

RESOURCE-USE EFFICIENCY AND DROUGHT TOLERANCE IN ADJACENT GREAT BASIN AND SIERRAN PLANTS¹

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Abstract. Using several adjacent Great Basin desert and Sierran montane trees and shrubs, we tested the prediction that water-use efficiency (WUE) is lower in more drought-tolerant species. We also measured maximum net photosynthetic rates and photosynthetic nitrogen-use efficiency (PNUE) to determine if these attributes decrease at high WUE. Differences in the physiological responses to resource availability were more clearly evident between growth forms, trees vs. shrubs, than between vegetation types, montane vs. desert. The shrubs (*Amelanchier alnifolia*, *Arctostaphylos patula*, and *Artemisia tridentata*) maintained higher rates of net photosynthesis at lower predawn water potential but had lower WUE than the trees (*Juniperus osteosperma*, *Pinus monophylla*, *P. jeffreyi*, and *P. ponderosa*). PNUE was highest in the shrubs that also had the highest foliage N content, and PNUE was inversely related to WUE. However, trees had higher nutrient retranslocation efficiency and growth-based NUE than shrubs.

Low WUE and high drought tolerance of shrubs suggests that maintaining high WUE under competitive water-limited conditions may not be advantageous. In contrast, conservative use of water (high WUE) and high growth-based NUE by trees lengthens the season of net carbon assimilation and more closely matches growth with low rates of nutrient availability on nutrient-poor sites.

Key words: *Artemisia*; carbon isotope ratio; desert; drought tolerance; Great Basin; net photosynthesis; photosynthetic nitrogen-use efficiency; *Pinus*; Sierra Nevada; water relations; water-use efficiency.

INTRODUCTION

Transpiration is often viewed as a “cost” associated with carbon acquisition by terrestrial plants, particularly in water-limited environments (Orians and Solbrig 1977). One method of assessing this cost is through measuring water-use efficiency (WUE), defined as the ratio of net photosynthesis to transpiration (Kramer 1983). Many morphological, phenological, and physiological attributes increase WUE, and most workers assume that the maintenance of high WUE is beneficial under desert conditions (Fischer and Turner 1978). However, many of the attributes that increase WUE may also impose limitations on carbon gain and compromise performance in competitive situations.

Stomatal closure causes a proportionately greater decrease in transpiration than in photosynthesis (Raschke 1979, Cowan 1982) because of additional resistances associated with diffusion of CO₂ relative to H₂O in the leaf (Nobel 1983). Thus, reduced conductance increases WUE but decreases the absolute rate of net photosynthesis. A reduction of stomatal conductance also may cause a decrease in photosynthetic nitrogen-use efficiency (Field et al. 1983). Instantaneous photosynthetic nitrogen-use efficiency (PNUE) is defined as the

rate of net carbon assimilation per mole of leaf nitrogen. For a fixed amount of leaf N, a decrease in stomatal conductance decreases PNUE while increasing WUE. Another cost of high WUE is that conserved water stored in the soil may be lost by evaporation or increase the availability of soil moisture to competitors (Cohen 1970). These potential consequences of efficient water use lead to speculation that the maintenance of high WUE is a conservative ecophysiological strategy that is disadvantageous to native plants in competitive water-limited environments (Cohen 1970, Passioura 1982).

The purpose of this study was to test the prediction that WUE is lower in more drought-tolerant species. We also measured maximum photosynthetic rates and PNUE to determine if these attributes decrease at high WUE and represent a “cost” of maintaining high WUE. To provide a range of moisture availability, measurements were made at four locations on the east slope of the Sierra Nevada and adjacent Great Basin desert.

The east-slope forests of the Sierra Nevada typically receive more than three times the annual precipitation of adjacent Great Basin desert (Barbour 1988, West 1988), and the dominant Sierran pines are considerably less drought tolerant than the dominant Great Basin shrub, *Artemisia tridentata* (DeLucia et al. 1988, DeLucia and Heckathorn 1989). Sierran pines also grow in the midst of sagebrush desert vegetation but are

¹ Manuscript received 21 March 1989; revised 23 March 1990; accepted 16 April 1990.

restricted to outcrops of hydrothermally altered rock (Billings 1950), presumably by competition for water with the more drought-tolerant sagebrush vegetation (DeLucia et al. 1988). Conversely, *Artemisia tridentata* and other desert plants are excluded from the pine stands by intolerance of the low-nutrient conditions of soils derived from hydrothermally altered rock (Billings 1950, DeLucia et al. 1989, Schlesinger et al. 1989). These disjunct forest ecosystems provide the opportunity to compare WUE and other aspects of plant water and nutrient relations in Sierran and Great Basin vegetation growing in a similar climate.

