYDROTHERMALLY ALTERED ROCK[1]

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Abstract. Unusual, nutrient-poor soils derived from hydrothermally altered bedrock support open forests of Sierran conifers (*Pinus ponderosa, P. jeffreyi,* and others) amongst the sagebrush and pinyon–juniper vegetation on typical desert soils of the Great Basin in western Nevada. As an index of soil moisture availability, we compared predawn xylem pressure potential (XPP) and diurnal patterns of stomatal conductance for various species at three sites, with paired, adjacent soils derived from unaltered and hydrothermally altered parent material.

At high soil moisture availability, Great Basin shrubs maintained higher maximum leaf conductance (2–3 mm/s) than Sierran conifers (< 1.2 mm/s). During the growing season XPP declined for all species at all sites, but during extended drought values for Great Basin shrubs (−2.70–−4.47 MPa) growing on unaltered soil were consistently lower than for Sierran conifers (−0.97–−1.12 MPa) growing on altered soil. While few species were found on both soil types, *Amelanchier alnifolia* showed lower predawn XPP on soils derived from unaltered (−3.22 MPa) than from altered (−2.05 MPa) parent materials.

These data suggest that shrubs rapidly deplete soil moisture in the Great Basin desert, restricting the establishment of Sierran conifers to soils derived from altered rocks, which otherwise support minimal vegetation cover. The $\delta^{13}C$ of foliage from conifers were higher than from Great Basin shrubs, suggesting that conifers maintain higher seasonally integrated water-use efficiencies.

Key words: altered andesite; Artemisia tridentata; *carbon isotope ratio; competition; conductance; desert shrubs; Great Basin, Nevada;* Pinus jeffreyi; Pinus ponderosa; *soil moisture; water relations; xylem pressure potential.*

INTRODUCTION

An unusual feature of the vegetation of western Nevada is the occurrence of disjunct populations of Sierran conifers in the midst of Great Basin sagebrush and pinyon–juniper communities. The eastern limits of the montane coniferous forest of the Sierra Nevada are on the east slope of these mountains. However, "tree islands" up to a size of several hectares are found as far as 60 km east of the climatic limits of the Sierran forest. These "island" communities consist primarily of *Pinus ponderosa* and *Pinus jeffreyi,* have very low shrub and herbaceous cover, and are largely devoid of characteristic Great Basin species, most notably *Artemisia tridentata* (Billings 1950). Moreover, these unique forested communities are restricted to bleached yellowish soils derived from hydrothermally altered bedrock (Billings 1950).

Andesite is a common parent material of soils supporting sagebrush and pinyon–juniper near Reno, Nevada. Hydrothermal alteration of andesites occurred at considerable depth during the Cenozoic Era, probably in the late Miocene (Gianella 1936, Billings 1950). Ascending hot water introduced sulfur that formed pyrites and resulted in considerable leaching of exchangeable bases. Surface weathering of pyrite produced acid that leached the altered substrate, forming a yellowish soil that is acidic (pH 3.3–5.5) and low in exchangeable bases and phosphorus (Billings 1950, Salisbury 1954, 1964).

The role of edaphic factors in locally modifying the regional distribution of vegetation governed by climate is readily apparent in serpentine communities (Kruckeberg 1954, 1969, 1984). There are many similarities in the physiognomy and dynamics of vegetation on serpentine and on hydrothermally altered soils including an open stand structure, the absence of intermediate vegetation size classes, xeromorphism, and a high proportion of endemics (Whittaker 1954). In the case of serpentine (Kruckeberg 1954) and hydrothermally altered soils (Billings 1950, Goldberg 1982, 1985) a two-part hypothesis has been proposed to explain the maintenance of unique edaphic communities in a matrix of regional climatic vegetation. Species from the infertile

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soil type (serpentine or altered andesite) are excluded from the more fertile soil by competition. Conversely, species from the more fertile soil are excluded from the less fertile soil by physiological intolerance to nutrient deficiency. We hypothesize that competition for water prevents the establishment of seedlings of *Pinus ponderosa* and *P. jeffreyi* in the native Great Basin sagebrush or pinyon–juniper communities, and intolerance to acidic and nutrient-deficient conditions prevents the establishment of Great Basin species on soils derived from altered rock.

In this study we addressed the factors restricting Sierran conifers to altered soils in the western Great Basin by examining the patterns of water use and availability in communities on both altered and unaltered soil. We predicted that water availability would be greater on the altered sites as a result of lower vegetation cover and the absence of Great Basin species, and that the Great Basin species would be more competitive for water under drought conditions. This hypothesis was tested by examining the diurnal pattern of stomatal conductance and xylem pressure potential in several species on each soil type during periods of high and low soil water availability. The $\delta^{13}C$ in foliage from several Great Basin and Sierran species was measured as an indicator of integrated seasonal water-use efficiency (Farquhar et al. 1982, Farquhar and Richards 1984, Ehleringer et al. 1985).

