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Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates

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Summary We examined the effects of increased transpiration demand on xylem hydraulic conductivity and vulnerability to cavitation of mature ponderosa pine (*Pinus ponderosa* Laws.) by comparing trees growing in contrasting climates. Previous studies determined that trees growing in warm and dry sites (desert) had half the leaf/sapwood area ratio (A_L/A_S) and more than twice the transpiration rate of trees growing in cool and moist sites (montane). We predicted that high transpiration rates would be associated with increased specific hydraulic conductivity (K_S) and increased resistance to xylem cavitation. Desert trees had 19% higher K_S than montane trees, primarily because of larger tracheid lumen diameters. Predawn water potential and water potential differences between the soil and the shoot were similar for desert and montane trees, suggesting that differences in tracheid anatomy, and therefore K_S, were caused primarily by temperature and evaporative demand, rather than soil drought. Vulnerability to xylem cavitation did not differ between desert and montane populations. A 50% loss in hydraulic conductivity occurred at water potentials between –2.61 and –2.65 MPa, and vulnerability to xylem cavitation did not vary with stem size. Minimum xylem tensions of desert and montane trees did not drop below –2.05 MPa. Foliage turgor loss point did not differ between climate groups and corresponded to mean minimum xylem tensions in the field. In addition to low A_L/A_S, high K_S in desert trees may provide a way to increase tree hydraulic conductivity in response to high evaporative demand and prevent xylem tensions from reaching values that cause catastrophic cavitation. In ponderosa pine, the flexible responses of A_L/A_S and K_S to climate may preclude the existence of significant intraspecific variation in the vulnerability of xylem to cavitation.

Keywords: hydraulic conductivity, leaf/sapwood area ratio, temperature, vapor pressure deficit, xylem cavitation.

Introduction

Transpiration depends on hydraulic conductivity and the continuity of the water column through the tree. Xylem cavitation, caused by high tension on the water column during transpiration, leads to the formation of air emboli in xylem conduits and is a major limit to water transport capacity in trees (Tyree and Ewers 1991). Trees may make hydraulic adjustments in response to atmospheric and soil water deficits that minimize the physiological impact of xylem cavitation. Some of these adjustments involve reducing evaporative water loss through stomatal closure or reductions in leaf area (Sperry 1995, Whitehead 1998). In contrast, other adjustments may act to raise leaf water supply through increases in the hydraulic conductance of the soil–leaf path. These mechanisms include increased allocation to sapwood, the maintenance of positive turgor, and more efficient water transport through the xylem (Tyree and Jarvis 1982, Mencuccini and Grace 1995, Maherali et al. 1997). Mechanisms that increase leaf water supply may have precedence in conifers because of high canopy boundary layer conductance (Whitehead and Jarvis 1981, Pallardy et al. 1995) and associated limits to stomatal control of water loss (Sandford and Jarvis 1986).

Whitehead and Jarvis (1981) proposed a framework for examining aboveground hydraulic adjustments of conifers in response to increased transpiration demands. The model, which integrates the pattern of aboveground biomass allocation and xylem transport efficiency with factors that influence transpiration (Whitehead and Jarvis 1981, Whitehead et al. 1984), is based on the Penman-Monteith equation (to describe water loss from the canopy) and Darcy's law (to describe water transport through the tree):

$$Dg_S = \frac{1}{A_L/A_S} K_S (\Delta\Psi/l)c, \qquad (1)$$

where A_L/A_S is leaf/sapwood area ratio, K_S is mean specific hydraulic conductivity (sapwood permeability), $\Delta\Psi/l$ is water potential gradient, g_S is canopy-weighted stomatal conductance, D is time-averaged vapor pressure deficit of the air, and c is a coefficient representing specific heat and density of air, the latent heat of vaporization and viscosity of water, and the psychrometric constant (Whitehead et al. 1984, Mencuccini and Grace 1995). In the absence of stomatal responses to D, the model predicts that, within a species, trees grown in climates with high evaporative demand will have low A_L/A_S. Thus, the expansion of conducting area relative to transpiring area increases leaf-specific hydraulic conductivity (Tyree and Ewers 1991).

An important limitation of predictions derived from Equation 1 is that they are restricted to mechanisms associated with the aboveground portions of the tree. Examples of tree responses to high transpiration demands that are independent of relationships described in Equation 1 include alterations in the axial and radial hydraulic properties of roots and the root–soil interface (Steudle 1994), rooting depth, and variation in root/leaf area ratio (Sperry et al. 1998). Nevertheless, shifts in aboveground tree structure have substantial implications for soil-to-leaf hydraulic conductance, because the bole and branches can constitute up to 85% of the total path resistance to water flow in conifers (Hellkvist et al. 1974, Tyree 1988).