METHODS AND MATERIALS

Four sites with different annual precipitation were selected near Reno, Nevada (Alpine County site, Virginia Mountains site, Peavine Mountain site, and Ramsey Mine site). Each site had both altered rock with Sierran vegetation and unaltered rock with Great Basin vegetation. The Alpine County site, a typical east-slope Sierran forest on all rock types, is the wettest, receiving an average of ≈ 950 mm (water equivalents) of precipitation annually. The Virginia Mountains site is pinyon-juniper woodland and the Peavine Mountain site is a sagebrush steppe. These sites receive ≈ 255 and 262 mm of precipitation, respectively. The Ramsey Mine site is a sagebrush steppe located ≈ 70 km east of the eastern climatic limit of the contiguous Sierran forest near Reno and is the driest of the four sites (≈ 200 mm precipitation). Sierran species are restricted to outcrops of hydrothermally altered rock at the Virginia Mountains, Peavine Mountain, and Ramsey Mine sites. At the Alpine County site, Sierran species occur on both rock types, but Great Basin species are excluded from altered rock. The first three sites were described in detail by DeLucia et al. (1988), and a map of all sites is provided by Schlesinger et al. (1989).

We measured the dominant Great Basin shrub *Artemisia tridentata* and a dominant Sierran pine, either *Pinus ponderosa* or *P. jeffreyi*, growing in adjacent soils derived from unaltered and hydrothermally altered bedrock at each site. Other dominant Great Basin and Sierran shrubs and trees were included when present (Tables 1 and 2). The Great Basin shrubs, *Amelanchier alnifolia* and *Purshia tridentata*, and two Great Basin trees, *Juniperus osteosperma* and *Pinus monophylla*, were included. *Arctostaphylos patula* was included as a Sierran shrub. When a species occurred on soils derived from hydrothermally altered and unaltered rock, it was sampled on both soil types (*Amelanchier alnifolia*, Virginia Mountains; *Arctostaphylos patula* and *Pinus jeffreyi*, Alpine County; and *Juniperus osteosperma*, Ramsey Mine). Intraspecific differences on contrasting soils, however, were generally small, and in most cases data within a species across soil types were grouped.

Physiological measurements were made in June and August 1987. In situ gas exchange was measured on

fully exposed shoots or leaves that were enclosed in a well-mixed 1-L cuvette, with a closed infrared gas analysis system (LI-COR, model LI-6200). Measurements were typically completed in 20–40 s under saturating irradiances ($> 1200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PAR). Relative humidity and CO_2 concentration in the cuvette were within 5% and $5 \mu\text{L/L}$, respectively, of ambient levels. Because of the short duration of the measurement and rapid air flow in the cuvette, foliage temperatures were within 2°C of ambient air temperature. Shoots of *Pinus monophylla*, *Juniperus osteosperma*, and *Artemisia tridentata* were trimmed to fit into the cuvette on the day prior to gas-exchange measurements. For species with more than one leaf cohort (*Pinus ponderosa*, *P. jeffreyi*, *P. monophylla*, and *Juniperus osteosperma*), measurements were made on foliage that had emerged during the previous summer. Measurements were made on five plants per species at each site and soil type, and two shoots were sampled on each plant.

Maximum gas-exchange rates occurred between 0800 and 1000 (Pacific Standard Time [PST]) (determined from diurnal response curves), and measurements were made during this period. Net photosynthesis (CO_2 uptake), stomatal conductance, and intercellular CO_2 concentration were calculated on a projected leaf area and dry mass basis as in von Caemmerer and Farquhar (1981). For calculation of stomatal conductance, we assumed that boundary layer resistance was 0.3 s/cm (boundary layer conductance for water = $\approx 1333 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for all species and that water flux through the leaf cuticle was negligible.

Bulk shoot water potential was measured on excised shoot tips (≈ 10 cm long), adjacent to those used for gas-exchange measurements, with a pressure chamber (SoilMoisture Equipment, Santa Barbara, California, USA) as described by Ritchie and Hinckley (1975). Measurements (two shoots/plant) were made between 0200 and 0400 (PST) and immediately following each gas-exchange measurement. Drought tolerance was defined as the ability to maintain positive rates of net photosynthesis at progressively lower water potentials, and was estimated from boundary-line plots of the maximum daily rate of net photosynthesis vs. predawn water potential. We also used the seasonal amplitude of predawn water potential as an index of drought tolerance. Insofar as predawn water potential reflects the ability of perennial plants to continue extracting soil moisture by maintaining stomatal conductance at progressively decreasing availability, the amplitude of predawn water potential should be positively correlated with drought tolerance.

