

Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats

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Summary In the Rocky Mountains, ponderosa pine (*Pinus ponderosa* (ssp.) *ponderosa* Dougl. ex P. Laws. & C. Laws) often co-occurs with Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco). Despite previous reports showing higher shoot vulnerability to water-stress-induced cavitation in ponderosa pine, this species extends into drier habitats than Douglas-fir. We examined: (1) whether roots and shoots of ponderosa pine in riparian and slope habitats are more vulnerable to water-stress-induced cavitation than those of Douglas-fir; (2) whether species-specific differences in vulnerability translate into differences in specific conductivity in the field; and (3) whether the ability of ponderosa pine to extend into drier sites is a result of (a) greater plasticity in hydraulic properties or (b) functional or structural adjustments. Roots and shoots of ponderosa pine were significantly more vulnerable to water-stress-induced cavitation (overall mean cavitation pressure, $\Psi_{50\%} \pm \text{SE} = -3.11 \pm 0.32$ MPa for shoots and -0.99 ± 0.16 MPa for roots) than those of Douglas-fir ($\Psi_{50\%} \pm \text{SE} = -4.83 \pm 0.40$ MPa for shoots and -2.12 ± 0.35 MPa for roots). However, shoot specific conductivity did not differ between species in the field. For both species, roots were more vulnerable to cavitation than shoots. Overall, changes in vulnerability from riparian to slope habitats were small for both species. Greater declines in stomatal conductance as the summer proceeded, combined with higher allocation to sapwood and greater sapwood water storage, appeared to contribute to the ability of ponderosa pine to thrive in dry habitats despite relatively high vulnerability to water-stress-induced cavitation.

Keywords: Douglas-fir, drought tolerance, hydraulic conductivity, leaf-to-sapwood ratio, ponderosa pine, sapwood water storage.

Introduction

The trade-off between carbon acquisition and water loss in plants dictates that the ability of plants to supply adequate water to foliage is crucial to their success in dry habitats. When xylem tensions exceed a critical value, xylem cavitation may occur with potentially severe negative consequences on over-

all water transport (Crombie et al. 1985, Sperry and Tyree 1990). Because water transport is interrupted in cavitating conduits, if stomatal control does not limit water loss, xylem tension in the remaining conduits increases, leading to a positive feedback process known as runaway or catastrophic xylem cavitation that results in plant death (Tyree and Sperry 1988). Comparisons of xylem characteristics of co-occurring species differing in drought resistance (Cochard 1992, Alder et al. 1996, Sperry and Ikeda 1997, Linton et al. 1998), and individuals of the same species growing in different habitats (Kavanagh et al. 1998, Brodribb and Hill 1999, Kolb and Sperry 1999) indicate that drought-resistant species or individuals growing in xeric habitats exhibit higher resistance to xylem cavitation than less drought-resistant species or individuals (Tyree and Ewers 1991, Linton et al. 1998, Kolb and Sperry 1999). Thus, increased resistance to water-stress-induced xylem cavitation appears to be central to the success of species in xeric habitats (Tyree and Ewers 1991).

Although xylem characteristics are fundamental for water transport, some woody plants rely on functional (e.g., stomatal control of water loss), structural (proportion of conducting versus transpiring tissues) and life history adjustments (e.g., drought-deciduous versus evergreen) for the maintenance of an adequate water supply to foliage (Kolb and Davis 1994, Comstock 2000, Maherali and DeLucia 2000, Piñol and Sala 2000). For instance, Piñol and Sala (2000) showed that, within co-occurring conifers of the northern Rocky Mountains, shoots of the more drought-resistant species (*Pinus ponderosa* Dougl. ex P. Laws & C. Laws and *Pinus contorta* Dougl. ex Loud.) were substantially more vulnerable to water-stress-induced cavitation than shoots of species considered less drought-resistant (e.g., *Pseudotsuga menziesii* (Mirb.) Franco). They suggested that other traits such as increased stomatal sensitivity and lower leaf-to-sapwood ratios in *P. ponderosa* and *P. contorta* contributed to their drought resistance. However, Piñol and Sala (2000) did not test whether differences in vulnerability to cavitation between the species they examined translated into differential xylem cavitation in the field. Further, these authors examined xylem properties of shoots only in species co-occurring at the same site. However, within spe-

cies, roots tend to be more vulnerable to water-stress-induced cavitation than shoots (Alder et al. 1996, Sperry and Ikeda 1997, Linton et al. 1998) and roots tend to exhibit greater plasticity along soil water gradients than shoots (i.e., greater increases in resistance to water-stress-induced cavitation from mesic to xeric sites; Alder et al. 1996, Kavanagh et al. 1998). It is unlikely that the more drought-resistant ponderosa pine experiences more cavitation in the field than Douglas-fir. Therefore, it is of interest to determine whether differences in root vulnerability to cavitation, in plasticity of xylem properties along soil water gradients or in functional and structural adjustments to maintain hydraulic continuity could offset the apparently counterintuitive differences in shoot vulnerability reported by Piñol and Sala (2000).

