

Species Variation in Water Relations and Xylem Vulnerability to Cavitation at a Forest-Woodland Ecotone

Dan F. Koepke and Thomas E. Kolb

Abstract: Xylem vulnerability to cavitation and response of water potential (Ψ), stomatal conductance (g_s), and net photosynthesis (P_n) to drought are potentially important mechanisms of drought resistance. We compared Ψ , g_s , P_n , and cavitation vulnerability of shoot and root xylem among co-occurring ponderosa pine (*Pinus ponderosa* var. *scopulorum* Dougl. Ex Laws.), pinyon pine (*Pinus edulis* Engelm.), and Utah juniper (*Juniperus osteosperma* [Torr.] Little) at a forest-woodland ecotonal site in northern Arizona to elucidate drought resistance mechanisms of these species. Juniper shoots partly regulated Ψ during drought via stomatal closure, but regulation was weaker than that for ponderosa and pinyon pines, which had similar water relations and P_n responses to drought. Midday g_s and P_n during summer drought were positive for juniper ($g_s = 14.3 \text{ mmol m}^{-2} \text{ s}^{-1}$, $P_n = 1.23 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) but near zero for ponderosa ($g_s = 0.7 \text{ mmol m}^{-2} \text{ s}^{-1}$, $P_n = -0.02 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) and pinyon ($g_s = 1.5 \text{ mmol m}^{-2} \text{ s}^{-1}$, $P_n = -0.18 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) pines. Cavitation vulnerability of shoots and roots was lower for juniper than for both pines. The water potential inducing 50% loss in xylem hydraulic conductivity (Ψ_{50}) for juniper was 5.0 MPa more negative for shoots and 3.9 MPa more negative for roots compared with the respective tissues of the pine species. Pinyon pine ($\Psi_{50} = -2.71 \text{ MPa}$) was slightly more vulnerable to cavitation than ponderosa pine ($\Psi_{50} = -3.42 \text{ MPa}$) for shoots, whereas root vulnerability was similar for both pines ($\Psi_{50} = -1.69 \text{ MPa}$ for pinyon; -1.98 MPa for ponderosa). Roots of all species were more vulnerable to cavitation than shoots. Our results show an important role of cavitation vulnerability in the greater drought resistance of Utah juniper than pinyon and ponderosa pines but not for the presumed greater drought resistance of pinyon pine than ponderosa pine. FOR. SCI. 59(5):524–535.

Keywords: Arizona, drought, *Juniperus osteosperma*, *Pinus edulis*, *Pinus ponderosa*

THE RESPONSE OF STOMATAL CONDUCTANCE (g_s) to drought is an important component of tree drought resistance (Sperry 2000, Sperry et al. 2002, Flexas et al. 2006) and mechanisms of drought-induced mortality (McDowell et al. 2008, Sala et al. 2010, McDowell 2011) because g_s regulates xylem water potential (Ψ) and net photosynthesis (P_n), which provides carbohydrates for plant metabolism (Flexas et al. 2006, Atkin and Macherel 2009) and defenses against some biotic agents (Raffa et al. 2008, Negrón et al. 2009, Kane and Kolb 2010). Xylem vulnerability to cavitation is another potentially important component of tree drought resistance (Linton et al. 1998, Pockman and Sperry 2000, Maherali et al. 2004) and drought-induced mortality and canopy dieback via hydraulic failure (Tyree et al. 1994, Rood et al. 2000, Davis et al. 2002, Rice et al. 2004, Anderegg et al. 2012). Moreover, xylem vulnerability to cavitation covaries with response of g_s to drought; species with high xylem vulnerability to water stress-induced cavitation typically exhibit strong control of transpiration via reduced g_s during drought to avoid Ψ values that cause extensive cavitation (Martínez-Vilalta et al. 2004, Sperry 2004, Maherali et al. 2006). Species with high vulnerability to xylem cavitation can occur on dry sites when high vulnerability is compensated for by other

drought adaptations that regulate xylem Ψ , such as high water storage in sapwood, strong stomatal regulation of water loss (Piñol and Sala 2000, Stout and Sala 2003, Martínez-Vilalta et al. 2004), and timing of growth during wet periods (Kolb and Davis 1994).