Because of potentially large errors associated with measurement of transpiration in closed cuvettes (Smith and Hollinger 1988) and questions regarding the significance of instantaneous values of WUE, we rely on the carbon isotope composition ($\delta^{13}\text{C}$) of foliage as an index of seasonally integrated WUE. Farquhar et al. (1982, 1989) developed the theoretical relationship be-

tween carbon isotope composition ($\delta^{13}\text{C}$) of foliage and the ratio of intercellular to ambient partial pressure of CO_2 (c_i/c_a). For C_3 plants:

$$\delta = \delta_{\text{env}} - a - (b_3 - a)c_i/c_a, \quad (1)$$

where δ is the ratio of $^{13}\text{C}/^{12}\text{C}$ in foliage relative to the PDB standard (Craig 1957), δ_{env} is the isotopic composition of the atmospheric CO_2 (-7.8‰), a is the fractionation caused by diffusion (4.4‰), and b_3 is the fractionation attributed to carbon fixation by ribulose biphosphate carboxylase (27‰). Current values for the parameters in this model are from O'Leary (1988). Carbon isotope composition provides an estimate of c_i , which in turn is negatively correlated with WUE (Farquhar and Richards 1984, Ehleringer and Cooper 1988). Based on an analogy to Ohm's law, WUE is expressed as:

$$A/E = (c_a - c_i)/(1.6 \times \text{LAVPD}), \quad (2)$$

where A is net photosynthesis, E is transpiration, and LAVPD is the leaf-to-air vapor pressure deficit. At comparable atmospheric CO_2 and LAVPD, water-use efficiency is therefore a function of c_i . For the purpose of interspecific or intersite comparisons, the relationship between WUE and $\delta^{13}\text{C}$ rests on the assumption that the plants are physiologically active at the same time of year, and their foliage experiences similar LAVPD. With the exception of *Arctostaphylos patula*, the species in this study have small or narrow leaves, reducing differences in boundary layer resistance and LAVPD. However, differences in rooting depth and phenology may contribute to variation in seasonal duration of physiological activity and introduce error in inferences regarding WUE.

Current-year foliage was collected in August 1987 from all plants used for gas-exchange measurements for determination of carbon isotope composition ($\delta^{13}\text{C}$). As suggested by Leavitt and Long (1986) a bulk sample was collected by combining tissue from the four cardinal points at mid-canopy. Foliage was dried to constant mass at 80° and ground in a Wiley mill to pass a $425\text{-}\mu\text{m}$ mesh. The carbon isotope composition of CO_2 derived from combustion of samples was measured with a mass spectrometer as in Ehleringer and Cooper (1988). Values for $\delta^{13}\text{C}$ are expressed relative to the PDB standard (Craig 1957). Samples also were collected in the same way from the same plants in June 1987 for analysis of nutrient content. Total N and P were determined as in Schlesinger et al. (1989) by the Agronomy Analytical Laboratory at Cornell University and cross-checked with samples traceable to the National Bureau of Standards.

The mean values for physiological and chemical characteristics among species at each site were compared with a one-way ANOVA and Tukey's multiple-range test ($P < .05$). The relationships between species were illustrated with scatter plots.