Ponderosa pine (*Pinus ponderosa* Laws.) trees growing under conditions of high evaporative demand (desert) have higher maximum stomatal conductance (DeLucia and Schlesinger 1991) and transpiration rates per unit leaf area (Maherali 1999) than trees growing in humid climates (montane). In summer, mean maximum transpiration rate was 2.7 times higher in desert trees than in montane trees (Figure 1). Consistent with Equation 1, desert stands have approximately half the A_L/A_S of montane stands (0.104 versus 0.201 $m^2\ cm^{-2}$) (Callaway et al. 1994). Mencuccini and Grace (1995) also found that A_L/A_S of *Pinus sylvestris* L. declined in response to increased D.

Based on the relationships described in Equation 1, transpiration rates of desert trees are higher than predicted based solely on the difference in A_L/A_S between desert and montane trees. Moreover, by reducing the ratio of photosynthetic to non-photosynthetic tissue, low A_L/A_S compromises growth potential (Poorter and Remkes 1990, Carey et al. 1998), suggesting that there may be a lower limit to reductions in leaf area in environments with high transpiration demand. Thus, other factors in addition to variation in A_L/A_S may contribute to differences in transpiration rate between desert and montane trees. We examined three additional mechanisms by which high transpiration at high D could occur in ponderosa pine. First, high transpiration rates at high D may be supported by increasing sapwood permeability (specific hydraulic conductivity, K_S; Whitehead et al. 1984, Whitehead 1998). Second, high transpiration rates may also be supported by the development of a large water potential difference from the soil to the shoot (Equation 1; Mencuccini and Grace 1995). This prediction implies that trees in dry climates may have increased resistance to drought-induced xylem cavitation, a variable that is not explicitly considered in Equation 1. Finally, changes in the capacity for osmotic adjustment and leaf tissue elasticity may influence transpiration by permitting the maintenance of positive turgor at negative xylem tensions (Tyree and Jarvis 1982).

We examined these three mechanisms by comparing the water relations and xylem physiology of ponderosa pine stands growing in contrasting climates. We predicted that ponderosa pine trees growing under conditions of high atmospheric evaporative demand would (1) have high specific hydraulic conductivity (K_S), (2) have high resistance to drought-induced xylem cavitation, and (3) maintain high leaf turgor with decreasing xylem tension.

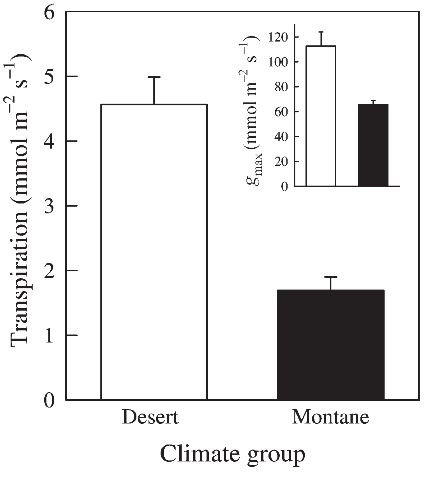

Figure 1. Mean (± 1 SE) maximum summer (June–August) transpiration rates for desert and montane trees. Transpiration per unit leaf area was calculated from the mean maximum (± 1 SE) summer stomatal conductance (g_{max}) of desert and montane trees (inset, reported by DeLucia and Schlesinger 1991) and mean maximum summer vapor pressure deficit (Table 1). Because conifer canopies are well-ventilated (Pallardy et al. 1995), we calculated transpiration based on the assumptions that needle boundary layer conductance was infinite and that air and leaf temperatures were identical (e.g., Tan et al. 1978, Whitehead and Jarvis 1981).

Methods

Study sites and plant material

We studied the same ponderosa pine populations used to measure climate-related variation in A_L/A_S (Callaway et al. 1994) and transpiration (Maherali 1999). In the eastern Sierra Nevada and adjacent Great Basin, open stands of ponderosa pine occur on islands of soil derived from hydrothermally altered andesite (Billings 1950, Delucia et al. 1988, Schlesinger et al. 1989, Callaway et al. 1994). In the arid Great Basin (desert sites), these tree islands occur in a matrix of sagebrush steppe vegetation and pinyon–juniper woodland. In the cool and humid Sierra Nevada and adjacent ranges (montane sites), the islands occur within a matrix of other conifers (*Pinus jeffreyi* Grev. & Balf. and *P. lambertiana* Dougl.). These open stands have similar density and nutrient status across the elevational gradient (Schlesinger et al. 1989). We selected one representative site in each climate group (Desert Research Institute (DRI) and Virginia Range) for measurements of xylem hydraulic conductivity, xylem anatomy, tissue water relations, and xylem water potential. We measured vulnerability to xylem cavitation on tissue collected at two sites in each climate group. Characteristics of the study sites are summarized in Table 1.