We have examined hydraulic properties and xylem vulnerability to water-stress-induced cavitation in shoots and roots of ponderosa pine (*Pinus ponderosa* subsp. *ponderosa* Dougl. ex P. Laws & C. Laws.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco) in riparian and slope habitats. Our objectives were to determine: (1) whether roots and shoots of ponderosa pine are more vulnerable to water-stress-induced cavitation than those of Douglas-fir; (2) whether the species exhibit differential plasticity with respect to xylem vulnerability to cavitation along soil water gradients; (3) whether differences in xylem vulnerability between species translate into differences in specific conductivity in the field; and (4) potential functional and structural adjustments that allow ponderosa pine to thrive in dry habitats despite its higher xylem vulnerability relative to Douglas-fir.

Materials and methods

Study site

The study area is located in Petty Creek drainage, about 4.8 km south of Alberton, MT (47°00' N, 114°28' W) in the Rocky Mountains. The climate is characterized by warm summers and cold winters, with mean January and July temperatures of -5.5 °C and 19.4 °C, respectively. Mean annual precipitation in nearby Missoula is 340 mm. However, precipitation during June and July 1998 was much higher than average (A. Sala, unpublished data). Within the study area, we identified two sites: a riparian site located along Petty Creek at an elevation of 975 m and a southwest-facing slope site adjacent to the Creek at an elevation between 1097 and 1151 m. Both sites contain mixed-age stands of ponderosa pine and Douglas-fir.

Field and laboratory measurements

Field measurements of gas exchange and predawn water potential, and sampling for laboratory measurements of hydraulic conductivity and sapwood relative water content took place during five consecutive days in each of June, July and August 1998. Ten individuals of ponderosa pine and Douglas-fir between 15 and 20 cm diameter at breast height (1.4 m) were sampled at both the riparian site and the adjacent slope site.

Stomatal conductance (g_s) of 1-year-old needles from the lower third of the canopy was measured in the field between 1100 and 1400 h with a Li-Cor LI-6200 portable photosynthesis system (Li-Cor, Lincoln, NE). Rates of transpiration were determined from independent measurements of air relative humidity and temperature (taken with the cuvette open), assuming leaf temperature is equal to air temperature (Campbell and Norman 1988). Measured shoots were placed in plastic bags, transported to the laboratory in a cooler and refrigerated the same day sampling occurred. The leaf area of the measured shoots was calculated with an image analysis system (Moccha Jandel Scientific, San Rafael, CA). Predawn water potentials were measured with a pressure chamber (PMS Instrument, Corvallis, OR) on terminal shoots sampled from the mid-canopy.

Immediately after the field gas exchange measurements, specific sapwood native conductivity was measured according to Sperry et al. (1988). One-meter-long branch segments were removed from the mid-canopy on the south side of each tree. Samples were placed in plastic bags and transported to the laboratory in a cooler. A smaller section of the branch was cut under water, and the bark and cambium were removed from 2 cm at each end of the branches. The proximal ends of the stems were then attached to a tubing system and perfused with a filtered (0.22 μm), degassed, acidified (pH 2) solution at pressures between 6.8 and 9 kPa. Flow from the distal ends of the stems (F ; kg s^{-1}) was collected in pre-weighed vials containing cotton. Hydraulic conductivity (K_h ; $\text{kg m MPa}^{-1} \text{ s}^{-1}$) was calculated as:

$$K_h = F/(dP/dx), \quad (1)$$

where dP/dx (MPa m^{-1}) is the pressure gradient needed to sustain flow.

Unfortunately, because we used excessively high flushing pressures (100 kPa) to remove embolisms and calculate maximum K_h , we were unable to calculate percent cavitation in stems. After flushing stems of both species at 100 kPa, ponderosa pine stems showed increased K_h as expected, but Douglas-fir showed strongly decreased K_h . A later test of several pressures showed that K_h of Douglas-fir shoots was greatest after prolonged flushing at 25–30 kPa, but declined at pressures greater than 50 kPa.