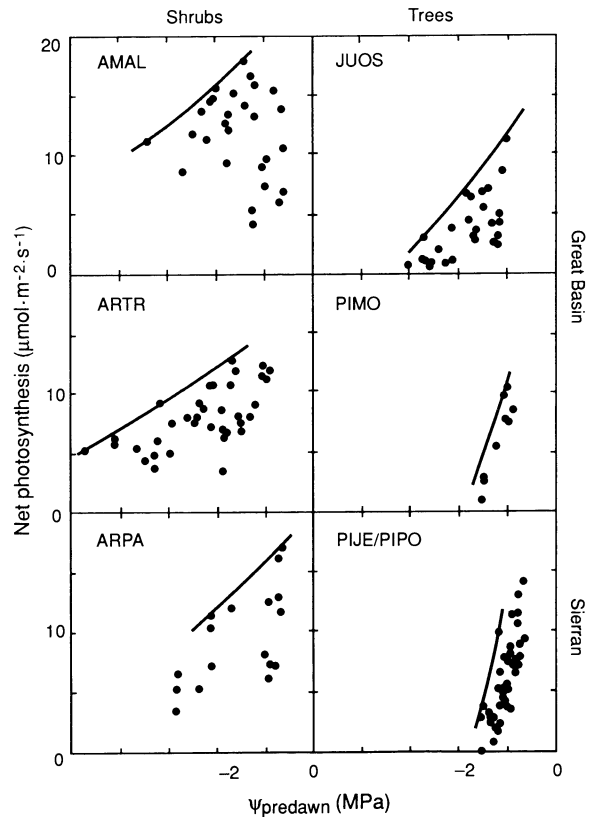


FIG. 1. Net photosynthesis (CO_2 uptake rate per unit leaf area) vs. predawn water potential for several Great Basin and Sierran shrubs and trees. Boundary lines were drawn through the highest photosynthetic rates for a given water potential. We assume that for points below the boundary lines net photosynthesis was limited by factors other than ψ_{predawn} . *Amelanchier alnifolia* (AMAL, Great Basin shrub); *Artemisia tridentata* (ARTR, Great Basin shrub); *Arctostaphylos patula* (ARPA, Sierran shrub); *Juniperus osteosperma* (JUOS, Great Basin tree); *Pinus monophylla* (PIMO, Great Basin tree); grouped data for *Pinus jeffreyi* and *P. ponderosa* (PIJE/PIPO, Sierran trees).

RESULTS

Because of large variations inherent in data collected at different locations and at different times of year, boundary lines were used to estimate the relationship between net photosynthesis and ψ_{predawn} (Fig. 1). We assume that factors other than soil moisture, such as LAVPD and temperature, limited photosynthesis for points below the boundary lines.

The cessation of net photosynthesis occurred at substantially higher ψ_{predawn} for the Great Basin and Sierran trees than for the shrubs (Fig. 1). *Pinus ponderosa*, *P. jeffreyi*, and *P. monophylla* maintained positive rates of carbon assimilation at water potentials greater than approximately -2.0 MPa. *Juniperus osteosperma* maintained positive photosynthetic rates at ≈ 1 MPa lower than the *Pinus* species. Although the minimum water potential supporting net carbon assimilation for

TABLE 1. Physiological, chemical, and structural characteristics of foliage for several dominant Great Basin and Sierran shrubs and trees.* Each value is a mean of five plants. Means were compared at each site with a one-way ANOVA and Tukey's multiple-range test. Means with different superscript letters are significantly different at $P < .05$.

Species	Growth form†	Community type‡	$A_{\max/a}$ ($\text{nmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	$A_{\max/m}$ ($\text{nmol} \cdot \text{g}^{-1} \cdot \text{s}^{-1}$)	PNUE ($\mu\text{mol} \cdot \text{mol}^{-1} \cdot \text{s}^{-1}$)	g_{\max} ($\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	ψ_{\min} (MPa)
Ramsey Mine							
<i>Artemisia tridentata</i>	Sh	GB	11.3 ^a	62.2 ^a	56.5 ^a	221 ^a	-3.33 ^a
<i>Juniperus osteosperma</i>	Mt	GB	3.4 ^b	5.3 ^b	8.8 ^b	62 ^b	-2.62 ^a
<i>Pinus ponderosa</i>	Tr	Sn	7.2 ^c	24.7 ^c	32.2 ^c	101 ^b	-1.24 ^b
Virginia Mountains							
<i>Amelanchier alnifolia</i>	Sh	GB	16.6 ^a	154.4 ^a	109.6 ^a	243 ^a	-2.66 ^a
<i>Artemisia tridentata</i>	Sh	GB	7.8 ^b	52.6 ^b	52.2 ^b	133 ^b	-2.33 ^a
<i>Juniperus osteosperma</i>	Mt	GB	3.1 ^c	4.8 ^c	8.8 ^c	40 ^a	-2.45 ^a
<i>Pinus monophylla</i>	Mt	GB	6.7 ^{bc}	9.0 ^c	14.0 ^{cd}	63 ^c	-1.52 ^b
<i>Pinus ponderosa</i>	Tr	Sn	4.9 ^{bc}	16.3 ^c	24.2 ^d	62 ^c	-1.50 ^b
Peavine Mountain							
<i>Artemisia tridentata</i>	Sh	GB	7.1 ^a	36.4 ^a	34.9 ^a	94 ^a	-3.85 ^a
<i>Purshia tridentata</i> §	Sh	GB	§	§	§	§	-0.75 ^b
<i>Pinus jeffreyi</i>	Tr	Sn	10.6 ^a	32.0 ^a	42.3 ^a	136 ^a	-0.84 ^b
<i>Pinus ponderosa</i>	Tr	Sn	9.7 ^a	29.0 ^a	40.4 ^a	124 ^a	-1.06 ^b
Alpine County							
<i>Artemisia tridentata</i>	Sh	GB	11.7 ^a	83.1 ^a	66.2 ^a	174 ^a	-2.80 ^a
<i>Arctostaphylos patula</i>	Sh	Sn	14.1 ^a	51.4 ^b	46.2 ^b	213 ^b	-2.74 ^a
<i>Pinus jeffreyi</i>	Tr	Sn	5.6 ^b	17.4 ^c	24.9 ^c	69 ^c	-1.31 ^b