Table 1. Elevation and climate characteristics of stands used for measurements of hydraulic conductivity, vulnerability to xylem cavitation, and tissue water relations. Mean temperature and precipitation are based on 30-year (1961–1990) summaries from weather stations located near each study site. Mean maximum daily temperatures are the average of monthly maxima. Vapor pressure deficit was calculated from temperature and relative humidity data obtained from the Vegetation Ecosystem Modeling and Analysis Project (VEMAP, Kittel et al. 1995).

Site	Elevation (m)	Latitude, Longitude	Precipitation (mm year^{-1})	Mean maximum temperature (°C)	Mean summer D (mol mol^{-1})
Montane					
Alpine County	2100	38°41′ N, 119°44′ W	550	14.9	0.024
Virginia Range	2030	39°22′ N, 119°41′ W	473	14.7	0.028
Desert					
Peavine Mtn.	1500	39°34′ N, 119°50′ W	245	18.2	0.038
Desert Research Inst.	1500	39°35′ N, 119°47′ W	225	19.3	0.043

Hydraulic conductivity

Fifty trees were sampled along two 250-m transects at each site. Portions of a single branch per tree (0.5 to 1 m long) were harvested. Branches (1- to 12-cm diameter) were placed underwater, and a 15- to 25-cm-long unbranched segment was excised. Stem segments were placed in a water bath at 4 °C for 2 h to reduce resin emission. Hydraulic conductivity (K_H) was measured as described by Tyree et al. (1983) and Sperry et al. (1988). Segments were cleared of air emboli by perfusing them at high pressure with a filtered (0.2 µm) solution of water adjusted to a pH of 2 with HCl. Preliminary experiments showed that ponderosa pine reached maximum flow rate (Q, kg s^{-1}) after 30 min flushing at 170 kPa, so all segments were flushed for 1 h before measurement. A hydrostatic pressure of 10 kPa was used to measure flow rate, which was calculated by collecting and weighing stem efflux at intervals. Flow rates were standardized to 25 °C.

Hydraulic conductivity (K_H; kg m MPa^{-1} s^{-1}) was expressed as flow rate divided by the pressure gradient ($Q/(dP/dx)$). After measuring hydraulic conductivity, stems were perfused with filtered (0.2 µm) 0.01% basic fuschin solution to determine the functional xylem area of each segment. Specific hydraulic conductivity (K_S; kg m^{-1} MPa^{-1} s^{-1}) was calculated by dividing K_H by the functional xylem area of the segment.

Xylem anatomy

Tracheid diameter and length were measured on a subsample of stem segments. Stem cross sections (20 µm thick) were made with a sliding microtome (American Optical Co., Buffalo, NY) and stained with toluidine blue. We measured radial strips of cells on sectors spaced at 90° intervals in the outermost portion (2–4 growth rings) of each cross section. Sixty to 80 tracheids were measured for each stem segment. Measurements were made with a light microscope and an ocular micrometer (Bausch and Lomb, Rochester, NY). Lumen diameter (L_D) was calculated as $L_D = 2xy/(x + y)$, where x and y are the short and long sides of the tracheid, respectively (Lewis and Boose 1995).

Tracheid length was measured on the outer portions of the stem segments. Several 2-cm-long slivers of wood were macerated by placing them in a 1:1 solution of 10% nitric acid and 10% chromic acid (Berlyn and Mischke 1976). After 24 h, samples were vortexed with 3-mm-diameter glass beads. The tracheids were washed with distilled water, stained with toluidine blue and mounted on a slide. The lengths of 10 tracheids per stem segment were measured with the aid of a light microscope.

Vulnerability to xylem cavitation

Vulnerability to drought-induced xylem cavitation was measured as the reduction in hydraulic conductivity of a stem as a function of xylem pressure (a "vulnerability curve," Sperry et al. 1988) created by air injection (Sperry and Saliendra 1994, Sperry and Ikeda 1997). Xylem cavitation was induced by successively increasing positive air pressures on a stem segment inside a double-ended pressure chamber. The positive air pressure causing a decrease in hydraulic conductivity is an estimate of the xylem tension causing cavitation in dehydrated stems (Sperry and Saliendra 1994).