Stem length, stem diameter and sapwood and heartwood areas were determined after conductivity measurements were completed. Sapwood area was visualized by staining the stem sections with bromocresol green (Kutscha and Sachs 1962). Sapwood specific native conductivity (K_s) was calculated as K_h divided by sapwood area. Because the visual method we used to estimate overall functional sapwood did not account for the area of conduits temporarily embolized (i.e., subjected to dynamic embolism and refilling), estimated K_s here is only an apparent measure. It may change seasonally as a result of the addition of late sapwood (although, according to the Hagen-Poiseuille law, it contributes little to the conductivity) and decreased water transport caused by dynamic embolism.

Sapwood relative water content was estimated in cores extracted from an additional 10 ponderosa pine and 10 Douglas-fir trees at each of the riparian and slope sites. Cored trees were adjacent to those used for all other field measurements. For each field sampling period (June, July and August), two cores, about 20 cm long and 5 mm in diameter, were extracted from the south side of each tree, tightly wrapped in plastic, double bagged and transported to the laboratory in a cooler. The sapwood portion of each core was weighed immediately on arrival in the laboratory (fresh mass, FM), soaked for 24 h in distilled water and weighed (saturation mass, SM), and then dried in an oven for 60–70 h at about 85 °C and reweighed (dry mass, DM). Sapwood relative water content was calculated as $100(\text{FM} - \text{DM})/(\text{SM} - \text{DM})$ (Borchert 1994).

Leaf area to sapwood area ratios (A_L/A_S) were measured on five of the 10 branches of ponderosa pine and Douglas-fir collected from each site in August for measurements of native specific sapwood conductivity. All distal needles were removed and the projected leaf area of a subsample was measured with an image analysis system (Moccha Jandel Scientific). All leaves from each branch were oven-dried at 100 °C for 72 h and weighed. The leaf mass ratio of the subsample was used to estimate the total projected leaf area of the corresponding branch. A subsample of needles from each branch was finely ground for carbon isotope ratio ($\delta^{13}\text{C}$) analysis. Samples were analyzed at the Stable Isotope Laboratory of the Institute of Ecology (University of Georgia, Athens, GA). Values were expressed relative to the PeeDee Belemnite standard.

Samples used to determine vulnerability to water-stress-induced cavitation were collected in November. Roots and stem sections free of lateral branches, about 20 cm long and 4 and 7 mm in mean diameter, respectively, were collected from five ponderosa pine and Douglas-fir trees at both sites and stored at 4 °C. Root sampling was done with a trowel by excavating a root from the base of the tree outward until a length of appropriate diameter was uncovered. Branches and roots were brought to room temperature overnight (about 12 h) and vulnerability curves were generated by the air-injection method (Sperry et al. 1988). Before mounting in the double-ended pressure chamber, the stems and roots were soaked in distilled water for 1 h and the bark and cambium removed. One-cm segments were cut from each end under water, and a sharp razor blade was used to remove a thin section from the ends to reduce any injury to tracheid openings. Three shallow cuts were made at the center of each measured segment to facilitate the entry of air into the tracheids. Segments were then mounted in the chamber, and the proximal ends were attached to the same tubing system used to measure hydraulic conductivity.

To eliminate any preexisting embolisms, a filtered (0.22 μm), degassed, acidified (pH 2) solution was flushed through the segments for 30 min at a pressure of 25 to 30 kPa. The solution was then perfused through the stems at a lower pressure (6.5–9.0 kPa) and water was collected from the distal ends of the branches in pre-weighed vials containing cotton.

Maximum hydraulic conductivity was calculated with Equation 1. Embolism was induced by injecting air into the chamber at a pressure of 0.5 MPa for roots and 1.0 MPa for shoots. After 10 min, any air trapped in the tubing system was released, and flow through the stems was reestablished. Hydraulic conductivity was remeasured. This process was repeated at pressures of 1, 2, 3, 5 and 7 MPa for roots and at 2, 3, 5, 6 and 7 MPa for shoots, or until the conductivity had dropped below 5%. A residual pressure of about 10 kPa was maintained inside the chamber during measurement of hydraulic conductivity to prevent lateral movement of water out of the stems.

Mean cavitation pressure ($\Psi_{50\%}$), the pressure at which 50% loss of conductivity is reached, was calculated as described by Pammenter and Vander Willigen (1998) by fitting vulnerability curves to the function:

$$\text{PLC} = 100 / (1 + \exp(a(P - b))), \quad (2)$$

where P is injection pressure, b is the pressure causing 50% loss of hydraulic conductivity ($\Psi_{50\%}$) and a is proportional to the slope of the curve.