Information on the vulnerability of multiple organs along the soil-plant-atmosphere continuum is needed to understand the role of xylem cavitation in tree drought resistance (Linton et al. 1998, Brodribb 2009). Root xylem often is more vulnerable to cavitation than shoot or twig xylem at a common Ψ (e.g., Sperry and Saliendra 1994, Alder et al. 1996, Jackson et al. 2000, Sperry and Hacke 2002, Stout and Sala 2003, McElrone et al. 2004, Hultine et al. 2006, Domec et al. 2004). There may be exceptions to this pattern, such as Utah juniper (*Juniperus osteosperma* [Torr.] Little), which has been reported to have similar vulnerability of shoots and roots (e.g., Linton et al. 1998, Willson et al. 2008). Root cavitation during extreme drought has been suggested to be more important than shoot cavitation in determining differences in drought resistance among species in semiarid environments (Linton et al. 1998, Domec et al. 2004).

Understanding of species differences in drought resistance is particularly important for regions that are predicted

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to be strongly affected by climate change, such as the southwestern United States. The climate in the southwestern United States is expected to become warmer and drier and include more frequent and severe droughts in the future (Intergovernmental Panel on Climate Change 2007, Seager et al. 2007, Overpeck and Udall 2010, Dai 2011). Tree growth in this region is strongly controlled by drought (Fritts 1976, Meko et al. 1995, Adams and Kolb 2005). Consistent with climate predictions, recent droughts have been unusually warm (Breshears et al. 2005) and have been associated with unusually high pulses of tree mortality and canopy dieback (Shaw et al. 2005, van Mantgem et al. 2009, Koepke et al. 2010, Ganey and Vojta 2011, 2012).

Little information is available about xylem vulnerability to cavitation for conifers that dominate woodlands and forests of the southwestern United States. For example, xylem vulnerability to cavitation of a widespread species, ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.) has been measured for populations from the Pacific Northwest (Domec et al. 2004, 2009), the northern Rocky Mountains (Piñol and Sala 2000, Stout and Sala 2003, Delzon et al. 2010), and the eastern Sierra Nevada Mountains (Maherali and DeLucia 2000), but not the Colorado Plateau of the southwestern United States where the largest contiguous forests occur (Burns and Honkala 1990). Xylem vulnerability to cavitation for two common woodland species, pinyon pine (*Pinus edulis* Engelm.) and Utah juniper, has been directly compared only for populations in Utah in the northern part of the widespread pinyon-juniper type (Linton et al. 1998, Delzon et al. 2010). Most subsequent comparisons of pinyon pine and Utah juniper, such as those of West et al. (2007) and McDowell et al. (2008) and reviews and syntheses of woody plant hydraulic architecture (e.g., Maherali et al. 2004, Martínez-Vilalta et al. 2004), used the xylem vulnerability curves of these species of Linton et al. (1998). For Utah juniper, xylem vulnerability to cavitation for populations in northern Arizona has been reported to vary considerably between studies (Willson and Jackson 2006, Willson et al. 2008).

Our study compared interannual, seasonal, and diurnal variation in shoot Ψ , leaf gas exchange, and xylem vulnerability to water stress-induced cavitation of shoots and roots among three gymnosperm species that differ in presumed drought resistance and commonly occur in forests and woodlands of the southwestern United States—ponderosa pine, pinyon pine, and Utah juniper. Similar to a common garden study (Clausen et al. 1940), we compared these species at an ecotonal site in northern Arizona where they co-occurred in the transition between woodland and forest to isolate inherent species differences from potential environmental sources of variation. Woody species common to both higher elevation forests and lower elevation woodlands occur in the forest-woodland ecotone in this region (Adams and Kolb 2005, Koepke et al. 2010). Our study builds on previous investigations of drought resistance of southwestern conifers (e.g., Linton et al. 1998, Williams and Ehleringer 2000, West et al. 2007, McDowell et al. 2008, Adams et al. 2009, Breshears et al. 2009) by including ponderosa pine in comparisons between pinyon pine and Utah juniper at a common site and by the creation of the first xylem vulnerability curves of both shoots and roots for populations of ponderosa pine and pinyon pine growing in Arizona.