* Physiological characteristics are: maximum photosynthetic (net CO_2 uptake) rate per unit leaf area ($A_{\max/a}$), maximum photosynthetic rates per unit leaf dry mass ($A_{\max/m}$), instantaneous photosynthetic nitrogen-use efficiency (PNUE, net CO_2 uptake rate per unit leaf N), maximum stomatal conductance to water vapor (g_{\max}), lowest predawn water potential during the summer (ψ_{\min}), and the amplitude of predawn water potential during the summer ($\Delta\psi$, MPa). Chemical characteristics are: foliar nitrogen content (N), foliar phosphorus content (P), and carbon isotope composition ($\delta^{13}\text{C}$). The structural characteristic is specific leaf mass (SLM).

† Growth forms are: Sh, shrub; Mt, multistem tree; Tr, single-stem tree.

‡ Community type is either Great Basin (GB), which includes shrub steppe and pinyon-juniper woodland, or Sierran montane forest (Sn).

§ Indicates this species was present but not measured at the site; otherwise, if the species is not listed it was not present at this location.

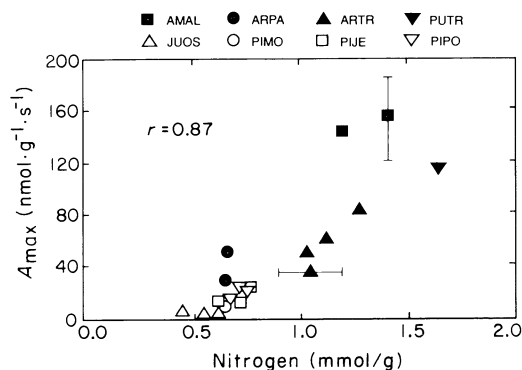


FIG. 2. Maximum daily net photosynthesis (A_{\max} , dry mass basis) vs. foliage N content for several Great Basin and Sierran shrubs and trees. Each point is the mean of five plants at each site, and the largest standard deviation for each axis is shown. Species codes are the same as in Fig. 1. Shrubs are shown with closed symbols and trees with open symbols. The slope of the regression (linear model) is significantly different from 0 at $P < .05$.

the shrubs could not be determined, these plants clearly had higher rates of photosynthesis at lower ψ_{predawn} than any of the tree species. *Artemisia tridentata* had positive carbon assimilation at ψ_{predawn} below -4.5 MPa.

The most drought-tolerant species, based on Fig. 1, also had the lowest minimum values and greatest amplitude of ψ_{predawn} during summer (Table 1). The amplitude of ψ_{predawn} for the *Pinus* species was consistently <0.5 MPa, compared to values >0.7 MPa for *Amelanchier alnifolia*, *Artemisia tridentata*, and *Arctostaphylos patula*. The minimum and seasonal amplitudes of ψ_{predawn} for *Juniperus osteosperma* were intermediate between *Artemisia tridentata* and *Pinus ponderosa* at Ramsey Mine, and were not significantly different from the shrubs at Virginia Mountains (Table 1). Unlike the other shrubs, *Purshia tridentata* at Peavine Mountain maintained high values and very little variation in ψ_{predawn} during summer (Table 1). Because these plants were large and values for ψ_{predawn} were unusually high, we suspect that *Purshia tridentata* was phreatophytic at the Peavine Mountain site.

Maximum net photosynthetic rates (A_{\max}), calculated on a dry mass basis, were positively correlated with foliage nitrogen content across species (Fig. 2). Trees had lower photosynthetic rates (expressed on a leaf dry

TABLE 1. Continued.

$\Delta\psi$ (MPa)	N (mmol/g)	P ($\mu\text{mol/g}$)	$\delta^{13}\text{C}$ (‰)	SLM (g/m^2)
Ramsey Mine				
1.49 ^a	1.01 ^a	81.7 ^a	-24.05 ^a	185.1 ^a
0.99 ^b	0.52 ^b	33.5 ^b	-23.05 ^b	644.0 ^b
0.28 ^c	0.75 ^c	28.4 ^b	-21.55 ^c	294.5 ^c
Virginia Mountains				
0.79 ^{ab}	1.30 ^a	50.9 ^a	-25.74 ^a	106.7 ^a
0.92 ^a	1.01 ^b	81.2 ^b	-25.40 ^a	150.3 ^a
1.18 ^a	0.54 ^c	35.6 ^c	-22.52 ^b	649.4 ^b
0.42 ^b	0.64 ^{cd}	38.2 ^c	-21.36 ^c	748.4 ^c
0.18 ^c	0.67 ^d	27.4 ^c	-22.26 ^b	297.7 ^d
Peavine Mountain				
1.94 ^a	1.04 ^a	85.6 ^a	-24.81 ^a	194.3 ^a
0.01 ^b	1.69 ^b	54.6 ^b	-24.15 ^b	†
0.09 ^b	0.77 ^c	34.7 ^c	-22.97 ^c	331.2 ^b
0.13 ^b	0.71 ^c	35.3 ^c	-22.23 ^c	334.8 ^b
Alpine County				
1.82 ^a	1.27 ^a	84.6 ^a	-25.90 ^a	140.8 ^a
1.78 ^a	0.64 ^b	43.7 ^b	-26.50 ^a	277.4 ^b
0.48 ^b	0.66 ^b	32.2 ^b	-22.22 ^b	324.2 ^b

