

The effect of soil drought on water-use efficiency in a contrasting Great Basin desert and Sierran montane species

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Abstract The effect of soil drought on water-use efficiency (WUE) and water relations was examined for potted *Artemisia tridentata* Nutt. and *Pinus ponderosa* Laws., a dominant Great Basin desert shrub and a Sierran montane tree, respectively. Before the onset of drought, *A. tridentata* had slightly higher photosynthetic rates than *P. ponderosa* and *A. tridentata* maintained positive photosynthetic rates at substantially lower water potentials (ψ). Complete stomatal closure and cessation of photosynthesis occurred at a ψ of ca. -2.5 MPa for *P. ponderosa* and less than -5.0 MPa for *A. tridentata*. Repeated drought cycles caused a small increase in bulk modulus of elasticity for *A. tridentata* and neither species exhibited significant osmotic adjustment. WUE was similar at $\psi \geq -1.0$ MPa but as ψ decreased *P. ponderosa* consistently maintained higher WUE than *A. tridentata*. The primary factor contributing to higher WUE for *P. ponderosa* was the rapid decrease in stomatal conductance with decreasing ψ . Comparatively low WUE for *A. tridentata*, a drought tolerant species, suggests that efficient use of water is a conservative ecophysiological 'strategy' that can be detrimental in a competitive water-limited environment. The combination of profligate use of water and a high degree of drought tolerance may be a more successful combination of physiological characteristics in certain dry habitats.

Key-words: *Artemisia tridentata*; drought tolerance; leaf gas exchange; *Pinus ponderosa*; photosynthesis; stomatal conductance; water relations; water-use efficiency.

Introduction

Water-use efficiency (WUE) is defined in agriculture or ecosystem science as the ratio of yield or net primary production to evapotranspiration and in plant physiology as the ratio of net photosynthesis to transpiration (Fischer & Turner, 1978; Kramer, 1982). In dry habitats high WUEs have been observed in plants having widely different physiognomies (Field, Merino & Mooney, 1983; Knapp & Smith, 1988; Monson, Sackschewsky & Williams,

1986), and greater WUE in plants using the C_4 photosynthetic pathway is well established (Osmond, Winter & Ziegler, 1982). It is often assumed that in dry environments natural selection should favour plants with high WUE; however, there may be physiological costs that potentially compromise the ecological benefits of maintaining high WUE (Cohen, 1970; Cowan, 1982).

Because of the non-linear relationship between photosynthesis and transpiration (Cowan, 1982; Nobel, 1983; Raschke, 1979), stomatal closure causes a proportionately greater decrease in transpiration than photosynthesis thereby increasing WUE. The maintenance of high WUE by decreasing stomatal conductance does, however, cause a decrease in the absolute rate of net photosynthesis and therefore reduces growth. High WUE can also be achieved by increasing the intrinsic photosynthetic capacity. This often involves an increase in nitrogen allocation to photosynthetic enzymes and possibly a reduction in nitrogen-use efficiency (Field & Mooney, 1986, 1987).

Water conservation by plants with high WUE increases the availability of soil moisture for potential competitors (Cohen, 1970). This may be particularly significant in habitats with strongly seasonal recharge of soil moisture where competition for water is intense during a relatively contracted period. The maintenance of high WUE is a conservative physiological strategy that may not be advantageous to native plants in competitive water-limited environments. Data for plants growing in one such habitat, the Great Basin desert of western North America, suggests that marginal increases in carbon assimilation in conjunction with the ability to tolerate low water potentials may be an ecologically more successful strategy in certain dry habitats (DeLucia, Schlesinger & Billings, 1988).

In this study, we examine the relationship between WUE and drought tolerance by comparing the photosynthetic and stomatal responses of *Artemisia tridentata* and *Pinus ponderosa* to soil drought. *Artemisia tridentata*, a low stature semi-deciduous shrub, is a dominant species of the western Great Basin steppe (West, 1988). *Pinus ponderosa* is the dominant tree species on adjacent east slope forests of the Sierra Nevada (Barbour, 1988), but also occurs in the midst of the Great Basin shrub community on

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outcrops of hydrothermally altered rock (Billings, 1950; DeLucia *et al.*, 1988). Great Basin shrubs exhibit greater drought tolerance than Sierran pines (Campbell & Harris, 1977; DeLucia *et al.*, 1988; Drivas & Everett, 1988), and competition for water may be an important factor excluding Sierran pines from desert shrub communities.