Materials and Methods

Three research sites were selected: one on the east slope of the Sierra Nevada and two on the nearest mountains of the Great Basin. The sites form a north-south transect ($\approx$100 km) from Reno, Nevada, to Alpine County, California. Representative pairs of plots on soils derived from hydrothermally altered and unaltered andesite were chosen at each location. The plots that constituted a pair were selected to have similar elevation, slope, and aspect (Table 1) and were contiguous. Annual precipitation and air temperature data for the three sites were obtained from nearby weather stations operated by the Desert Research Institute (University of Nevada) or the National Weather Service. Vegetation in the tree size class ($\geq$2.5 cm diameter at breast height) was sampled with a standard 0.1-ha plot, with 50 subplots (4 m^2) for shrubs (<2.5 cm), and a line intercept (50 m) for herbs (cf. Whittaker 1956).

The Alpine County site (38°41′ N, 119°43′ W) is the wettest of the three sites and receives an average of 950 mm of precipitation (water equivalent) annually. The site is in the Sierran montane forest and *Pinus jeffreyi* is the dominant species in the tree size class on both soil types (Table 1). The Virginia Mountains site (39°23′ N, 119°43′ W) is in pinyon–juniper woodland and receives an average of 255 mm of precipitation annually (Billings 1950, Billings et al. 1954). The dominant tree species on the altered and unaltered plots are *Pinus ponderosa* and *P. monophylla,* respectively. The third site is on the southeast shoulder of Peavine Mountain (39°33′ N, 119°53′ W) and receives an annual average of 262 mm of precipitation. *Pinus ponderosa* and *P. jeffreyi* occur on the altered soil at this site though *P. ponderosa* has a slightly higher importance value (Table 1). Thus *Pinus jeffreyi* occurs in both soil types at the Alpine County site, but in the Great Basin desert, *P. jeffreyi* and *P. ponderosa* are restricted to altered soils. Shrubs, particularly *Artemisia tridentata* v. *tridentata,* are strongly dominant on the unaltered soils at the Virginia and Peavine Mountains (Billings 1950). Total density (tree + shrub) and herbaceous cover were consistently greater on the unaltered soils at all three research sites (Table 1).

Diurnal measurements of stomatal conductance and xylem pressure potential (XPP) were made on individuals of several dominant tree and shrub species at each site. At most sites only a few species occurred on both soil types, making intraspecific comparisons on the different soils difficult. Measurements were made on *Pinus ponderosa, P. jeffreyi,* and *Artemisia tridentata* wherever they occurred. Species with lower importance values were included if they occurred in sufficient numbers on both soil types. *Amelanchier alnifolia* occurred on altered and unaltered soil at the Virginia Mountains site, although infrequently, and was examined intensively. At that site measurements were also made on *Pinus monophylla* and *Juniperus osteosperma* on both soils.

Stomatal conductance was measured with a LI-COR 1600 steady-state porometer during May, July, and September 1986. Diurnal measurements were made at 3-h intervals between 0500 and 1830 (Pacific Standard Time [PST]) on two fully exposed branches on each of three plants per species on each soil type. Conductance was calculated on a total-leaf-area basis for all species and was measured on needles that matured during the previous summer for the *Pinus* species. The porometer was also used to measure leaf and air temperature, photosynthetically active irradiance, and relative humidity. Atmospheric vapor pressure deficit (VPD) was calculated at the daily maximum air temperature.

Predawn xylem pressure potential was measured with a pressure chamber as an index of soil water availability at different times during the summer on each soil type (Ritchie and Hinckley 1975). Measurements were made on foliage-bearing branches of five plants per species between 0200 and 0400 PST. Measurements of XPP were also made concurrent with the diurnal conductance measurements described above. Water content of the surface soil was measured at the Virginia Mountains site at several times during the summer. Gravimetric moisture determinations were made on 15 soil samples collected from 2 to 10 cm deep on each soil type. Water content was calculated as a percentage of oven-dry mass (105°C). The relationship between gravimetric water content and soil water potential was

TABLE 1. Vegetation summary of research sites. Density (DEN = number/ha), dominance (DOM [basal area] = m^2/ha), and importance value (IV, %) are shown for all species in the tree size class. Density, frequency (FRQ, %), and importance value are shown for the two species in the shrub size class with the highest IV. IV for plants in the tree size class was calculated as the mean of the relative density and relative dominance. IV for plants in the shrub size class was calculated as the mean of the relative density and relative frequency. Nomenclature follows Munz and Keck (1968).