Data were subjected to one-, two- or three-way ANOVA (SAS Institute, Cary, NC) to determine significant differences due to site, species, plant segment (roots or shoots) or time. Time was treated as a repeated measures factor when included in the ANOVA model. Some variables were log-transformed to meet assumptions of normality.

Results

Overall, ponderosa pine was more vulnerable to water-stress-induced cavitation (higher a and lower $\Psi_{50\%}$) than Douglas-fir ($P_{\text{species}} < 0.001$ for a and $\Psi_{50\%}$; three-way ANOVA with species, site and plant segment) and roots were more vulnerable than shoots ($P_{\text{segment}} < 0.001$ for a and $\Psi_{50\%}$; Figure 1, Table 1). Species differences remained significant when roots and shoots were analyzed separately ($P < 0.03$ in all cases) and segment differences remained significant when the species were analyzed separately ($P < 0.001$ in all cases). Site differences in vulnerability to cavitation were generally small and were apparent only with an overall significantly greater a value (slope of the curve) at the riparian site relative to the slope site ($P_{\text{site}} = 0.03$; three-way ANOVA; Figure 1, Table 1), indicating higher vulnerability to cavitation in trees at this site. Site differences, however, were less apparent (and not statistically significant) when roots and shoots were analyzed separately ($0.05 < P_{\text{site}} < 0.08$ in all cases). A significant species \times site interaction for the slope of the curve for roots (a value; $P < 0.04$) indicated that plasticity in root vulnerability was greater for ponderosa pine (where roots were more vulnerable at the riparian site) than for Douglas-fir (Figures 1c and 1d, Table 1).

Native sapwood specific hydraulic conductivity (K_s , permeability on a sapwood area basis) declined significantly throughout the summer (Figure 2; $P_{\text{date}} < 0.01$; three-way ANOVA, with species, site and date) and this decline was similar for both species ($P_{\text{date} \times \text{species}} > 0.05$). In general, K_s was

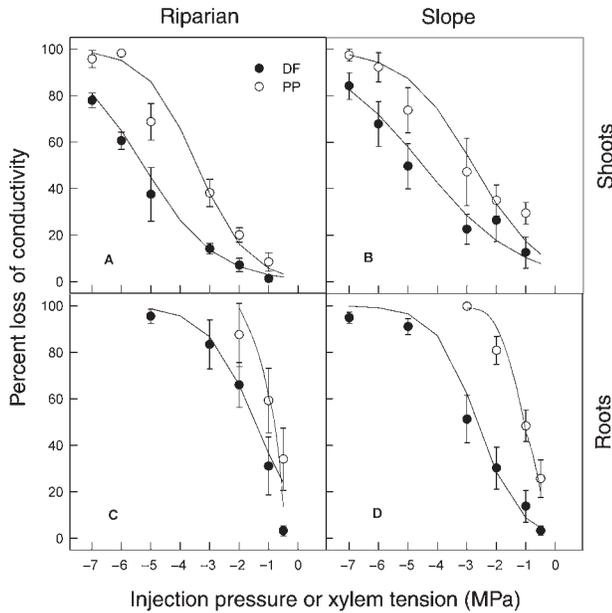


Figure 1. Vulnerability curves for shoots and roots of ponderosa pine (PP) and Douglas-fir (DF) sampled at riparian and slope sites. Error bars represent one standard error. Sample size varied between three (ponderosa pine roots at the riparian site) and five (all slope data).

higher in trees at the riparian site ($P_{\text{site}} < 0.001$), although site differences were larger for ponderosa pine than for Douglas-fir ($P_{\text{site} \times \text{species}} < 0.01$). There were no species differences in K_s on any sampling date, except in August at the riparian site where the more vulnerable ponderosa pine maintained greater K_s relative to Douglas-fir ($P_{\text{site} \times \text{species}} = 0.018$; two-way ANOVA per date).

Predawn water potential (Ψ_{PD}) declined in both ponderosa pine and Douglas-fir throughout the summer from mean values of -0.72 MPa in June to -1.5 MPa in August (Figure 3; $P_{\text{date}} < 0.001$; three-way ANOVA). Overall, Ψ_{PD} was lower in

Table 1. Mean (\pm SE) slope (a) and $\Psi_{50\%}$ (b) for the function $\text{PLC} = 100/(1 + \exp(a(P - b)))$ adjusted to the vulnerability data for Douglas-fir and ponderosa pine. Asterisks indicate significant site differences within a species and segment ($P < 0.05$). In all cases, roots were significantly more vulnerable than shoots, and ponderosa pine roots and shoots were significantly more vulnerable than those of Douglas-fir.