Segments (30 cm long) were excised from branches on six trees at each of two desert and two montane sites. Stem segments were debarked and immersed in a water bath at 4 °C for 2–3 h to reduce resin emission. Each segment was notched (0.5 to 1 mm deep) with a razor blade to provide an entry point for air and then placed in the pressure chamber. To determine maximum hydraulic conductivity (K_{max}) before the induction of cavitation, the segment was cleared of existing air emboli. Hydraulic conductivity was measured after each pressurization at a hydrostatic pressure of 10 kPa. During measurement of hydraulic conductivity, the chamber was maintained at 30 kPa to prevent the refilling of embolized tracheids. Percent loss in conductivity (PLC) following each pressurization of the chamber was calculated as PLC = $100((K_{max} - K_h)/K_{max})$, where K_h is the hydraulic conductivity of the segment measured after each chamber pressurization.

Shoot water relations

During July 1997, we harvested 0.5-m-long branches from 15 trees at one desert and one montane site. Branches were bagged and returned to an air-conditioned laboratory for pressure–volume analysis. Single shoots were recut under water and placed in distilled water to rehydrate for 12–16 h. Pressure–volume curves were constructed by the repeat-pressurization method described by Parker and Colombo (1996) with a pressure chamber (Plant Moisture Status Instrument Company, Corvallis, OR). Bulk tissue estimates of shoot osmotic potential at saturation and at turgor loss as well as shoot relative water content at turgor loss were calculated as described by Parker and Colombo (1996). Bulk modulus of elasticity of the shoot was calculated as described by Tyree and Jarvis (1982). Pressure–volume curves were corrected for oversaturation plateaus (Kubiske and Abrams 1991).

Water potential

We measured predawn and midday shoot water potentials *in situ* during mid-June and late August 1997 at the Desert Research Institute and the Virginia Range sites with a pressure chamber. Predawn measurements were made between 0400 and 0500 h PST and midday measurements were made between 1230 and 1330 h PST. We measured exposed shoots on six trees at each site. Tree sizes varied from 21 to 59 cm in diameter at 1.4 m aboveground (DBH).

Statistical analysis

For size-dependent variables (K_S, tracheid diameter, and length), statistical comparisons between climate groups were made by analysis of covariance (ANCOVA, Sokal and Rohlf 1995) with stem diameter as the covariate. Data were log-transformed where appropriate to meet assumptions for ANCOVA. We tested differences among slope coefficients by including the climate × size interaction term in each model. If the interaction term was nonsignificant (i.e., the slopes were homogeneous), we removed it from the model and tested for differences between climate groups (intercepts).

Vulnerability curves were fit with an exponential sigmoid equation (Pammenter and Vander Willigen 1998):

$$\mathrm{PLC} = \frac{100}{1 + \exp(a(\Psi - b))}, \tag{2}$$

where Ψ is the negative of the injection pressure, a is a measure of the degree that conductivity responds to injection pressure (curve shape) and b represents the Ψ at which a 50% loss in conductivity occurs (curve displacement along the x-axis). Coefficients a and b were estimated with a linear version of Equation 2 (Pammenter and Vander Willigen 1998).

Differences in shoot pressure–volume parameters and water potential for trees growing in desert and montane climates were determined with an independent samples t-test. Differences in the vulnerability of xylem to cavitation (coefficients a and b) between sites within climates and between climates were determined with a nested analysis of variance, with site nested within climate. Statistical analyses were made with Systat 5.2.1 (SPSS, Evanston, IL).

Results

Specific hydraulic conductivity (K_S) increased ($P < 0.05$) with the log of stem diameter in both montane and desert trees (Figure 2). Desert trees, however, had significantly higher K_S than montane trees as stem diameter increased (a 37% increase in slope for desert versus montane trees, $P < 0.05$). Mean (± 1 SE) K_S for all stems was 0.64 ± 0.04 kg $\mathrm{m^{-1}\ MPa^{-1}\ s^{-1}}$ in desert trees and 0.54 ± 0.03 kg $\mathrm{m^{-1}\ MPa^{-1}\ s^{-1}}$ in montane trees, a difference of 19%. Tracheid diameter (Figure 3A) and tracheid length (Figure 3B) also increased with stem diameter. Desert trees had 10% larger tracheid diameters than montane trees across all stem sizes ($P < 0.05$), whereas montane trees had 11% longer tracheids than desert trees across all stem sizes ($P < 0.05$).

The loss of hydraulic conductivity with increasing injection pressures, representing the induction of xylem cavitation, was similar for trees from desert (Desert Research Institute and Peavine Mtn.) and montane (Virginia Range and Alpine Co.) populations (Figure 3). The mean water potential at which 50% loss in conductivity occurred ranged between –2.61 and –2.65 MPa and did not differ between populations within climates or across climates (Table 2). The mean slope of the vulnerability curve ranged from 1.20 to 1.50, and did not differ between populations within climates or across climates (Table 2). The relatively shallow vulnerability curve slopes indicated that cavitation occurred over a wide range of xylem pressure potentials. The relationship between turgor loss of foliage and water potential was also similar between desert and montane trees (Figure 4), indicating that turgor loss occurred following relatively limited cavitation (about 20–30%). There was no relationship between stem diameter and vulnerability to drought-induced cavitation at the 20% loss in conductivity ($\mathrm{LC_{20}}$) or 50% loss in conductivity ($\mathrm{LC_{50}}$) values.