Materials and methods

Experiments were conducted with potted *Artemisia tridentata* Nutt. and *Pinus ponderosa* Laws. grown from seeds in a greenhouse. *Pinus ponderosa* seeds were collected from large trees growing on soils derived from hydrothermally altered rock in the Virginia Mountains near Reno, Nevada, U.S.A. *Artemisia tridentata* seeds were collected from several plants growing nearby on native Great Basin soils (Xerolic Haplargids). Collections were made from open-pollinated plants in the fall of 1985. Seeds were planted in 300 cm³ pots containing a soil mixture of equal parts of clay-loam, perlite and peat moss. Following emergence plants were fertilized regularly with a commercially prepared N-P-K fertilizer. After 3 months, plants were repotted in 2 dm³ pots and, after an additional 3 months, were transferred to a growth chamber where constant environmental conditions could be maintained. The conditions in the growth chamber were: irradiance, 550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) at pot height; photoperiod, 16 h day/8 h night; air temperature, 26 °C day/20 °C night; and relative humidity, 30%. Plants were grown under these conditions for 10 d before beginning the experiment.

Drought was imposed by withholding water for 14 d. Gas-exchange parameters including net photosynthesis and transpiration were measured on three randomly selected plants of each species every other day during the drought treatment. Immediately after the gas exchange measurements, water potential (ψ) of the shoot was measured with a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, U.S.A.).

Gas exchange was measured with a closed IR gas analysis system (model LI-6200, LICOR Inc., Lincoln, NE, U.S.A.). The entire shoot was enclosed in a well-mixed 4 dm³ cuvette. Humidity in the cuvette was generated by transpiration and maintained at 40 \pm 5% by diverting a portion of the incoming air through a column containing magnesium perchlorate (anhydrous). Transpiration was calculated by measuring the rate of change in humidity in the cuvette (which was maintained close to 0) and correcting for the addition of dry air. Flow rate through the desiccant and into the cuvette was measured with a mass flow meter. The initial CO₂ concentration in the cuvette was approximately 400 cm³ m³ and the measurement was initiated once the plant had depleted the atmosphere to 350 cm³ m³ CO₂. Measurements were made over a

3–5 cm³ m³ CO₂ depletion and typically took 20–60 s. The cuvette was cooled with an external fan and heat-exchanger so that foliage temperature inside the cuvette was 25 \pm 2 °C. Measurements were made at an irradiance of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) provided by a multi-vapour metal halide lamp (1000 W) projected through 5 cm of water. All gas exchange parameters were calculated on a projected leaf area basis using the equations of von Caemmerer & Farquhar (1981). A boundary layer conductance of 1.3 mol m⁻² s⁻¹ was assumed for both species.

The response of net photosynthesis to intercellular CO₂ concentration (c_i) was measured under non-steady state conditions by the method described by Davis, Arkebauer & Norman (1987). The concentration of CO₂ was increased to approximately 1000 cm³ m³ by breathing into the cuvette and measurements were made as the plant depleted the CO₂ concentration. After each measurement, the cuvette CO₂ concentration was depleted rapidly to the next ambient CO₂ concentration (approximately 100 cm³ m³ increments) by passing air entering the cuvette through a soda-lime column. The leak rate at several chamber CO₂ concentrations was measured by placing a plastic stem facsimile into the cuvette. Photosynthetic rates were then corrected for the leak rate occurring at each CO₂ concentration. Breathing into the cuvette caused a negligible change in humidity which was maintained at 40 \pm 5% as described above.

Additional water relations characteristics of *A. tridentata* and *P. ponderosa* in response to short-term drought were determined from analysis of pressure-volume (PV) curves (Tyree & Hammel 1972), using a technique similar to Davis & Mooney (1986). PV curves were constructed for five or six plants of each species prior to and following a 7-d drought and three consecutive 7-d drought cycles. Pots were watered to saturation on days 7 and 14 of the 21-d drought cycle. Because of differences in the degree of drought tolerance between these two species, they were dried to different levels during the drought cycle. *Pinus ponderosa* was dried to a shoot ψ of approximately -1.5 MPa whereas *A. tridentata* was dried to approximately -2.5 MPa. Whole shoots were harvested 12–14 h prior to use and allowed to rehydrate overnight with the cut end of the stems submerged in distilled water and the shoot at 100% RH. Shoot ψ and relative water content (RWC) were measured at approximately 10 intervals as the tissue dehydrated. Relative water content was plotted against inverse ψ , and zero turgor (the point where the curve becomes linear) was estimated visually, thus providing estimates of RWC and ψ_{π} at zero turgor (RWC₀ and $\psi_{\pi 0}$), respectively. Osmotic potential at full turgor ($\psi_{\pi 100}$) was determined by extrapolation of the linear portion of the curve back to 100% RWC.