Because of differences in presumed drought resistance

among these species (juniper > pinyon > ponderosa; Ninemets and Valladares 2006) and previous reports that drought-susceptible species with high xylem vulnerability to cavitation strongly control transpiration and xylem water potential to avoid extensive cavitation (Sperry 2000, Martínez-Vilalta et al. 2004, Sperry 2004), we predicted that ponderosa pine shoots and roots would be most vulnerable to xylem cavitation and show the strongest isohydric behavior (e.g., little temporal variation in shoot Ψ and large reductions of g_s and P_n in response to drought and vapor pressure deficit [VPD]), pinyon pine would be intermediate, and Utah juniper would be least vulnerable to cavitation and show the weakest isohydric behavior. This prediction is consistent with the greater dominance of Utah juniper at drier and lower elevations, codominance of juniper and pinyon pine at medium elevations, and greater dominance of ponderosa pine at wetter and higher elevations in the southwestern United States (Brown 1982, Burns and Honkala 1990). It also is consistent with the greater survival of juniper than pinyon and ponderosa pines during severe drought (Mueller et al. 2005, Koepke et al. 2010) and with a previous review of Ψ causing 50% loss of shoot xylem conductivity (Ψ_{50}) that included data for these species from different studies and locations (Martínez-Vilalta et al. 2004). In that review, the shoot Ψ_{50} of ponderosa pines sampled in Montana and eastern California ranged between -2.6 and -3.4 MPa and was -4.5 MPa for pinyon pine and -6.6 MPa for Utah juniper, both sampled in Utah. An alternative prediction regarding ponderosa and pinyon pines is that there would be little species difference in xylem vulnerability to cavitation and water relations behavior. This prediction is based on the similar percent mortality reported for these species during the severe 2002 drought at ecotonal sites where they co-occurred in northern Arizona (Koepke et al. 2010) as well as similar shoot Ψ_{50} (approximately -4 MPa) in a recent comparison of ponderosa pine sampled from Montana and pinyon pine sampled from Utah (Delzon et al. 2010).

Methods

Study Site

We conducted the study at one site located at the ecotone between ponderosa pine forest and pinyon-juniper woodland in northern Arizona, just north of Walnut Canyon National Monument ($35^{\circ}10'49.1''$ N, $111^{\circ}29'46.7''$ W; elevation 2,000 m). The soil was derived from sandstone parent material and is classified as a fine sandy loam Typic Haplustalf with approximately 30% rock content. Dominant trees of the site included ponderosa pine, pinyon pine, Utah juniper, alligator juniper (*Juniperus deppeana* Steud.), one-seed juniper (*Juniperus monosperma* [Engelm.] Sarg.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and Gambel oak (*Quercus gambelii* Nutt.) (Koepke et al. 2010). Total basal area of the site ($19.2 \text{ m}^{-2} \text{ ha}^{-1}$) (Adams and Kolb 2005) was dominated by ponderosa pine (57%), followed by pinyon pine (26%) and Utah juniper (3%). Total number of stems was higher for pinyon pine (164 ha^{-1}) than ponderosa pine (35 ha^{-1}) and Utah juniper (23 ha^{-1}). Precipitation at the site is characterized by a moist fall and winter followed by a distinctively drier spring that receives only 11% of the approximately 460 mm annual precipitation

(Hereford 2007, Western Regional Climate Center 2010). June is typically dry (11 mm) and warm (mean maximum air temperature 28°C). Late summer rains between July and September typically supply about 38% of annual precipitation.

Seasonal and Interannual Variation in Water Potential

We measured shoot Ψ of each species during predawn (Ψ_{PD} ; 2:00–5:00 am) and midday (Ψ_{MD} ; 11:00 am–2:00 pm) during spring and summer of 2005 and 2006. Both seasons were wetter and cooler in 2005 than 2006. Specifically, the Palmer drought severity index for the spring (+5.2) and summer (+4.4) of 2005 indicated unusually moist conditions; in contrast, the Palmer drought severity index for the respective seasons in 2006 was –3.1 and –4.5 or extremely dry (Heim 2002, National Oceanic and Atmospheric Administration 2008). The spring Ψ measurements occurred on May 31 in 2005 and about 2 weeks earlier (May 11) in 2006 because of the severe drought in 2006. The summer Ψ measurements were made on July 16 in 2005 and on July 1 in 2006.