	Unaltered site			Altered site		
		Alpine County				
Elevation (m)		2088			2088	
Slope (°)		14			21	
Aspect (° from true N)		170			182	
Trees (all species)	DEN	DOM	IV	DEN	DOM	IV
*Pinus jeffreyi**	510	36.0	98	260	23.9	100
Abies concolor	10	<0.1	1	—†	—	—
Cercocarpus ledifolius	10	<0.1	1	—	—	—
Shrubs	DEN	FRQ	IV	DEN	FRQ	IV
*Arctostaphylos patula**	50	2	6	150	6	17
*Purshia tridentata**	2300	42	72	—	—	—
Pinus seedlings‡	600	10	18	1500	18	83
Other	100			50		
Total tree + shrub density	3580			1960		
Total herb cover (%)	0.1			<0.1		
		Virginia Mountains				
Elevation (m)		1615			1615	
Slope (°)		16			15	
Aspect (° from true N)		268			268	
Trees (all species)	DEN	DOM	IV	DEN	DOM	IV
*Pinus ponderosa**	—	—	—	100	3.9	83
*Pinus monophylla**	40	6.2	100	10	0.2	6
*Juniperus osteosperma**	—	—	—	30	<0.1	11
Shrubs	DEN	FRQ	IV	DEN	FRQ	IV
*Artemisia tridentata**	4200	68	30	—	—	—
Chrysothamnus parryi	350	10	4	5050	40	68
Eriogonum wrightii	9450	66	45	450	6	8
Pinus seedlings‡	—	—	—	800	20	20
Other	2400			100		
Total tree + shrub density	16 420			6540		
Total herb cover (%)	3.4			0.1		
		Peavine Mountain				
Elevation (m)		1710			1735	
Slope (°)		15			19	
Aspect (° from true N)		117			192	
Trees (all species)	DEN	DOM	IV	DEN	DOM	IV
*Pinus ponderosa**	—	—	—	70	3.3	58
*Pinus jeffreyi**	—	—	—	60	2.3	42
Shrubs	DEN	FRQ	IV	DEN	FRQ	IV
*Artemisia tridentata**	6550	88	47	550	14	31
*Tetradymia glabrata**	6600	94	48	—	—	—
Eriogonum sp.	—	—	—	1200	18	51
Other	400			350		
Total tree + shrub density	13 550			2230		
Total herb cover (%)	1.2			0.2		

* Diurnal water relations measurements were made on these species.
† — = species was not present in the sample.
‡ *Pinus* seedlings were either *P. ponderosa* or *P. jeffreyi.*

measured from −1.5 and −0.03 MPa with a pressure plate.

Current-year foliage was collected in September for carbon isotope ratio ($\delta^{13}C$) determinations from representative Great Basin and Sierran species at each site. Tissue was sampled at several points around each of five plants per species (Leavitt and Long 1986) and was oven dried (80°) and ground in a Wiley mill to pass a 425-μm mesh. The isotopic composition was measured in whole leaf tissue and in cellulose extracted from ground foliage by the method of Green (1963). The carbon isotope ratios were measured with a mass

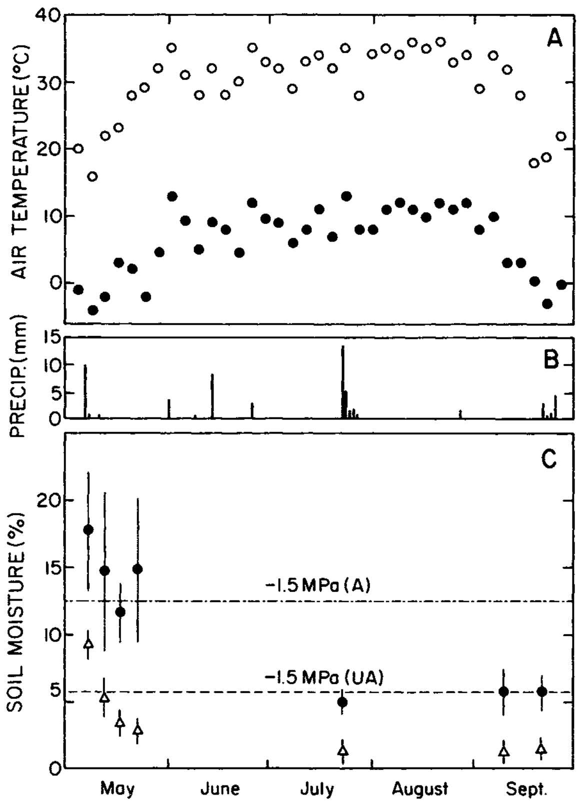

FIG. 1. (A) Maximum (O) and minimum (●) air temperatures for the previous 4 d and (B) precipitation, measured by the National Weather Service near the Virginia Mountains site during the summer of 1986. (C) Percentage moisture for the altered (●) and unaltered (△) soil at the Virginia Mountains site. The dashed lines indicate the percentage soil moisture for altered (A) and unaltered (UA) soil at −1.5 MPa.

spectrometer by Dr. J. R. Ehleringer (University of Utah) and are expressed relative to the PDB standard (Craig 1957).

RESULTS

At the National Weather Service Station near the Virginia Mountains site, maximum and minimum air temperatures increased rapidly during May and began to decrease in early September (Fig. 1A). Maximum air temperature was between 26° and 36°C for most of the summer, and, with the exception of the first measurement date, minimum air temperature remained above freezing during the portion of the day when diurnal conductance measurements were made. The range in maximum air temperatures and VPDs (vapor pressure deficits) recorded during porometer measurements was 3.1° and 0.55 kPa, respectively (Fig. 2). Less than 26 mm of precipitation fell during May and June (Fig. 1B), but a series of consecutive late-afternoon thunderstorms in mid-July was sufficient to saturate surface soils for a few hours beginning on the afternoon of 22 July. Heavy precipitation also occurred at the Alpine County and Peavine sites in mid-July (data not shown).