Bulk modulus of elasticity (ϵ) was calculated from the ψ_p versus RWC relationship for each plant

following Wilson *et al.* (1979). The response of ψ_p to RWC was sigmoidal in both *A. tridentata* and *P. ponderosa*, a response characterized as Type III by Roberts, Strain & Knoerr (1981). Values of ϵ reported here are maximum values.

Results

Withholding water produced a strong decrease in net photosynthesis and stomatal conductance (Fig. 1a, b). Before the onset of drought *A. tridentata* had slightly higher photosynthetic rates than *P. ponderosa*, and *A. tridentata* maintained positive rates of carbon uptake at substantially lower ψ s. Cessation of net photosynthesis and nearly complete stomatal closure occurred at a ψ of approximately -2.5 MPa for *P. ponderosa* and less than -5.0 MPa for *A. tridentata*. Most of the *P. ponderosa* seedlings died following exposure to this level of water stress. Photosynthesis was positively correlated with stomatal conductance for both species and the function was markedly curvilinear (Fig. 2). The slope of the photosynthesis/conductance function was greater at conductances below than above $100 \text{ mmol m}^{-2} \text{ s}^{-1}$, indicating a shift from stomatal to primarily non-stomatal limitations to photosynthesis at this conductance.

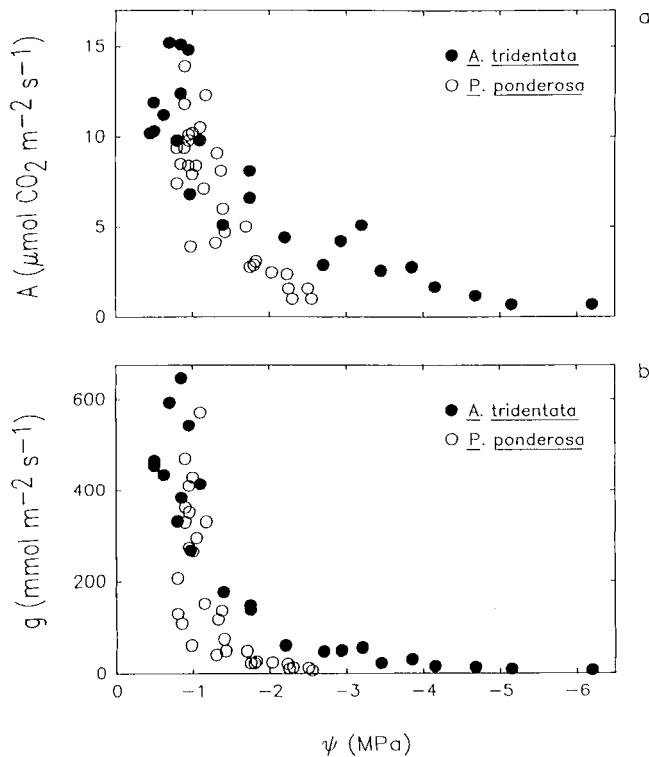


Figure 1. Effect of soil drought on (a) net photosynthesis and (b) stomatal conductance to water vapour in *Artemisia tridentata* (●) and *Pinus ponderosa* (○). Shoot water potential (ψ) was measured immediately after the gas exchange measurements. Each point represents a measurement made on a single plant.

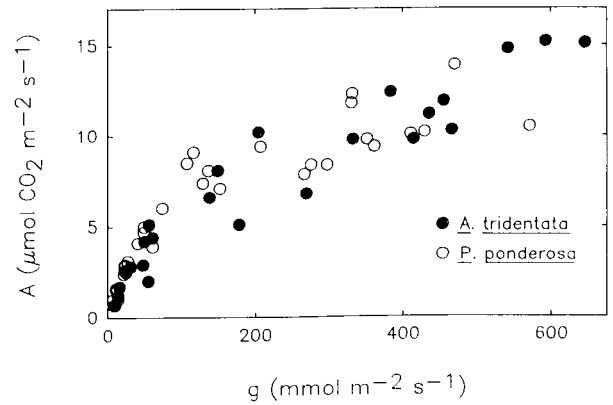


Figure 2. The relationship between net photosynthesis (A) and stomatal conductance to water vapour (g) for *Artemisia tridentata* (●) and *Pinus ponderosa* (○) during the drought cycle. Each point represents a measurement made on a single plant.