On each date, we sampled five mature individuals of each species for measurement of Ψ by collecting a terminal twig (pinyon pine and Utah juniper) or needle (ponderosa pine) from approximately mid-canopy and immediately sealing it into a plastic bag containing a slightly moist paper towel (no free water). The samples were stored in a dark cooler and measured using a Scholander-type pressure chamber (model 1000; PMS Instruments, Corvallis, OR) (Scholander et al. 1965) within 2 hours of collection, a procedure that does not change leaf Ψ of conifers (Kaufmann and Thor 1982). Two or three samples per tree were measured for the highly resinous pines to assure accurate observation of the endpoint. The dbh of the measured trees averaged 27.1 cm for ponderosa pine, 22.1 cm for pinyon pine, and 23.2 cm for Utah juniper. Height of the measured trees averaged 5.8 m for ponderosa pine, 3.5 m for pinyon pine, and 3.9 m for juniper. All sampled trees were reproductively mature as indicated by cone or strobilus production and were at least 50 years old based on ring counts of similar sized trees at the study site (Adams and Kolb 2005). We used two-way analysis of variance with season and year as factors and Tukey mean comparisons to compare temporal variation in Ψ_{PD} and Ψ_{MD} for each species. Best-fit regressions based on coefficient of determination were used to evaluate the relationship between Ψ_{MD} and Ψ_{PD} pooled over seasons and years for each species.

Diurnal Variation in Leaf Gas Exchange and Water Potential

We selected two representative mature and healthy (i.e., no recent canopy dieback) plants of each species in an open sunlit area for measurements of leaf gas exchange and Ψ . One plant per species was selected from each of two nearly flat (slope <2%) locations within the study site. The dbh of the sampled trees (mean of 33.5, 22.0, and 23.5 cm for ponderosa pine, pinyon pine, and Utah juniper, respectively) was similar to that of trees sampled for the study of seasonal and interannual variation in Ψ . On one day during a moist period in early May (spring) and one day during a

drier period in late June (summer) in 2006, we measured temporal variation on both plants of each species in shoot xylem Ψ using a Scholander-type pressure chamber and in leaf gas exchange (g_s , P_n) using a Li-Cor 6400 portable photosynthesis system (Li-Cor Inc.; Lincoln, NE). These measurements were made every 1–2 hours between sunrise and midafternoon in the mid-canopy for all species.

For the leaf gas exchange measurements, we inserted a single fascicle (pines) or twig tip (juniper) into the cuvette (2 × 3 cm model) and made three consecutive measurements that were averaged for each plant. For the pines, gas exchange was measured on fascicles formed in the previous year, and each fascicle included multiple needles (two for pinyon pine and three for ponderosa pine). Relative humidity and temperature in the cuvette during measurements were close (within 10%) to ambient air outside the cuvette. Measurements were conducted under mostly cloud-free skies, which provided high light intensity (photosynthetically active radiation >600 $\mu\text{mol m}^{-2} \text{s}^{-1}$) without using a lamp. Light intensity for all midday (10:00 am–2:00 pm) measurements was greater than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas light intensity for measurements between 7:00 and 10:00 am and between 2:00 and 4:00 pm was often between 600 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Net photosynthetic rate of individual ponderosa pine leaves saturates at a light intensity of approximately 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Kolb and Robberecht 1996, Bickford et al. 2005). Net photosynthetic rate of whole pinyon pine trees has been reported to saturate at a light intensity of 1,100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Nowak et al. 1999), which strongly suggests saturation of individual leaves at an intensity less than 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. We measured projected area of the leaves contained in the cuvette using AgImage Plus software (version 1.08; Decagon Devices). Leaf-to-air VPD was calculated for each measurement by the LiCor 6400 based on water vapor pressure, leaf temperature, and air temperature in the cuvette. We measured shoot Ψ concurrently with gas exchange using the same procedures described for the study of seasonal and interannual variation. We tested relationships between g_s and Ψ and between g_s and VPD using best-fit regressions on diurnal (hourly) data for each season and species.

We measured volumetric soil water content on the same spring and summer days in 2006 using time domain reflectometry (Robinson et al. 2003). We inserted a 15-cm probe vertically into the soil at the outer edge of the canopy of each sampled tree, recorded three measurements at each of the cardinal directions, and averaged these measurements for each tree. For each species, we used one-way analysis of variance to test for seasonal differences in soil water content.

Xylem Vulnerability to Cavitation

We measured xylem vulnerability to water stress-induced cavitation of roots and shoots of mature, healthy trees of each species sampled at the same site used for measurements of Ψ and leaf gas exchange. Root and shoot segments were sampled from five trees of each species during the summers of 2005 and 2006. The dbh of the sampled trees (mean of 26.7, 21.0, and 23.7 cm for ponderosa pine, pinyon pine, and Utah juniper, respectively) was similar to that of

the trees sampled for the study of seasonal and interannual variation in Ψ .