Water content of the surface soils (2–10 cm) at the Virginia Mountains site decreased rapidly during May, particularly on the unaltered soil (Fig. 1C). The percentage water content on the unaltered site was within 2% of the lowest summer values by 20 May. Altered soil had a higher percentage water content than unaltered soil at water potentials from −1.5 to −0.03 MPa (Fig. 3). The percentage soil moisture at −1.5 MPa was 6.6% for unaltered soil and 12.6% for altered soil. The water potential of surface soil (2–10 cm) at the unaltered site decreased below −1.5 MPa in early May, at least 1 wk earlier than at the altered site (Fig. 1C).

At all sites predawn XPPs were highest in May and decreased as the soil dried during the summer (Table 2). The July XPP measurements at the Peavine Mountain and Alpine County sites were made after a series of thunderstorms and were consequently higher than the values measured at the Virginia Mountains site. Predawn values for *Pinus ponderosa* and *P. jeffreyi* at Peavine Mountain decreased from ≈−0.70 MPa in May to −1.00 MPa in September. Predawn XPP for *Pinus ponderosa* at the Virginia Mountains site decreased from −0.99 to −1.12 MPa over the same interval and a somewhat larger decrease was observed for *P. jeffreyi* at the Alpine County site (Table 2). Among growth forms XPPs were similar for trees and shrubs at all sites in May (Table 2); however, in contrast to the trees, the shrub species showed large decreases in XPP at all sites during the summer. Predawn XPP for *Artemisia tridentata, Purshia tridentata* (Alpine County site), *Tetradymia glabrata, Amelanchier alnifolia, Arctostaphylos patula,* and *Cercocarpus ledifolius* in May were between −0.39 and −1.03 MPa and decreased to −2.05 to −4.47 MPa by September. *Purshia tridentata* at the Peavine (unaltered) site was an exception, showing little seasonal fluctuation in XPP. The lowest predawn values were observed for *Artemisia* (−4.47 MPa). Values for the Great Basin conifers, *Pinus monophylla* and *Juniperus osteosperma,* were generally intermediate between the Sierran conifers and shrub species.

Predawn XPP for *Amelanchier alnifolia,* which occurs on both soils at the Virginia Mountains site, was 0.15 MPa higher on unaltered than on the altered soil in May. This trend was reversed in July and by September predawn XPPs on the unaltered and altered soil were −3.32 and −2.05 MPa, respectively. Predawn XPPs for *Pinus jeffreyi* and *Arctostaphylos patula* at the Alpine County site were also slightly higher on unaltered soil in May and July and became significantly lower than their counterparts on altered soil in September (Table 2). Thus at sites where species occurred on both soil types, predawn XPP following an extended dry period was always lower on unaltered than on altered soil.

For species at the Virginia Mountains site, maxi-

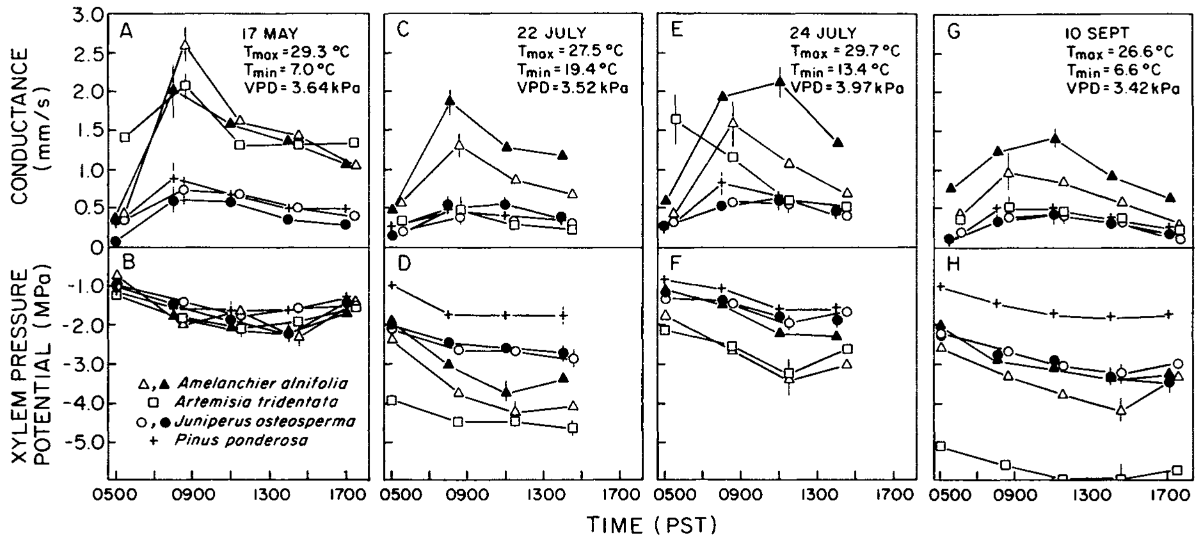

FIG. 2. The diurnal (0500-1830) pattern of stomatal conductance (upper graphs) and xylem pressure potential (lower graphs) during the summer of 1986 for representative species on altered (closed symbols) and unaltered (open symbols) soil at the Virginia Mountains site. The measurement date, maximum air temperature (T_{max}), and vapor pressure deficit (VPD) during the measurement and the minimum air temperature (T_{min}) for the previous night are indicated in each panel. Each point is the mean of six independent measurements. The largest standard deviation for each species is shown. PST = Pacific Standard Time.