mass or area basis), maximum stomatal conductances, and N contents than did shrubs (Table 1). *Amelanchier alnifolia* had the highest photosynthetic rate, but *Purshia tridentata*, a nitrogen-fixing plant (Virginia and Delwiche 1982), had the highest foliage N content. Among the shrubs, *Arctostaphylos patula* had the lowest assimilation rate and N content. This species also had values of specific leaf mass intermediate between the trees and other shrubs. When calculated on an area basis, however, photosynthetic rates of *Arctostaphylos patula* were similar to the other shrubs (Table 1). Across species, photosynthetic rates were not significantly correlated with foliage P content ($r = 0.45$, $P > .05$), although there was a significant positive correlation between foliage N and P content ($r = 0.64$, $P < .05$).

There was a negative correlation between A_{max} and $\delta^{13}\text{C}$ (Fig. 3a). Shrubs had higher maximum photosynthetic rates and more negative values of $\delta^{13}\text{C}$, indicating shrubs had lower WUE integrated over the growing season than trees. When expressed on a dry mass basis, A_{max} for *Arctostaphylos patula* was similar to the trees; however, $\delta^{13}\text{C}$ values were significantly lower and similar to values observed for the Great Basin shrubs (Table 1). There was also a negative correlation between instantaneous PNUE and $\delta^{13}\text{C}$ (Fig. 3b), resulting from the strong positive correlation between PNUE and A_{max} (Fig. 4). Because photosynthetic rates were measured under ambient conditions, we calculated instantaneous PNUE as the maximum daily rate of CO_2 assimilation per tissue N content, rather than using photosynthesis measured under optimal conditions as in Field et al. (1983). Instantaneous PNUE was also positively correlated with foliage N ($r = 0.74$, $P < .05$). Thus, for

shrubs high foliar N supports high A_{max} , g_{max} , and PNUE, but low WUE compared to trees.

Seasonally integrated c_i , calculated using Eq. 1 and assuming $c_a = 350 \mu\text{L/L}$, was consistently greater for shrubs than for the Sierran or Great Basin trees. The mean ($\pm 1\text{SD}$) calculated c_i for shrubs and trees were 211 ± 24 and $155 \pm 10 \mu\text{L/L}$, respectively. These values were significantly different ($P < .05$), but differences between data grouped for Great Basin and Sierran plants were not. For the shrubs, calculated c_i values were: *Amelanchier alnifolia*, 240 $\mu\text{L/L}$; *Arctostaphylos patula*, 221; *Artemisia tridentata*, 199; and *Purshia tridentata*, 185. Values for the trees were: *Juniperus osteosperma*, 166 $\mu\text{L/L}$; *Pinus monophylla*, 142; *P. jeffreyi*, 159; and *P. ponderosa*, 152.

DISCUSSION

Artemisia tridentata, the dominant Great Basin shrub, had substantially higher drought tolerance and lower WUE, determined by carbon isotope composition, than the dominant Sierran trees, *Pinus ponderosa* and *P. jeffreyi*. However, when all species were considered, differences in the physiological responses to resource