Species	Site	Segment	a (slope)	b (intercept)
Douglas-fir	Riparian	Shoot	0.824 (\pm 0.111)	5.251 (\pm 0.428)
		Root	1.215 (\pm 0.181)	1.454 (\pm 0.495)
	Slope	Shoot	0.620 (\pm 0.143)	4.487 (\pm 0.586)
		Root	1.424 (\pm 0.170)	2.652 (\pm 0.281)
Ponderosa pine	Riparian	Shoot	1.157 (\pm 0.097)	3.430 (\pm 0.293)
		Root	4.590 (\pm 0.735)*	0.905 (\pm 0.245)
	Slope	Shoot	0.875 (\pm 0.118)	2.786 (\pm 0.515)
		Root	2.444 (\pm 0.588)*	1.071 (\pm 0.191)

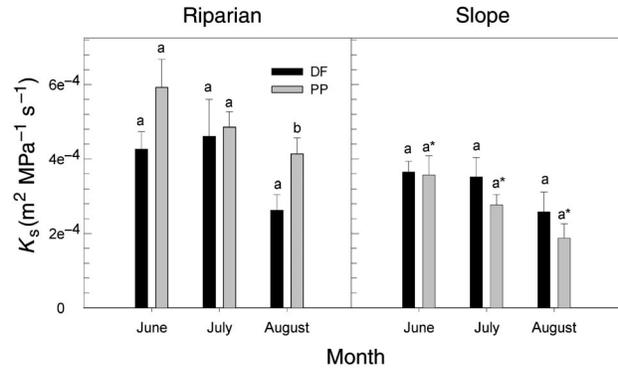


Figure 2. Sapwood specific native conductivity (K_s) of Douglas-fir (DF) and ponderosa pine (PP) shoots sampled at riparian and slope sites in June, July and August 1998. Letters indicate significant differences between species within a site and month ($P < 0.05$). Asterisks represent significant site differences within a species ($P < 0.05$). Error bars represent one standard error; $n = 10$.

ponderosa pine than in Douglas-fir ($P_{\text{species}} < 0.01$) and lower in trees at the slope site than at the riparian site ($P_{\text{site}} < 0.01$). These differences, however, were small and when dates were analyzed separately, species and site differences were significant only in June ($P_{\text{species}} = 0.003$, $P_{\text{site}} = 0.035$). None of the interactions were significant, indicating that seasonal declines in Ψ_{PD} were similar for the two species and at the two sites.

Overall, sapwood relative water content (RWC) was highest in June ($P_{\text{date}} < 0.05$; three-way ANOVA, with species, site and date), higher at the slope site than at the riparian site ($P_{\text{site}} < 0.01$) and higher in ponderosa pine than in Douglas-fir ($P_{\text{species}} < 0.01$; Figure 4). When dates were analyzed separately, however, species differences were statistically significant only in June ($P_{\text{species}} < 0.01$; two-way ANOVA per date; Figure 4). Seasonal changes in sapwood RWC varied depending on the species and the site (Figure 4). At the riparian site, both species exhibited similar seasonal changes in sapwood RWC ($P_{\text{date} \times \text{species}} > 0.05$; two-way ANOVA per site), whereas

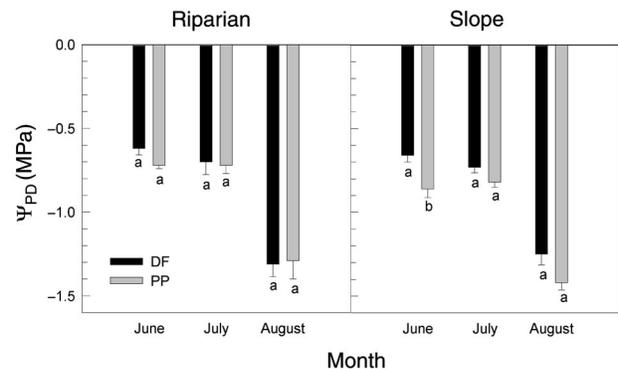


Figure 3. Predawn water potentials (Ψ_{PD}) of Douglas-fir (DF) and ponderosa pine (PP) shoots sampled at riparian and slope sites in June, July and August 1998. Letters indicate significant differences between species within a site and month ($P < 0.05$). Error bars represent one standard error; $n = 10$.