Neither shoot osmotic potential at full turgor nor water potential at turgor loss differed between montane and desert climates (Table 3). In contrast, desert trees had higher relative

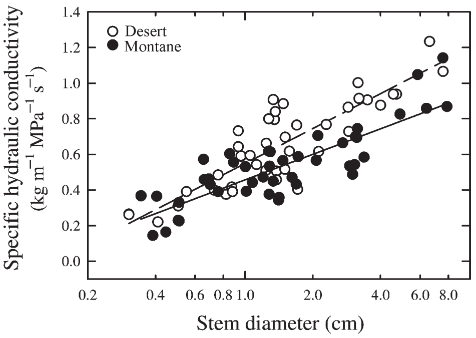

Figure 2. Specific hydraulic conductivity (K_S) as a function of stem diameter (DIA) for ponderosa pine trees growing in desert and montane climates. For desert trees, $K_S = 0.652 \log(\mathrm{DIA}) + 0.548$, $r^2 = 0.76$, $P < 0.001$, $n = 44$. For montane trees, $K_S = 0.477 \log(\mathrm{DIA}) + 0.457$, $r^2 = 0.70$, $P < 0.001$, $n = 42$. Slopes differed significantly (ANCOVA, $P < 0.05$).

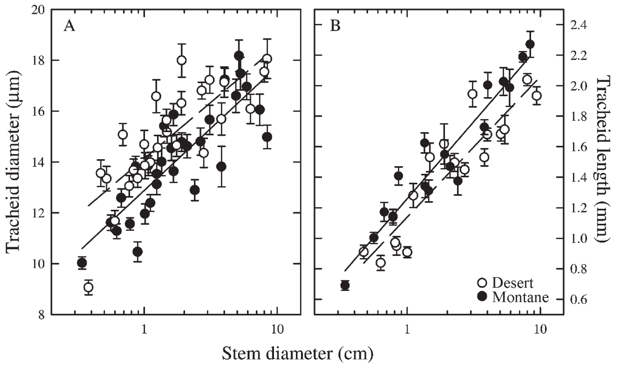

Figure 3. (A) Mean (± 1 SE) tracheid lumen diameter (L_D) as a function of stem diameter (DIA) for ponderosa pine trees growing in desert and montane climates. For desert trees, $L_D = 1.91 \log(\text{DIA}) + 14.14$, $r^2 = 0.64$, $P < 0.001$, $n = 26$. For montane trees $L_D = 2.11 \log(\text{DIA}) + 12.88$, $r^2 = 0.70$, $P < 0.001$, $n = 30$. Intercepts differed significantly (ANCOVA, $P < 0.001$). (B) Mean (± 1 SE) tracheid length (L) as a function of stem diameter (DIA) for ponderosa pine trees growing in desert and montane climates. For desert trees, $L = 0.427 \log(\text{DIA}) + 1.14$, $r^2 = 0.83$, $P < 0.001$, $n = 17$. For montane trees, $L = 0.438 \log(\text{DIA}) + 1.26$, $r^2 = 0.92$, $P < 0.001$, $n = 17$). Intercepts differed significantly (ANCOVA, $P < 0.05$).

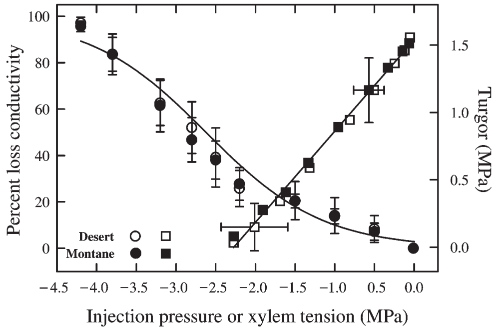

Figure 4. Mean (± 1 SD) percent loss in hydraulic conductivity as a function of injection pressure (circles), and mean (± 1 SD) turgor pressure as a function of xylem tension (squares) for desert (open symbols) and montane (closed symbols) populations of ponderosa pine. Because vulnerability to xylem cavitation and turgor pressure loss with xylem tension did not differ between climates (Table 2), a single curve was fit to each relationship. Curves were fit to raw data with Equation 2. The relationship between turgor loss and xylem tension was estimated from pressure–volume curves and the largest standard deviation for each climate group is shown.

water content at turgor loss ($P < 0.05$) and higher bulk modulus of elasticity than montane trees ($P < 0.05$).