mum conductances generally occurred early in the day, between 0830 and 1100 PST (Fig. 2). In May, when soil water availability was high, the diurnal patterns of conductance for *Artemisia tridentata* and *Amelanchier alnifolia* were similar but different from the pattern observed for *Pinus ponderosa* and *Juniperus osteosperma* (Fig. 2A). Maximum conductance for *Artemisia* and *Amelanchier* was between 2.0 and 2.6 mm/s compared with 0.6–0.9 mm/s for the two conifers. Furthermore, the predawn and minimum XPPs were generally higher in the conifers (Fig. 2B, D, F, H). Similar to XPP, maximum conductance for *Amelanchier* in May was higher on unaltered than on altered soil. This pattern was reversed as soil water availability decreased and *Amelanchier* maintained higher conductance and XPP values on altered soil for the duration of the growing season. After ≈5 wk with little precipitation, conductance and XPP decreased for the other species at the Virginia Mountains site (Fig. 2C and D). The largest decrease in conductance and XPP between 17 May and 22 July was observed in *Artemisia* on unaltered soil. Conductance decreased by ≈80% and predawn XPP decreased from −1.24 to −3.95 MPa (Fig. 2A–D). Approximately 20 mm of precipitation fell at the Virginia Mountains site between measurements made on 22 and 24 July (Fig. 1B). An increase in conductance and XPP was evident in all species as a result of the increase in soil moisture (Fig. 2C–F).

At the Virginia Mountains site the lowest conductance and XPP values were measured in September (Fig. 2G and H). At that time maximum conductance for *Amelanchier* on the altered soil was 1.35 mm/s and was 31% lower on unaltered soil. Predawn and minimum XPP were also lower for *Amelanchier* on unaltered than on altered soil. In September maximum conductance for *Artemisia* was similar to that of *Pinus ponderosa* and *Juniperus osteosperma* (0.35–0.50 mm/s), however, predawn and minimum XPP for *Artemisia* were considerably lower (≤−5.0 MPa).

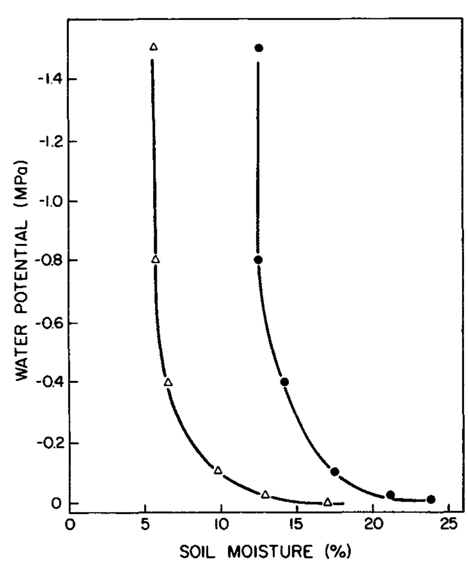

FIG. 3. Soil water potential vs. soil moisture (% of dry mass) for altered (●) and unaltered (△) soils collected from the Virginia Mountains site. Each point is the mean of 10 independent measurements. The standard deviation is within the symbols.

TABLE 2. Predawn xylem water potential (MPa) for representative species growing on soil derived from altered (A) or unaltered (UA) andesite. (t test comparing the mean values for XPP in cases where the same species was sampled on both soil types.) Data are $\bar{X} \pm$ SD. * $P \leq .05$. No measurable precipitation fell in the 10 d prior to predawn XPP measurements except for the July measurements at Alpine County and Peavine Mountain and the September measurements at Peavine Mountain.

Species	Site	May	July	September
		Alpine County		
Pinus jeffreyi	A	−0.69 ± 0.15	−0.69 ± 0.03*	−1.36 ± 0.09*
Arctostaphylos patula	A	−0.52 ± 0.10	−0.56 ± 0.10	−2.22 ± 0.16*
Pinus jeffreyi	UA	−0.64 ± 0.11	−0.63 ± 0.04*	−1.50 ± 0.04*
Arctosatphylos patula	UA	−0.49 ± 0.08	−0.47 ± 0.11	−2.62 ± 0.17*
Cercocarpus ledifolius	UA	−0.39 ± 0.11	−0.35 ± 0.01	−2.28 ± 0.20
Purshia tridentata	UA	−0.65 ± 0.11	−1.16 ± 0.16	−2.90 ± 0.09
		Virginia Mountains		
Pinus ponderosa	A	−0.99 ± 0.14	−1.09 ± 0.05	−1.12 ± 0.05
Pinus monophylla	A	−1.07 ± 0.10	...	−1.59 ± 0.13
Juniperus osteosperma	A	−1.03 ± 0.08	−1.96 ± 0.11	−2.24 ± 0.27
Amelanchier alnifolia	A	−1.00 ± 0.08*	−1.96 ± 0.53	−2.05 ± 0.21*
Artemisia tridentata	UA	−1.02 ± 0.10	−3.71 ± 0.50	−4.47 ± 0.99
Pinus monophylla	UA	−0.91 ± 0.10	...	−1.72 ± 0.15
Juniperus osteosperma	UA	−1.00 ± 0.09	−2.12 ± 0.20	−2.41 ± 0.31
Amelanchier alnifolia	UA	−0.85 ± 0.09*	−2.76 ± 0.56	−3.32 ± 0.54*
		Peavine Mountain		
Pinus ponderosa	A	−0.69 ± 0.15	−0.76 ± 0.10	−1.08 ± 0.08
Pinus jeffreyi	A	−0.71 ± 0.13	−0.75 ± 0.05	−0.97 ± 0.11
Artemisia tridentata	UA	−0.60 ± 0.03	−1.15 ± 0.08	−2.87 ± 0.39
Purshia tridentata	UA	−0.93 ± 0.10	−0.73 ± 0.10	−0.93 ± 0.17
Tetradymia glabrata	UA	−0.65 ± 0.03	−1.83 ± 0.09	−2.70 ± 0.63