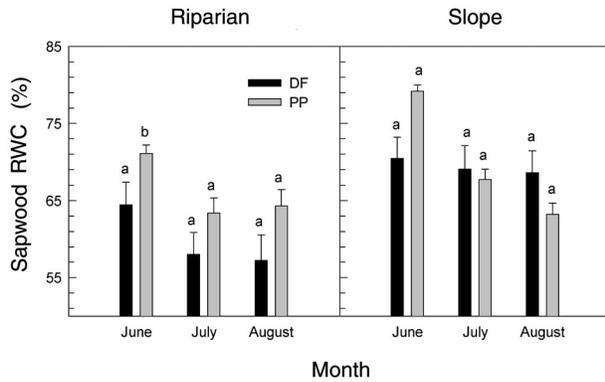


Figure 4. Percent sapwood relative water content (RWC) of Douglas-fir (DF) and ponderosa pine (PP) at riparian and slope sites in June, July and August 1998. Letters denote significant differences between species within a site ($P < 0.05$). Error bars represent one standard error; $n = 10$.

at the slope site sapwood RWC declined significantly during the summer, but only in ponderosa pine (Figure 4; $P_{\text{date} \times \text{species}} = 0.013$; two-way ANOVA per site).

Stomatal conductance was substantially higher in ponderosa pine than in Douglas-fir ($P_{\text{species}} < 0.001$; three-way ANOVA) and declined significantly throughout the summer in both species ($P_{\text{date}} < 0.001$; Figure 5). Species differences were greatest in June, and became less pronounced later in the summer because of large declines in g_s throughout the summer in ponderosa pine ($P_{\text{date} \times \text{species}} < 0.03$; three-way ANOVA). In general, site differences were small and significant only in July when g_s was higher at the slope site than at the riparian site ($P_{\text{site}} < 0.01$; two-way ANOVA per date).

The A_L/A_S ratios for terminal shoots at the riparian and slope sites were significantly lower in ponderosa pine than in Douglas-fir (Table 2). However, A_L/A_S did not vary between sites in either species. Sapwood-area-based transpiration rates for terminal shoots were consistently higher for ponderosa

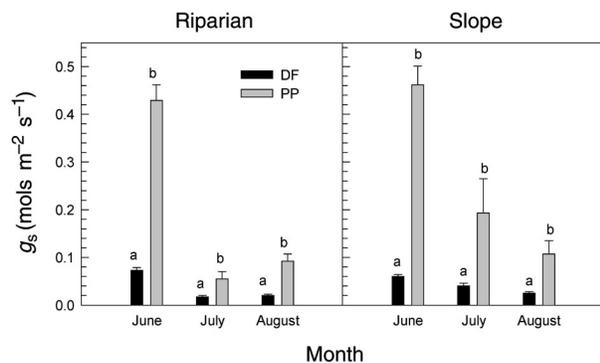


Figure 5. Stomatal conductance (g_s) for Douglas-fir (DF) and ponderosa pine (PP) at riparian and slope sites in June, July and August 1998. Letters represent significant differences between species within a site. Error bars represent one standard error. Sample size varied between six and 10.

Table 2. Leaf area to sapwood area ratios (A_L/A_S) and carbon isotope ratios ($\delta^{13}\text{C}$) for Douglas-fir and ponderosa pine at riparian and slope sites. Letters indicate significant species differences within a site ($P < 0.05$). Standard errors are in parentheses.

Species	Site	A_L/A_S ($\text{m}^2 \text{cm}^{-2}$)	$\delta^{13}\text{C}$ (‰)
Douglas-fir	Riparian	0.805 (± 0.116) a	-27.45 (± 0.156)
	Slope	0.739 (± 0.158) a	-26.97 (± 0.23)
Ponderosa pine	Riparian	0.190 (± 0.035) b	-27.81 (± 0.271)
	Slope	0.255 (± 0.032) b	-27.03 (± 0.315)

pine than for Douglas-fir ($P_{\text{species}} < 0.01$; data not shown). However, based on species-specific published A_L/A_S ratios and mean leaf-area-based transpiration rates for the slope and riparian sites on each date, estimated whole-tree sapwood-area-based transpiration rates were higher for ponderosa pine than for Douglas-fir in June, but not in July and August ($P_{\text{species} \times \text{date}} < 0.05$; two-way ANOVA; Figure 6). On average, $\delta^{13}\text{C}$ values of trees at the riparian site were significantly lower than at the slope site ($P_{\text{site}} < 0.05$; two-way ANOVA with species and site), but $\delta^{13}\text{C}$ values did not vary significantly between species ($P > 0.05$).