Desert trees had marginally higher predawn and midday water potentials than montane trees in mid-June (Table 4, $P < 0.10$). In late August, after several weeks of little rain (4 and 15 mm at the Desert Research Institute and Virginia Range sites, respectively), desert and montane trees had similar predawn and midday water potentials. Water potential differences between the soil and the shoot ($\Delta\Psi$) were similar for montane and desert trees at both measurement periods (Table 4).

Discussion

Desert trees had higher K_S than montane trees (Figure 2), supporting the prediction that the transport efficiency of xylem, as measured by specific hydraulic conductivity (K_S), increases with increasing transpiration rate in ponderosa pine trees grown in environments with high evaporative demand. However, desert and montane trees did not differ with respect to the vulnerabiliy of xylem to cavitation or the xylem tension at which needle turgor was lost (Figure 4). Desert and montane trees also developed similar minimum and maximum xylem tensions (Table 4). Thus, we obtained no evidence that desert trees could support higher transpiration rates than montane trees through the development of a larger soil-to-leaf water potential difference (Figure 1). Our results suggest that, in addition to a low leaf/sapwood area ratio (A_L/A_S) (Callaway et al. 1994, Mencuccini and Grace 1995), a high K_S helps support high transpiration rates of trees growing in environments with high atmospheric evaporative demand.

Higher K_S in desert trees than in montane trees was caused by differences in tracheid anatomy (Figure 3). Tracheid conductance and thus K_S increases with the square of the lumen radius (Hägen-Poiseuille law; Zimmermann 1983). Through an increase in the number of pits connecting adjacent tracheids (Pothier et al. 1989*b*), longer tracheids will also increase K_S.

Table 2. Mean (± 1 SD) slopes (a) and intercepts (b) of Equation 2, fitted to the vulnerability curves of individuals from desert and montane populations. There were no significant differences ($P > 0.05$) in parameters between climate groups.

Climate	Site	a	b (MPa)
Desert	Desert Research Inst.	1.20 ± 0.29	–2.65 ± 0.20
	Peavine Mtn.	1.41 ± 0.38	–2.62 ± 0.29
Montane	Virginia Range	1.50 ± 0.12	–2.61 ± 0.19
	Alpine County	1.31 ± 0.25	–2.61 ± 0.35

Table 3. Mean (± 1 SD) tissue water relations parameters measured during July 1997 for ponderosa pine trees growing in desert ($n = 15$) and montane ($n = 11$) climates. Significant differences ($P < 0.05$) in parameters between climate groups are indicated by different letters.

Parameter	Desert	Montane
Osmotic potential at full turgor (Ψ_{po}, MPa)	–1.57 ± 0.18 a	–1.59 ± 0.17 a
Water potential at turgor loss (Ψ_{tlp}, MPa)	–2.23 ± 0.12 a	–2.31 ± 0.10 a
Relative water content at turgor loss (R_P)	0.85 ± 0.03 a	0.80 ± 0.03 b
Maximum modulus of elasticity (ε_{max}, MPa)	12.6 ± 2.14 a	9.76 ± 2.30 b

Table 4. Mean (± 1 SD) predawn (Ψ_{PD}) and midday (Ψ_{MD}) water potentials (MPa) and water potential difference ($\Delta\Psi$, MPa) for trees growing in desert ($n = 6$) and montane ($n = 6$) climates. There were no differences ($P > 0.05$) in Ψ_{PD}, Ψ_{MD} or $\Delta\Psi$ between desert and montane trees in June or August.

Parameter	Desert	Montane
June		
Ψ_{PD}	–0.65 ± 0.04	–0.74 ± 0.09
Ψ_{MD}	–1.85 ± 0.10	–1.99 ± 0.09
$\Delta\Psi$	1.19 ± 0.13	1.25 ± 0.09
August		
Ψ_{PD}	–0.96 ± 0.09	–0.96 ± 0.11
Ψ_{MD}	–1.98 ± 0.10	–2.05 ± 0.10
$\Delta\Psi$	1.02 ± 0.13	1.09 ± 0.13

Desert trees had 10% wider tracheid lumens than montane trees (Figures 3A and 3B). In contrast, montane trees had longer tracheids than desert trees. Because K_S was higher in desert trees than in montane trees, we conclude that larger tracheid lumen diameter is the primary factor increasing xylem hydraulic conductivity in ponderosa pine. Calculations based on the Hägen-Poiseuille law also support this conclusion. If it is assumed that all other anatomical characteristics influencing xylem permeability are similar in desert and montane trees, a 10% increase in tracheid diameter corresponds to a 21% increase in K_S. We observed a 19% higher mean K_S in desert trees compared with montane trees (Figure 2). It is also possible that high K_S in desert trees was caused by high permeability between bordered pits linking adjacent tracheids (Calkin et al. 1986). However, high pit permeability also increases vulnerability to cavitation (Pallardy et al. 1995). We observed no differences in vulnerability to cavitation across climates (Figure 4) or with stem size, suggesting that pit permeability was not a significant factor influencing differences in K_S between desert and montane ponderosa pine.