WUEs were similar among species at $\psi \geq -1$ MPa, but as ψ decreased *P. ponderosa* consistently maintained a higher WUE than *A. tridentata* (Fig. 3). The relationship between WUE and stomatal conductance was similar for both species (Fig. 4). WUE decreased with increasing conductances up to approximately $250 \text{ mmol m}^{-2} \text{ s}^{-1}$ and remained constant thereafter; however, *P. ponderosa* had slightly higher WUEs at conductances of less than $50 \text{ mmol m}^{-2} \text{ s}^{-1}$.

The relationship between photosynthesis and intercellular CO_2 concentration (c_i) was examined at several levels of ψ (Fig. 5). Under well-watered conditions, photosynthesis for both species saturated at $500\text{--}600 \text{ cm}^3 \text{ m}^{-3} c_i$. As ψ decreased, the maximum rates of photosynthesis (at CO_2 saturation) as well as the initial slope of the A vs c_i curve decreased. As was observed for photosynthesis measured at ambient external CO_2 concentrations (Fig. 1a), net carbon uptake at CO_2 saturation ceased at a ψ between

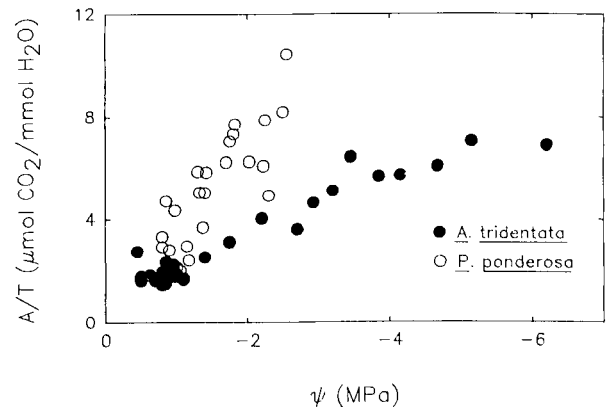


Figure 3. The effect of soil drought on water-use efficiency (A/T) and shoot water potential (ψ) for *Artemisia tridentata* (●) and *Pinus ponderosa* (○). Each point represents a measurement made on a single plant.

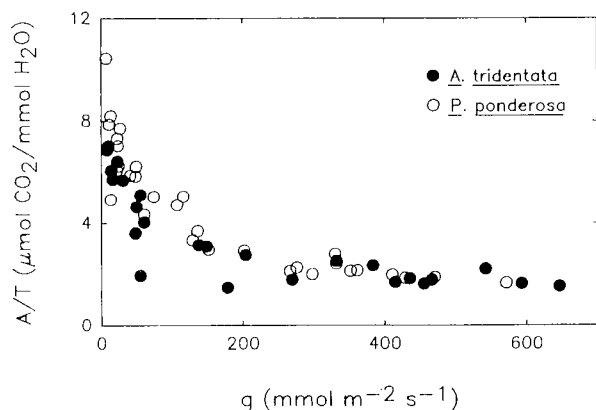


Figure 4. The relationship between water use efficiency (A/T) and stomatal conductance to water vapour (g) during the drought cycle for *Artemisia tridentata* (●) and *Pinus ponderosa* (○). Each point represents a measurement made on a single plant.

–2.0 and –2.5 MPa for *P. ponderosa* (Fig. 5a) and between –4.2 and –6.5 MPa for *A. tridentata* (Fig. 5b).