Stomatal conductance in *Pinus ponderosa* and *Artemisia tridentata* was significantly correlated with predawn XPP (Fig. 4). Low values of predawn XPP, which can result in stomatal closure, were not observed for *P. ponderosa* so a value from Running (1976) was included for the purpose of curve fitting. The relationship between conductance and predawn XPP was best described by a negative exponential curve for both species (least squares regression). A similar relationship between conductance and predawn XPP was observed for other species. However, at all sites conifers followed a different curve than the shrub species (Fig. 5). Conductance was higher at a given predawn XPP in the shrubs *Artemisia tridentata, Purshia tridentata, Arctostaphylos patula,* and *Amelanchier alnifolia* than in the Sierran or Great Basin conifers *Pinus ponderosa, P. jeffreyi, P. monophylla,* and *Juniperus osteosperma. Purshia tridentata* on the unaltered site at Alpine County maintained relatively high conductance at low XPP and was not included in the regression (Fig. 5A).

The carbon isotope ratios (cellulose component) for representative Great Basin and Sierran species were inversely related to maximum stomatal conductances measured during the summer (Fig. 6). The Great Basin conifers *Pinus monophylla* and *Juniperus osteosperma* had the lowest maximum conductances and highest $\delta^{13}C$ values, whereas the shrubs *Artemisia* and *Amelanchier* had the highest maximum conductances and lowest $\delta^{13}C$ values. The Sierran conifers *Pinus ponderosa* and *P. jeffreyi* had intermediate values. The $\delta^{13}C$ ratio for whole leaf tissue was highly correlated with that for cellulose [$\delta^{13}C_{\text{whole tissue}} = 0.98(\delta^{13}C_{\text{cellulose}}) - 1.00$, $r^2 = 0.99$], but whole leaf tissue was 1.5 ± 0.3‰ lighter than the cellulose component.

DISCUSSION

Early in the spring, when water availability was high, there were no significant differences between predawn XPP in *Arctostaphylos patula* and *Pinus jeffreyi* on the altered and unaltered soils at the Alpine County site. The spring values for *Amelanchier alnifolia* were actually higher on the unaltered soil at the Virginia Mountains site (Table 2). After an extended period without precipitation predawn XPPs for these species were significantly lower on the unaltered soils. Although not statistically different, predawn XPPs for *Pinus monophylla* and *Juniperus osteosperma* were also consistently lower on the unaltered soil (Virginia Mountains site) during the summer drought. Gravimetric determinations of soil moisture content suggest that the surface soil dries earlier in the summer on the unaltered than on the altered soil type (Fig. 1B).

There is a strong correlation between plant cover, evapotranspiration, and the depletion of soil moisture in desert shrub communities (Bronson et al. 1976, Miller et al. 1982, Schlesinger et al. 1987). Although total plant cover and leaf area index were not measured at our sites, the density of woody vegetation and herbaceous cover were considerably greater on unaltered soils (Table 1). At the drier sites, Virginia and Peavine mountains, the density of shrubs and trees was an order of magnitude greater on the unaltered soils. The higher percentage herbaceous cover, including a high proportion of the annual grass *Bromus tectorum,* undoubtedly contributed to depletion of surface soil water earlier in the summer on the unaltered soil at these sites.

The composition of the vegetation on the two soil types was also important in establishing seasonal differences in water availability. Shrubs, particularly *Artemisia tridentata* at Virginia and Peavine mountains, were dominant on the unaltered soil type, whereas Sierran conifers dominated the altered soil. As a physiognomic group the shrub species maintained substantially higher leaf conductances over a range of predawn XPPs from −0.5 to <−5.0 MPa (Figs. 4 and 5). Maximum conductance values for the shrubs were generally between 2 and 3 mm/s compared with <1.2 mm/s for *Pinus ponderosa* and *P. jeffreyi.* Other workers have reported that *Artemisia tridentata* maintains high conductance values and growth rates at very low soil water potentials and can strongly deplete soil water to a depth of ≈2 m in deep soils (Campbell and Harris 1977, Sturges 1977, Black and Mack 1986). Vegetative growth in *Artemisia* can continue at soil water potentials below −3.0 MPa, and reproductive growth and relatively high conductance values are observed below −6.0 MPa (Campbell and Harris 1977). The ability of shrubs to maintain high conductances at low soil water potential would lead to depletion of water in the rooting zone of soils derived from unaltered rocks. Moreover, the presence of greater herbaceous cover, composed largely of *Bromus tectorum,* on the unaltered soil should rapidly deplete surface moisture early in the summer. *Bromus tectorum* has rapid early season root growth and