We excavated root segments from a depth of 15–50 cm at the base of each tree and cut shoot segments from a sunlit location in the middle of the canopy. We selected root and shoot samples containing an approximate 15-cm-long straight section with little branching and a sapwood diameter of 5–15 mm. Following the sampling procedure of Hultine et al. (2006), the segments were cut under water, sealed with a moist paper towel into three black plastic bags, and then transported to the laboratory.

In the laboratory, we removed side branches and then recut the sample ends under water to prevent introduction of additional emboli. The final segment length was approximately 14 cm. At each end, a 1-cm length of bark/root cortex was removed so tubing could be tightly clamped onto the segments. A tubing manifold was fitted at the proximal end of the segments to induce a gravitational gradient pressure head of approximately 5.5 and 10.5 kPa for root and shoot segments, respectively. Because roots have larger diameter tracheids than shoots (Jackson et al. 2000) and therefore greater hydraulic conductivity at a given pressure head, a reduced pressure head was used for roots to avoid disruption of the torus-margo pits (Pittermann et al. 2006). We used distilled and filtered (0.22 μm) water without added ions (e.g., KCl) because of previous reports that KCl has little effect on xylem hydraulic conductance (Boyce et al. 2004) and vulnerability to cavitation (Cochard et al. 2010) in conifers. For each flow rate (Q ; kg s^{-1}) measurement, effluent was collected in vials with cotton wool tared on an electronic balance (10^{-4} g) after flow rate equilibrated. The setup of the tubing manifold was similar to that described by Sperry et al. (1988), except that we measured flow rates of up to three segments at one time.

To remove embolized tracheids and ensure that water was transported through all functional xylem, we originally flushed the segments at 100 kPa as is commonly done with both angiosperm (Pockman and Sperry 2000, Hultine et al. 2006) and gymnosperm (Piñol and Sala 2000) species. However, because the postflush (at 100 kPa) hydraulic conductivity was frequently less than the native (preflush) flow rate, we subsequently reduced the pressure to 15 kPa and flushed the segments for 20–30 minutes, as was used by Sperry et al. (2005) for gymnosperm species with torus-margo pits. The low flush pressure reduced the likelihood of a sudden disequilibrium of conduit pressure from occurring, leading to membrane aspiration of the torus over the pit aperture (Domec et al. 2007, Hacke and Jansen 2009) and preventing the torus from becoming stuck in an aspirated position (Hacke et al. 2004), which was a likely cause of the reduced postflush conductivity.

We estimated xylem vulnerability curves for ponderosa and pinyon pines using the centrifuge method (Pockman et al. 1995, Alder et al. 1997). For juniper, we used the centrifuge method for pressures less than 6.5 MPa and the air-injection method (Sperry and Saliendra 1994) for pressures of 6.5 MPa and greater because 6.5 MPa was the maximum pressure induced by our centrifuge and rotor. All juniper samples had less than 95% loss of conductivity at pressures less than 6.5 MPa; thus, the air-injection method

was required to produce complete vulnerability curves. Both methods have been shown to produce similar results (Pockman et al. 1995, Linton and Nobel 1999).

For the air-injection method, we made several notches after flushing with a needle 0.5–1.0 mm deep and 3–5 cm apart along the segment surface to directly expose the xylem to air and decrease the time to pressurize segments (Sperry and Saliendra 1994). The segments were then inserted through a double-ended pressure sleeve (Sperry and Saliendra 1994, Pockman and Sperry 2000) and pressurized at 0.1 MPa for 20 minutes to allow the air to fill any potentially open tracheids (Hultine et al. 2006), which excluded them from subsequent measurements of xylem hydraulic conductivity (K_x ; $\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$). K_x is the hydraulic conductivity ($K_h = Q/\Delta\Psi/\Delta x$; $\text{kg m s}^{-1} \text{MPa}^{-1}$) or flow rate (Q ; kg s^{-1}) per pressure head gradient ($\Delta\Psi$; MPa) per segment length (Δx ; m), standardized by the cross-sectional sapwood area (A ; m^2) of the segment ($K_x = K_h/A$) (Sperry et al. 2002). The pressure within the sleeve was returned to atmospheric pressure (Pockman and Sperry 2000, Hultine et al. 2006), and the flow rate through the segment was equilibrated for at least 10 minutes before initial measurement of conductivity ($K_{x,0.1}$). After the initial measurement, the process was repeated at progressively higher pressures ($K_{x,p}$) in increments of 0.5 or 1.0 MPa. The procedure continued until $\geq 95\%$ loss of conductivity (PLC) occurred, where