Although direct comparisons of water relations between species are not possible because of different levels of drought preconditioning (see ‘Methods’), successive drought cycles induced a small increase in bulk modulus of elasticity (ϵ) for *A. tridentata* but not

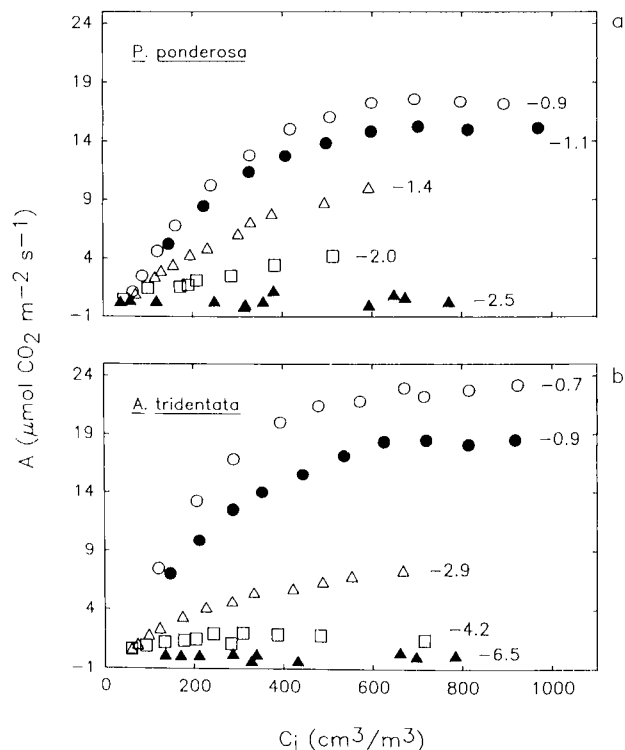


Figure 5. Net photosynthesis (A) as a function of intercellular CO_2 concentration (c_i) for (a) *Pinus ponderosa* and (b) *Artemisia tridentata* measured at several levels of ψ . ψ s (MPa) are shown next to each curve.

Table 1. Selected water relations parameters measured by PV analysis for *Artemisia tridentata* and *Pinus ponderosa*. Measurements were made before the initiation of the drought cycles (C), and after one (D1) or three (D3) drought cycles. Bulk modulus of elasticity (ϵ), and osmotic potential at full turgor ($\psi_{\pi 100}$) and at the turgor loss point ($\psi_{\pi 0}$) are in MPa. Relative water content at the turgor loss point (RWC_0) is expressed as a percentage. Mean values within a species designated with the same letter are not significantly different at $P < 0.05$ (ANOVA, Fischer’s LSD test). $n = 5$, or 6 ± 1 SD

Parameter	Treatment	<i>A. tridentata</i>		<i>P. ponderosa</i>	
		Mean	SD	Mean	SD
ϵ	C	6.39	(0.27) ^a	5.67	(0.30) ^a
	D1	6.30	(0.32) ^a	5.63	(0.65) ^a
	D3	7.73	(0.38) ^b	6.33	(0.42) ^a
$\psi_{\pi 100}$	C	–0.88	(0.13) ^a	–0.83	(0.17) ^a
	D1	–1.05	(0.13) ^{ab}	–0.93	(0.27) ^a
	D3	–1.17	(0.17) ^b	–1.07	(0.27) ^a
$\psi_{\pi 0}$	C	–1.28	(0.15) ^a	–1.22	(0.13) ^a
	D1	–1.51	(0.15) ^{ab}	–1.33	(0.29) ^{ab}
	D3	–1.71	(0.30) ^b	–1.67	(0.32) ^b
RWC_0	C	82.6	(2.63) ^a	84.1	(2.91) ^a
	D1	83.8	(2.48) ^a	84.5	(3.39) ^a
	D3	80.4	(3.74) ^a	81.7	(3.07) ^a

P. ponderosa (Table 1). Osmotic adjustment occurred for both species as indicated by the decrease in osmotic potential at full turgor ($\psi_{\pi 100}$) and at the turgor loss point ($\psi_{\pi 0}$), but the magnitudes of these changes were small (< 0.3 and 0.5 MPa, respectively). Exposure to successive drought cycles did not cause a significant change in relative water content at zero turgor (RWC_0).

Discussion

Artemisia tridentata exhibited substantially greater drought tolerance than *Pinus ponderosa*. Photosynthesis ceased at a ψ of approximately –2.5 MPa for *P. ponderosa* whereas *A. tridentata* maintained positive rates of carbon assimilation below –5.0 MPa. These results are consistent with observations of field-grown plants (DeLucia *et al.*, 1988). Complete stomatal closure for many western conifers including *P. ponderosa* generally occurs at ψ s above –2.0 MPa (Lassoie, Hinckley & Grier, 1985; Lopushinsky & Klock, 1974; Running, 1976; Smith, 1985). In contrast, *A. tridentata* and other desert shrubs can maintain relatively high values of stomatal conductance at shoot water potentials below –6.0 MPa (Caldwell, 1985; Campbell & Harris, 1977).