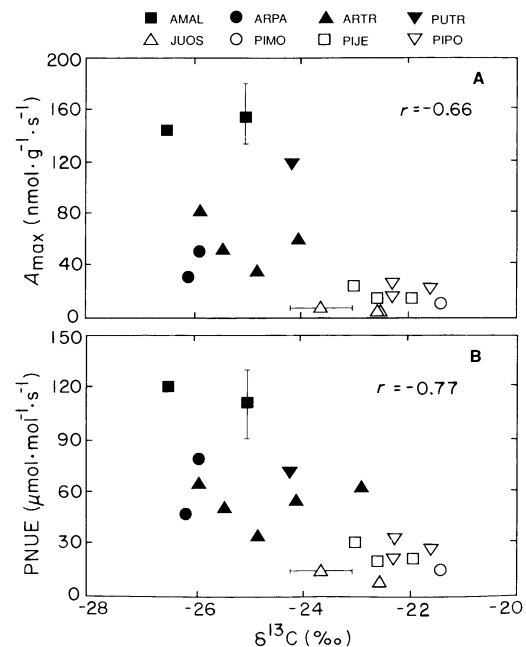


FIG. 3. Maximum net photosynthetic (CO_2 uptake) rates per unit leaf dry mass, A_{max} (a) and photosynthetic nitrogen-use efficiency (PNUE, net CO_2 uptake per unit leaf nitrogen) (b) vs. foliage carbon isotope composition ($\delta^{13}\text{C}$) for several Great Basin and Sierran shrubs and trees. Species codes are the same as in Fig. 1. Each point is the mean of five plants at each site, and the largest standard deviation for each axis is shown. The r values are indicated and the slopes of the regressions (linear model) are significantly different from 0 at $P < .05$.

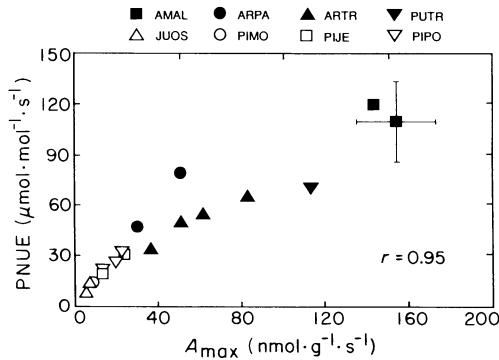


FIG. 4. Photosynthetic nitrogen-use efficiency (PNUE) vs. A_{\max} for several Great Basin and Sierran shrubs and trees. (Variables defined as in Fig. 3.) Species codes are the same as in Fig. 1. Each point is the mean of five plants at each site, and the largest standard deviation for each axis is shown. The slope of the regression (linear model) is significantly different from 0 at $P < .05$.

availability were more clearly evident between growth forms, trees vs. shrubs, than between community types, montane vs. desert (Table 2). For most physiological characteristics, the Great Basin trees, *Juniperus osteosperma* and *Pinus monophylla*, performed similarly to the Sierran pines. Both Sierran and Great Basin shrubs had greater drought tolerance and photosynthetic nitrogen-use efficiency (PNUE), and lower WUE than trees. When calculated on a dry mass basis, higher maximum photosynthetic rates were found in shrubs.

Fischer and Turner (1978) proposed that in dry habitats natural selection should favor plants with high WUE. For dominant Great Basin and Sierran plants the opposite appears to be the case; low WUE is associated with a high degree of drought tolerance as exemplified by the shrubs (Table 2). We rely on $\delta^{13}\text{C}$ values of foliage for estimating seasonally integrated WUE. This method is based on the negative relationship between c_i and WUE (Eq. 2), and for interspecific

comparisons we must assume that plants experience similar LAVPD over the growing season at each research site. This assumption may not be entirely valid. For broader leaf shrubs, high boundary layer resistance and LAVPD at the same c_i would cause an underestimate of WUE compared to narrow-leaf conifers. However, using gas-exchange techniques under controlled growth chamber conditions, DeLucia and Heckathorn (1989) found that *Pinus ponderosa* consistently maintained higher WUE than *Artemisia tridentata* over a range of water potentials, thus providing partial corroboration for inferences based on $\delta^{13}\text{C}$ data.

For Great Basin and Sierran plants there is an inverse relationship between WUE and A_{\max} and PNUE (Fig. 3). Shrubs have high PNUE and A_{\max} and low WUE, while the opposite is true of trees. A similar relationship between WUE measured by gas exchange and PNUE for several C_3 evergreen shrubs was observed by Field et al. (1983) and Lajtha and Whitford (1989). The balance between WUE and PNUE represents a functional compromise between attributes that maximize net photosynthesis and physiological and morphological adaptations to drought. For C_3 plants high rates of photosynthesis are associated with factors that increase c_i and consequently decrease WUE (Eq. 2), such as high foliar N and high stomatal conductance. Diffusional limitations caused by low stomatal conductance increase WUE but decrease c_i and PNUE (Field and Mooney 1986). Average seasonally integrated c_i s calculated for trees and shrubs were 155 and 211 $\mu\text{L/L}$, respectively. This difference indicates that trees had relatively higher diffusional limitations to gas exchange than shrubs.