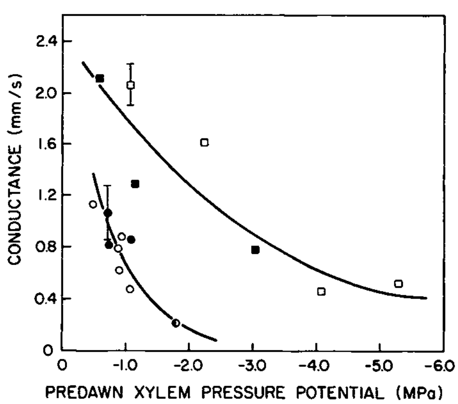

FIG. 4. Maximum stomatal conductance vs. predawn xylem pressure potential for *Artemisia tridentata* (□, ■) and *Pinus ponderosa* (O, ●, ◐). Each point is the mean of six independent measurements from the Virginia Mountains (open symbols) and Peavine Mountain (closed symbols) sites. Datum from Running (1976) is indicated by the half-filled circle. The curves were fitted by least-squares regression. For *P. ponderosa* conductance = $2.796e^{(-1.444\mathrm{XPP})}$, $r^2 = 0.84$. For *A. tridentata* conductance = $2.508e^{(-0.341\mathrm{XPP})}$, $r^2 = 0.85$. The largest standard deviation for each species is shown.

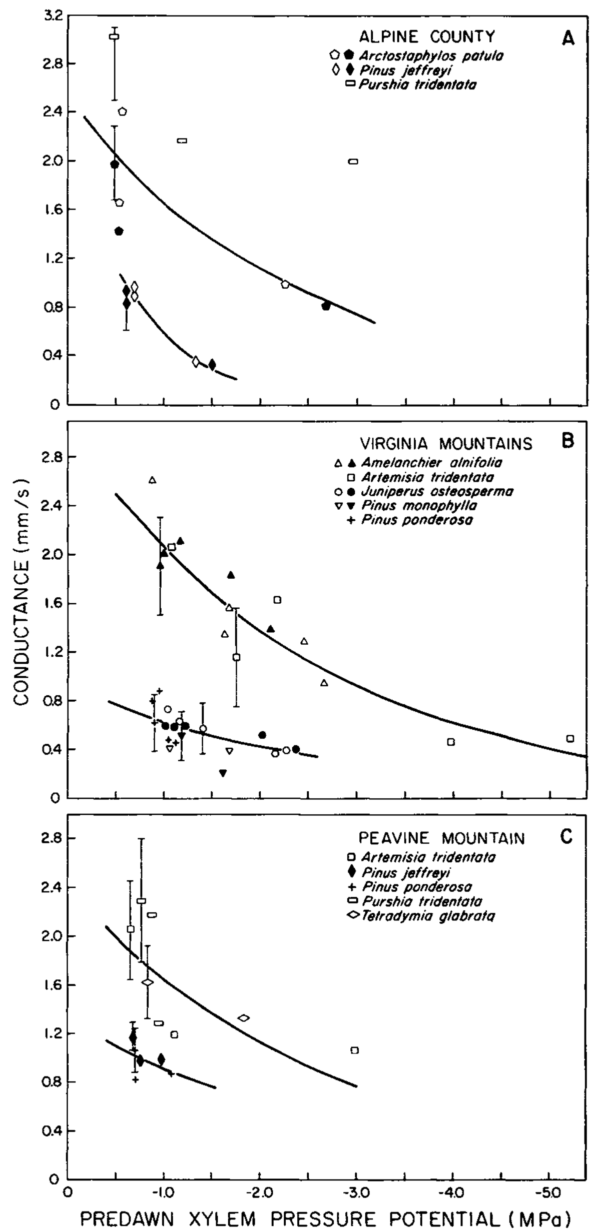

FIG. 5. Composite curves for stomatal conductance vs. predawn xylem pressure potential for shrubs and trees at the Alpine County (A), Virginia Mountains (B), and Peavine Mountain (C) sites. Open and closed symbols designate unaltered and altered soil, respectively. The curves were fitted by least-squares regression. The largest standard deviation for each species is shown. The regression equations are as follows. A_{shrub}: conductance = $2.105e^{(-0.035\mathrm{XPP})}$, $r^2 = 0.87$; A_{tree}: conductance = $1.993e^{(-0.125\mathrm{XPP})}$, $r^2 = 0.96$; B_{shrub}: conductance = $3.074e^{(-0.040\mathrm{XPP})}$, $r^2 = 0.88$; B_{tree}:conductance = $0.924e^{(-0.038\mathrm{XPP})}$, $r^2 = 0.60$; C_{shrub}: conductance = $2.396e^{(-0.037\mathrm{XPP})}$, $r^2 = 0.68$; C_{tree}: conductance = $1.297e^{(-0.036\mathrm{XPP})}$, $r^2 = 0.20$.