Discussion

Ponderosa pine and Douglas-fir have broad and overlapping distributions along climate gradients in western US forests. In low-elevation forests of the interior northwest, however, ponderosa pine extends into drier sites than Douglas-fir (Daubenmire and Daubenmire 1968, Pfister et al. 1977) and is

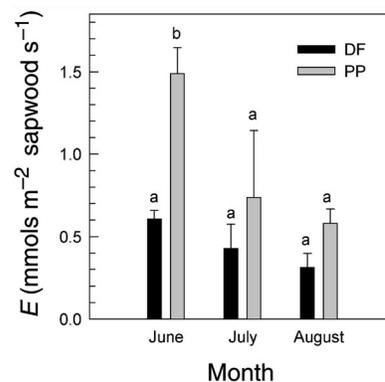


Figure 6. Water loss (E) per unit of sapwood area in June, July and August 1998. Values are the product of mean transpiration rates from the riparian and slope sites and published local A_L/A_S means for Douglas-fir (DF) ($0.46 \text{ m}^2 \text{cm}^{-2}$) (Sala et al. 2001a) and ponderosa pine (PP) ($0.17 \text{ m}^2 \text{cm}^{-2}$) (O'Hara and Valappil 1995). Letters denote significant differences between species ($P < 0.05$). Error bars represent one standard error. Sample size varied between five and 11.

considered more drought-resistant (Minore 1979). Contrary to the expectation that species extending into xeric sites are more resistant to water-stress-induced cavitation than species limited to mesic sites, we found that shoots and roots of ponderosa pine were more vulnerable to cavitation than those of Douglas-fir. Several functional and structural adjustments in ponderosa pine apparently offset its relatively high vulnerability to cavitation and resulted in seasonal changes in native specific hydraulic conductivity similar to those in Douglas-fir. Such adjustments may provide alternative mechanisms by which ponderosa pine can thrive in dry habitats.

Higher vulnerability to cavitation in roots than in shoots of the species examined are consistent with results reported elsewhere (Alder et al. 1996, Sperry and Ikeda 1997, Kavanagh et al. 1998, Linton et al. 1998). Alder et al. (1996) proposed that higher vulnerability in roots than in shoots might be adaptive if root cavitation in response to water stress limits water transport, thereby delivering a hydraulic signal to shoots that triggers stomatal closure (e.g., Sperry and Pockman 1993, Meinzer et al. 1999). This suggestion is consistent with our results showing that decreases in g_s in ponderosa pine from June to July were greater in trees at the riparian habitat, where root vulnerability tended to be greater (see below), than at the slope habitat. If root vulnerability serves as a sensitive mechanism to deliver hydraulic signals in response to water stress, higher root vulnerability in ponderosa pine than in Douglas-fir may be advantageous, particularly if coupled with other mechanisms to conserve water.

We also determined the degree to which plasticity in vulnerability to cavitation along environmental gradients (toward reduced vulnerability at drier sites) was greater in ponderosa pine than in Douglas-fir, thus providing an alternative mechanism by which ponderosa pine can extend into xeric sites. Although overall vulnerability to cavitation was higher in trees at the riparian site than at the slope site, differences were small and trends were similar for both species. Contrary to expectation, however, similar A_L/A_S in terminal shoots (a parameter sensitive to drought) and the lack of strong differences in Ψ_{PD} between sites suggest that trees at both sites may have had similar access to soil water. If this is the case, in the long-term, it could account for the small site differences in vulnerability to cavitation that we observed. However, the unusually wet spring of 1998 may also account, at least in part, for the small differences in Ψ_{PD} at the two sites. Further, whole-tree A_L/A_S may differ between the two sites despite similar values in terminal branches. Therefore, it is possible that, in the long term, the two sites differ in water availability and that plastic responses in vulnerability to cavitation are small and similar for both species.

Despite the greater vulnerability to water-stress-induced cavitation in ponderosa pine than in Douglas-fir, K_s values and seasonal trends were similar for both species at each site. An exception was a greater K_s in August at the riparian site for ponderosa pine than for Douglas-fir. Although we were unable to calculate % cavitation, these results suggest that ponderosa pine did not cavitate more in the field than Douglas-fir, particularly if maximum conductivity remained constant

throughout the season for both species. This is a reasonable assumption because, according to the Hagen-Poiseuille law, as the summer proceeds, the addition of late wood comprising small diameter xylem conduits is expected to contribute little to total hydraulic conductivity. Further, there was no significant seasonal change in the ratio of heartwood to sapwood for either species (data not shown), suggesting that the addition of late wood was small. Therefore, the seasonal decreases in K_s appear to be a result of dynamic embolism rather than addition of late sapwood. Similar decreases in K_s for both species suggest that seasonal dynamic embolism was also similar.