Reich and Schoettle (1988) found that PNUE in white pine (*Pinus strobus*) was positively correlated with the efficiency of nutrient use in growth, i.e., dry mass of carbon added per unit of nutrient uptake. Such a relation is not seen in the comparison across growth forms in our study (Table 2). Shrubs have lower NUE

TABLE 2. Summary of some physiological and growth characteristics for several Great Basin and Sierran trees and shrubs.*

Species	Growth form	Community type	Drought tolerance	WUE	PNUE	NUE (growth)	Fractional reabsorption
<i>Amelanchier alnifolia</i>	Sh	GB	+++	--	+++	†	†
<i>Artemisia tridentata</i>	Sh	GB	+++	--	++	--	--
<i>Purshia tridentata</i>	Sh	GB	†	--	++	†	†
<i>Arctostaphylos patula</i>	Sh	SN	++	--	++	†	--
<i>Juniperus osteosperma</i>	Mt	GB	-/+	++	--	†	++
<i>Pinus monophylla</i>	Mt	GB	--	+++	--	++	++
<i>Pinus jeffreyi</i>	Tr	SN	--	+++	--	†	++
<i>Pinus ponderosa</i>	Tr	SN	--	+++	--	+++	++

* Growth forms are: Sh, shrub; Mt, multistem tree; Tr, single-stem tree. Community type is either Great Basin (GB), which includes shrub steppe and pinyon-juniper woodland, or Sierran montane forest (SN). + Plus and -- minus signs indicate a high or low degree, respectively, for each physiological parameter. The rankings for drought tolerance are based on the photosynthesis vs. water potential relationship and the seasonal amplitude of predawn water potentials. Water-use efficiency (WUE) is based on carbon isotope discrimination. Photosynthetic nitrogen-use efficiency (PNUE) is based on gas exchange data. Growth-based nutrient-use efficiency (NUE growth) and fractional reabsorption of P prior to leaf abscission were determined from data in Schlesinger et al. (1989).

† Insufficient data.

than trees (Schlesinger et al. 1989). Instantaneous PNUE is only one facet of nutrient-use efficiency in growth, which is also affected by leaf longevity, internal nutrient allocation, and nutrient reabsorption before leaf abscission (Vitousek 1982). Sierran conifers show higher NUE in growth and reabsorption efficiency than Great Basin shrubs, particularly for phosphorus (Schlesinger et al. 1989).

These patterns of differences in physiology between trees and shrubs, but not between species with different distributions relative to soil type and climate, raise several questions about the causes of their distribution patterns. For evergreen coniferous trees growing in Sierran montane forest, on altered rock in the desert, or in pinyon-juniper woodland, relatively high and stable values for predawn water potential indicate that these plants become deeply rooted and largely free of competition for water with the smaller shrubs. Deep root penetration would also put a high proportion of the root systems of trees in a region of the soil profile with relatively low rates of mineralization. We propose that conservative use of water (high WUE) by trees and high growth-base NUE and retranslocation efficiency associated with evergreen habit (Chabot and Hicks 1982) lengthen the season favorable for net carbon assimilation and more closely match growth with low rates of nutrient availability on nutrient-poor sites (Chapin 1980). High WUE may contribute to lower competitive ability of trees than shrubs (Shainsky and Radosevich 1986), confining Sierran trees growing in the desert to nutrient-poor soils on hydrothermally altered rock, which excludes Great Basin vegetation. In contrast, shrubs require high foliar N and P contents to support higher photosynthetic rates than trees and may rely on shallower root distribution to acquire these nutrients. A shallower root system is consistent with the profligate use of water and greater drought tolerance observed for shrubs (Cohen 1970). Greater precipitation in high-elevation Sierran forests may ameliorate the effect of these physiological differences between shrubs and trees, thus permitting co-occurrence of *Arcostaphylos patula* and the Sierran pines.

It is intriguing that the Great Basin trees, *Pinus ponderosa* and *Juniperus osteosperma*, have similar WUE and drought tolerance to the Sierran trees, yet grow with sagebrush vegetation. We speculate that lower rates of growth and presumably respiration for Great Basin trees (DeLucia et al. 1989) confer a higher probability of surviving extended periods of low soil water availability than the Sierran trees.

ACKNOWLEDGMENTS

We thank W. D. Billings, S. A. Heckathorn, and J. L. Naeherling for assistance with the field work, and the Desert Research Institute, Reno, Nevada, for providing logistical support. Editorial assistance provided by D. Goldberg and L. D. Schlesinger is gratefully acknowledged. $\delta^{13}\text{C}$ determinations were made by Dr. J. R. Ehleringer, University of Utah. This project was funded by NSF grant number BRS 85-04859

(Ecology Program) to W. H. Schlesinger and W. D. Billings. Additional support was provided by USDA competitive grant (Forest Biology Program) to E. H. DeLucia.

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