can develop very high root densities, indicating that it may be important in depleting soil moisture from the upper 100 cm (Harris 1967). Similarly, rapid depletion of surface soil moisture by *Bromus trinii* plays an im-

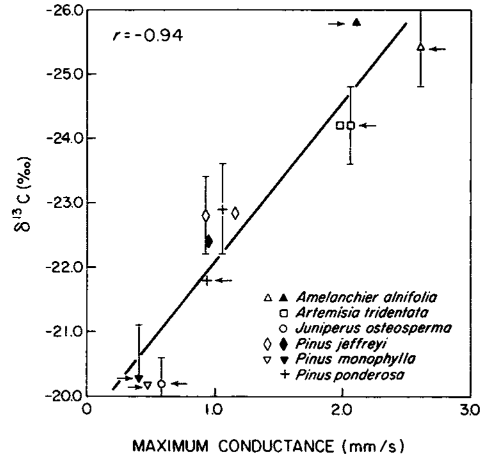

FIG. 6. Foliage $\delta^{13}C$ ratio vs. maximum stomatal conductance for several Great Basin and Sierran species. Isotopic composition was measured in cellulose extracted from current-year foliage. Open and closed symbols designate unaltered and altered soil, respectively, and the arrows indicate plants sampled at the Virginia Mountains site. The curve was fitted by least-squares regression ($\delta^{13}C$ ratio = 2.47 × conductance + 19.6, $r^2 = 0.89$). The largest standard deviation for each species is shown ($N = 5$).

portant role in restricting the establishment of evergreen chaparral species into adjacent grasslands in southern California (Davis and Mooney 1985).

The relatively high values and small fluctuation in predawn XPP for *Pinus ponderosa* and *P. jeffreyi* during the summer suggest that these species are deeply rooted in the altered rocks and have a reliable water supply. However, negative carbon balance associated with stomatal closure at relatively high soil water potentials suggests that seedlings of *Pinus ponderosa* or *P. jeffreyi* utilizing the upper 10–50 cm of the soil profile could not effectively compete for water with *Artemisia* and other Great Basin shrubs on unaltered soils. Stomatal closure for many western conifers occurs at soil water potentials above −2.0 MPa (Lassoie et al. 1985, Smith 1985) and at ≈ −1.8 MPa for *Pinus ponderosa* (Lopushinsky 1969, Lopushinsky and Klock 1974, Running 1976). Shainsky and Radosevich (1986) report a reduction in the growth of *P. ponderosa* seedlings in the presence of *Arctostaphylos patula* in the Sierra Nevada, but under the mesic montane conditions the effect is not so extreme as to restrict *P. ponderosa* to sites without shrubs.

The stomatal behavior of the Great Basin conifers, *Juniperus osteosperma* and *Pinus monophylla*, is more like that of the Sierran conifers than the Great Basin shrubs (Figs. 2 and 5), yet they become established amongst *Artemisia* and other shrubs. *Juniperus osteosperma* and *Pinus monophylla* may have superior drought tolerance than the Sierran conifers enabling these species to coexist with the Great Basin shrubs until they can establish a deeper root system. The higher predawn XPPs of mature junipers and pinyons during drought (Fig. 2) indicate that these species are more deeply rooted than *Artemisia* and the other Great Basin shrubs.

Recent investigations have shown a correlation between the ratio of stable carbon isotopes ($\delta^{13}C$) in leaf tissue, the internal CO_2 concentration of the leaf, and water-use efficiency (Farquhar et al. 1982, Farquhar and Richards 1984, Ehleringer et al. 1985). However, this relationship requires that the tissue being compared is exposed to similar leaf-to-air vapor pressure differences. With the possible exception of *Amelanchier*, the species examined in this study have small, narrow leaves and low boundary layer resistances. We assume that the species within a site experience similar leaf-to-air vapor pressure differences. The Great Basin conifers *Pinus monophylla* and *Juniperus osteosperma* had the highest isotopic ratios, the Sierran conifers *Pinus ponderosa* and *P. jeffreyi* had intermediate values, and the shrubs *Artemisia* and *Amelanchier* had the lowest values (Fig. 6). This suggests that shrubs function at higher internal CO_2 concentrations and lower water-use efficiencies than the Great Basin or Sierran conifers. In the Great Basin desert selection may favor higher carbon assimilation rates for the shrubs rather than higher water-use efficiencies, at least when water is abundant.

Although competition for water between the Sierran conifers and Great Basin shrubs was not assessed directly, the patterns of water use intrinsic to these species suggest that seedlings of the Sierran pines could not effectively compete with the suite of shrub species in desert soils of the Great Basin. Soil moisture in the western Great Basin is recharged mainly during the winter. Seedlings of *Pinus ponderosa* and *P. jeffreyi* germinate early in the spring when water availability is high. However, on unaltered soil rapid growth of annual and perennial grasses in the late winter and early spring followed by relatively high rates of water use by shrub species depletes soil water to a level unavailable to the Sierran conifer seedlings by June. Stands of *Pinus ponderosa* and *P. jeffreyi* in the midst of Great Basin vegetation are maintained on the altered soil type to a large extent by greater water availability on these sites.

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