Temperature and D covary and may affect tracheid lumen diameter, and therefore K_S, in similar ways. Large tracheid lumen diameter was associated with high temperatures in *Pinus radiata* D. Don (Richardson 1964, Jenkins 1975) and *P. sylvestris* (Antanova and Stasova 1993), although these studies did not control for vapor pressure deficit. Whitehead et al. (1983) observed that *P. sylvestris* seedlings grown with a daytime D of 2.0 kPa had marginally higher tracheid lumen diameter than seedlings grown with a daytime D of 1.0 kPa or below. Because atmospheric evaporative demand and temperature are correlated in nature, we could not directly determine which of these factors influenced tracheid lumen diameter and K_S in desert and montane ponderosa pine. However, transpiration is driven primarily by D in conifers (Sandford and Jarvis 1986) and is coordinated with whole-path conductance (Meinzer and Grantz 1990, Tyree and Ewers 1991, Sperry and Pockman 1993), suggesting that the most probable explanation for larger tracheid diameter at high temperature is high D.

The potential impacts of other factors that influence tracheid size and K_S in pines, such as stand density, nutrient availability, water stress, and tree growth rate (Pothier et al. 1989*a*, 1989*b*), can be ruled out in this experiment. The study stands were open-grown and occurred on similar soil substrates (Schlesinger et al. 1989). Although trees grew in contrasting climates, they had similar predawn water potentials during the growing season (Table 4), suggesting that desert and montane trees had relatively similar access to soil water. Based on patterns observed in other studies (Whitehead et al. 1984, Pothier et al. 1989*b*), the lower growth rate of desert trees relative to montane trees (Callaway et al. 1994, Carey et al. 1998) should have reduced mean tracheid lumen diameter, a result opposite to that observed. Therefore, the difference in growth rates between montane and desert trees could not have contributed to higher K_S in desert trees. Tracheid length, however, is correlated with growth rate (Whitehead et al. 1984, Pothier et al. 1989*b*) and may explain why we observed longer tracheids in montane trees than in desert trees (Figure 3B).

Higher xylem conducting efficiency and larger tracheid diameter in desert trees than in montane trees may be related to phenotypic plasticity or may represent a genetic adaptation in response to selection by climate. In a growth chamber study, we observed that ponderosa pine seedlings from a single genetic source responded to elevated temperatures and D by increasing K_S (Maherali and DeLucia 2000). A common garden experiment revealed no ecotypic differences between desert and montane populations (Maherali 1999), suggesting that increased xylem efficiency in desert trees relative to montane trees is largely phenotypic.

In contrast to our prediction, we found that vulnerability to drought-induced xylem cavitation (Figure 4, Table 2) did not vary between desert and montane populations. The similarity in vulnerability to cavitation in contrasting climates was corroborated by the observation that soil-to-shoot water potential differences, both early in the growing season and following a summer drought, were very similar between desert and montane trees (Table 4). Values of water potential at turgor loss (about –2.3 MPa) also did not differ between desert and montane trees, and corresponded to the mean minimum midday shoot water potential observed in the field (–2.05 MPa) and the water potential at which stomata close (DeLucia et al. 1988). We conclude that desert trees do not acclimate to high evaporative demand by increasing resistance to xylem cavitation. Our results also indicate that there is no clear trade-off between variation in K_S and the vulnerability of xylem to cavitation in ponderosa pine shoots.

Observations from other studies suggest that minimum xylem tensions in ponderosa pine rarely drop below –2.0 MPa (Running 1976, Lassoie et al. 1985, Smith 1985, DeLucia et al. 1988). The relatively high minimum xylem tension in shoots suggests that cavitation may have reduced hydraulic conductivity in ponderosa pine branches by about 20–30%. Xylem tension in the bole, where the majority of sapwood is contained (Callaway et al. 1994), will be less negative than in the shoots. Therefore, xylem cavitation in the bole sapwood was probably small, and may not be a significant factor limiting water transport in desert and montane ponderosa pine.