Based on our vulnerability curves and Ψ_{PD} results, predicted root embolism in August was high in both ponderosa pine (70%) and Douglas-fir (50%). It is possible that measured Ψ_{PD} was not in equilibrium with soil water potential. Although this has not been explored in ponderosa pine, a predawn disequilibrium has been reported in Douglas-fir and other conifers, including *Picea abies* (L.) Karst. and *Pinus contorta* (Donovan et al. 2001). If disequilibrium occurs, roots might have higher water potentials and experience lower cavitation than predicted here.

How does the more vulnerable ponderosa pine maintain a similar degree of cavitation in the field as Douglas-fir? Our data suggest that the relatively high xylem vulnerability of ponderosa pine is offset by several functional and structural adjustments, including greater stomatal sensitivity to water stress, shifts in biomass allocation and enhanced capacity to store water. Consistent with other studies showing greater gas exchange and leaf-area-based water use in early successional species with lower A_L/A_S (Sala et al. 2001a, 2001b), g_s was higher in ponderosa pine than in Douglas-fir. This difference was particularly large in June, when estimated sapwood-area-based water loss was significantly greater in ponderosa pine than in Douglas-fir. However, as the summer proceeded, greater declines in g_s for ponderosa pine resulted in similar sapwood-area-based water loss in both species later in the summer. Therefore, increased stomatal sensitivity in ponderosa pine combined with low A_L/A_S resulted in proportionally greater control of water loss as the summer proceeded relative to Douglas-fir. In ponderosa pine, sensitive stomatal responses to midday leaf-to-air vapor pressure deficits may also explain the strong decreases in g_s from June to July despite constant Ψ_{PD} . Stomatal control of transpiration in ponderosa pine is thought to prevent cavitation-inducing pressures (Piñol and Sala 2000). Contrary to other studies (Marshall and Zhang 1994, Piñol and Sala 2000), higher stomatal sensitivity in ponderosa pine than in Douglas-fir was not reflected in less negative $^{13}\delta C$, perhaps because of the small sample size ($n = 5$).

A characteristically low A_L/A_S ratio in ponderosa pine relative to other Rocky Mountain non-pine conifers (see Callaway et al. 2000) is an effective structural adjustment that minimizes whole-tree water loss and maintains a homeostatic balance between water supply and water transport (DeLucia et al. 2000). Although our small sample sizes did not reveal significant differences in A_L/A_S for terminal shoots between riparian and slope sites, previous studies have shown strong structural acclimation (decreases in whole-tree A_L/A_S) in ponderosa pine

along climate gradients (DeLucia et al. 2000). According to published values of whole-tree A_L/A_S for the interior Rocky Mountains, lower A_L/A_S for ponderosa pine than for Douglas-fir mitigated the large difference in stomatal conductance between species. Such structural acclimation, combined with relatively high stomatal sensitivity, allows ponderosa pine to maximize leaf-area-based water transport (leaf specific conductivity; Maherali and DeLucia 2000) and gas exchange during favorable conditions, while minimizing overall water use during water stress. Comstock (2000) reported similar strategies in desert shrubs.

The large proportion of sapwood in ponderosa pine, combined with the overall high sapwood RWC, may provide this species with a substantial capacity for water storage. Stem water storage is known to act as an important buffer during soil water deficits for several species (Waring and Running 1978, Borchert 1994, Stratton et al. 2000) and can contribute significantly to transpirational water demand (Waring et al. 1979). Seasonal decreases in sapwood RWC in ponderosa pine, which were particularly strong at the slope site, suggest that this species may draw stored water to meet transpiration demand. Because water storage may buffer changes in leaf water status by reducing apparent hydraulic resistance (Stratton et al. 2000), stored stem water in ponderosa pine may be important in preventing xylem cavitation in critical leaf-bearing stems. Retrieval of sapwood stored water in ponderosa pine throughout the season at the slope site could have contributed to maintaining August Ψ_{PD} values similar to those at the riparian site. Similar use of stored water has been shown in Scots pine (Jackson et al. 1995).

In conclusion, despite being able to extend into xeric sites, ponderosa pine is substantially more vulnerable to water-stress-induced cavitation than the co-occurring Douglas-fir. However, ponderosa pine did not cavitate more than Douglas-fir in the field as the summer proceeded because of functional (higher stomatal sensitivity) and structural (greater proportion of sapwood combined with higher sapwood water storage) adjustments that apparently offset its high vulnerability to cavitation. Therefore, effective drought-avoiding mechanisms appear to confer higher drought resistance on ponderosa pine relative to the more drought-tolerant Douglas-fir.

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