Many studies have suggested that the degree of drought tolerance is associated with the ability to undergo changes in ϵ and $\psi_{\pi 100}$ (Abrams, 1988; Pallardy *et al.*, 1983; Parker *et al.*, 1982; Roberts & Knoerr, 1977). A drought-induced increase in ϵ would permit the maintenance of a large ψ gradient through the soil-plant-atmosphere continuum with little change in RWC and therefore increase the ability to extract soil moisture from progressively

drier soil. Similarly, a decrease in $\psi_{\pi 100}$ resulting from osmotic adjustment permits the maintenance of positive turgor at progressively lower leaf ψ s. However, the magnitude of the changes in ϵ for *A. tridentata* and in $\psi_{\pi 100}$ for both species were minor relative to changes observed for other species that acclimate to low ψ (Ike & Thurtell, 1981; Melkonian, Wolfe & Steponkus, 1982; Turner & Jones, 1980). It is unlikely that these changes are the primary factors enabling *A. tridentata* to maintain a higher degree of drought tolerance than *P. ponderosa*.

Despite a lower degree of drought tolerance, *P. ponderosa* had higher WUEs than *A. tridentata* over the range of ψ supporting net carbon uptake. The primary factor contributing to higher WUE for *P. ponderosa* was the rapid decrease in stomatal conductance at ψ s from -1 to -2.5 MPa. Stomatal closure causes a proportionately greater decrease in transpiration than photosynthesis (Nobel, 1983; Raschke, 1979) resulting in an increase in WUE, and the onset of soil drought caused a more rapid decrease in A and conductance for *P. ponderosa* than for *A. tridentata*.

Greater WUE for *P. ponderosa* is consistent with field observations based on carbon isotope discrimination ($\delta^{13}\text{C}$). The $\delta^{13}\text{C}$ values for foliage of *P. ponderosa* growing at several locations in the western Great Basin were between -22 and -23‰ compared to $< -24\text{‰}$ for *A. tridentata* (DeLucia *et al.*, 1988). Higher $\delta^{13}\text{C}$ for *P. ponderosa* indicates that this species operates at a lower seasonally integrated c_i than *A. tridentata* which, if we assume both species experience similar leaf-to-air vapour pressure deficits, translates to greater WUE (Ehleringer *et al.*, 1985; Farquhar, O'Leary & Berry, 1982; Farquhar & Richards, 1984; Martin & Thorstenson, 1988).

The relationship between high WUE and a low degree of drought tolerance observed in this study raises several questions regarding the ecological significance of WUE. Given the potential costs of maintaining a high WUE, namely lower rates of photosynthesis and growth, Cohen (1970) argues that selection for high WUE would only be advantageous if conserved soil moisture is available for uptake later in the season. Although *A. tridentata* can develop root systems up to 2 m deep, a high proportion of its roots are in the upper 0.5 m where there is intense competition for water with grasses, especially *Bromus tectorum* (Campbell & Harris, 1977; Sturges, 1977). Therefore it is unlikely that surface moisture conserved by *A. tridentata* would be available later in the growing season. The small magnitude of changes in predawn water potential observed seasonally for *P. ponderosa* growing on altered substrate (DeLucia *et al.*, 1988) suggests that this species is deeply rooted and largely free of competition for water with the adjacent Great Basin shrubs and annuals. Also, many of the Great Basin species are excluded from altered soil by intolerance to low pH and nutrient deficiency (DeLucia, Schlesinger & Billings, 1989;

Schlesinger, DeLucia & Billings, 1989). Under these conditions, conservation of water by high WUE in *P. ponderosa* would effectively lengthen the time during the year that is favourable for carbon assimilation.

Drought tolerance and comparatively low WUE in *A. tridentata*, and the proposal that *P. ponderosa* and other Sierran conifers are excluded from the matrix of Great Basin vegetation by competition for water (DeLucia *et al.*, 1988), support our prediction that the maintenance of high WUE is a conservative ecophysiological 'strategy' that may be detrimental in a highly competitive milieu. The combination of profligate use of water (low WUE) and high degree of drought tolerance, as exemplified by *A. tridentata*, may be a more ecologically successful combination of physiological characteristics in most water-limited habitats.

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