Roots are generally more vulnerable to cavitation than shoots in conifers (Sperry and Ikeda 1997, Kavanagh et al. 1999) and may influence water transport in different ways than shoots. Cavitation in the roots could represent the major limit to transpiration under periods of water stress (Sperry et al. 1998) as well as increase the overall resistance that roots contribute to the soil–leaf hydraulic pathway. Vulnerability to cavitation may be a more phenotypically plastic trait in roots than in shoots (Sperry and Ikeda 1997), raising the possibility that roots from desert trees were more resistant to xylem cavitation than roots from montane trees. Although the vulnerability of roots to cavitation is not known for ponderosa pine, the minimum predawn water potentials of about –1.0 MPa observed in desert and montane environments were not low enough to induce cavitation in other similar conifer species (Sperry and Ikeda 1997, Kavanagh et al. 1999). These data suggest that root cavitation had limited impact on transpiration differences between desert and montane trees.

Turgor loss as a function of water potential and osmotic potential at full turgor was similar for trees growing in contrasting climates (Table 3), suggesting that these mechanisms do not enable desert trees to tolerate higher evaporative demands than montane trees. High tissue elasticity permitted foliage on montane trees to have a lower relative water content at zero turgor (R_P) than desert trees (Table 3). These results were unexpected because high tissue elasticity and low R_P are properties of pines exposed to relatively high drought stress (Tognetti et al. 1997). However, there was no evidence that montane and desert trees differed in access to soil water (Table 4). High tissue elasticity and low R_P in montane trees may be indicative of increased shoot water storage capacity (Tyree and Jarvis 1982), although the functional significance of this phenotype is not clear.

The significance of variation in A_L/A_S and K_S for supporting high transpiration rates can be examined by substituting the relative differences between desert and montane trees in these variables into Equation 1. A 48% decrease in A_L/A_S coupled with a 19% increase in K_S, without any adjustment in $\Delta\Psi/l$, leads to a predicted 2.30-fold increase in transpiration rate in desert trees relative to montane trees. The predicted increase is 15% less than the observed 2.70-fold higher summer transpiration rate in desert trees relative to montane trees (Figure 1). Without adjustments in A_L/A_S and K_S, higher transpiration rates in desert trees could only be supported by a 2.70-fold increase in soil-to-leaf water potential difference from a seasonal value of 1.1 to 2.97 MPa. Assuming a seasonally averaged predawn water potential of –0.81 MPa (Table 4), such an increase would require minimum midday xylem tensions in desert trees to drop to –3.78 MPa, causing cavitation in stems to reach about 85%. Thus, A_L/A_S and K_S adjustments in desert trees are critical for supporting high transpiration rates and preventing the induction of lethal xylem cavitation.

A tacit assumption of Equation 1 is that it is representative of the entire soil-to-leaf hydraulic pathway. However, several components, other than stem K_S and A_L/A_S, can affect transpiration and may have also responded to climate. For example, root K_S may have been higher in desert trees than in montane trees. Non-vascular components, such as restrictions to radial water flow at the soil–root interface, can contribute substantial hydraulic resistance to whole-plant water transport (Steudle 1994). Although we could not measure this component, water transfer across the soil–root interface may be similar for desert and montane trees because they are rooted in similar substrates (Schlesinger et al. 1989) and experience similar soil water availability (Table 4). Nevertheless, it is possible that climate-dependent variation in root hydraulic properties accounted for the difference between predicted and observed transpiration rates.

Previous tests of Equation 1 suggest that leaf/sapwood area ratio is phenotypically plastic, and that low A_L/A_S is the primary mechanism that permits increased transpiration in environments with high evaporative demand (Margolis et al. 1995, Mencuccini and Grace 1995, DeLucia et al. 2000). A potential cost of a decline in A_L/A_S is that by decreasing the ratio of photosynthetic to non-photosynthetic tissue, carbon assimilation and growth are also reduced (Poorter and Remkes 1990, Carey et al. 1998). In contrast, there is no trade-off between high K_S and the carbon cost of sapwood construction in ponderosa pine (Carey et al. 1997). Thus, the combination of low A_L/A_S and high K_S in desert trees provides a way to increase whole-tree hydraulic conductivity without further reducing carbon gain.

The development of high resistance to xylem cavitation in woody plants is considered an important adaptation to arid environments (Franks et al. 1995, Kolb and Sperry 1999, Sparks and Black 1999). Despite an apparent lack of intraspecific variation in this trait, ponderosa pine is still among the more drought-tolerant species of the Pinaceae and often becomes the dominant species in arid forest ecosystems (Daubenmire 1968, Kolb and Robberecht 1996). We suggest that the ability of ponderosa pine to increase hydraulic conductivity, mediated by high K_S and low A_L/A_S, is necessary to maintain water potentials within limits that prevent the occurrence of catastrophic xylem cavitation. The flexible responses of A_L/A_S and K_S to climate may preclude the existence of significant intraspecific variation in the vulnerability of xylem to cavitation in ponderosa pine.

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