$$\text{PLC} = 100 \left(\frac{1 - K_{x,p}}{K_{x,0.1}} \right).$$

For the centrifuge method, we removed the segment from the tubing after flushing and secured it in the center of a centrifuge rotor (Sorvall Superspeed RC₂B). Up to three segments were spun at one time. We used the immersed method of Alder et al. (1997) in which the segment ends were placed in an “L” shape Plexiglas reservoir cup containing water at the outer rim of the centrifuge, which prevented open-ended conduits from losing water and artificially increasing the amount of embolism. After the postflush K_x measurement, the segments were initially spun at 244 radians s^{-1} (2,330 rpm) to induce a xylem tension of 0.1 MPa for 5 minutes; then the segment was reattached to the tubing manifold, and the flow was allowed to equilibrate for at least 10 minutes before measurement of $K_{x,0.1}$. The procedure was repeated at progressively greater tensions until at least 95% loss of K_x occurred. We calculated the average tension induced in the xylem from the equation $2/3P_{\text{xylem}}$ (Alder et al. 1997), where $P_{\text{xylem}} = -0.5\rho\omega^2r_{\text{max}}^2$ (dynes cm^{-2}) (Briggs 1950), ρ is the density of water (g cm^{-3}), ω is the angular velocity (radians s^{-1}), and r_{max} is the radius of the segment from the axis to the meniscus in the cup.

We created xylem vulnerability curves for shoots and roots of each species by plotting mean percentage loss of conductivity (PLC) against xylem Ψ . We estimated the xylem Ψ that induced 50 PLC (Ψ_{50}) by fitting the PLC and Ψ data to a modified version of the Pammenter and Van der Willigen (1998) sigmoidal equation,

$$\text{PLC} = \theta_1 + \frac{\theta_2 - \theta_1}{1 + e^{\theta_3(\Psi - \theta_4)}},$$

where θ_1 adjusts the x -intercept close to zero, θ_2 adjusts the y -intercept close to 100, θ_3 is the slope of the curve at the inflection point, and θ_4 is the Ψ value at the inflection point, which is approximately equal to Ψ_{50} (Pittermann et al. 2006). We used the modified four-parameter equation because it fit the data better than the two-parameter Pammenter and Van der Willigen (1998) equation; both equations produced similar Ψ_{50} (within 0.2 MPa) for all tissues and species. This Ψ_{50} is similar to the mean cavitation pressure used in other studies (e.g., Linton et al. 1998, Hacke et al. 2006). The SE of Ψ_{50} was estimated using SAS JMP 7.0 software as the SE of θ_4 .

Results

Seasonal and Interannual Variation in Water Potential

Less soil water was available to all species in summer than in spring of both years. The Ψ_{PD} was significantly lower (i.e., more negative) in summer than in spring for all species in both 2005 and 2006 (Table 1). Soil water content was significantly ($P < 0.05$) lower in summer than in spring for each species. The mean (SE) soil volumetric water content for pinyon pine, ponderosa pine, and juniper in spring was 10.4 (0.3), 9.8 (1.0), and 9.8 (0.6), respectively, and in summer was 8.5 (0.7), 6.4 (1.5), and 7.4 (0.6).

With regard to annual variation, Ψ_{PD} of all species was significantly lower in 2006 than in 2005 for both spring and summer (Table 1). The Ψ_{MD} of pinyon pine was similar in 2005 and 2006 for both spring and summer. For ponderosa pine and juniper, Ψ_{MD} was similar in 2005 and 2006 in spring but in summer was significantly lower in 2006 than 2005 (Table 1).

There was no relationship between seasonal/annual variation in Ψ_{MD} and Ψ_{PD} for ponderosa and pinyon pines (Figure 1A). In contrast, Ψ_{MD} for juniper was positively and strongly ($P = 0.015$) related to Ψ_{PD} (Figure 1A). The difference between Ψ_{MD} and Ψ_{PD} ($\Delta\Psi_{MD-PD}$) decreased significantly ($P \leq 0.05$) for all species as Ψ_{PD} became more negative (Figure 1B). The relationship between Ψ_{PD} and Ψ_{MD-PD} was linear for ponderosa and pinyon pines and curvilinear for juniper (Figure 1B). Both ponderosa and pinyon pines had little difference between Ψ_{PD} and Ψ_{MD} when Ψ_{PD} was more negative than -1.5 MPa, whereas this

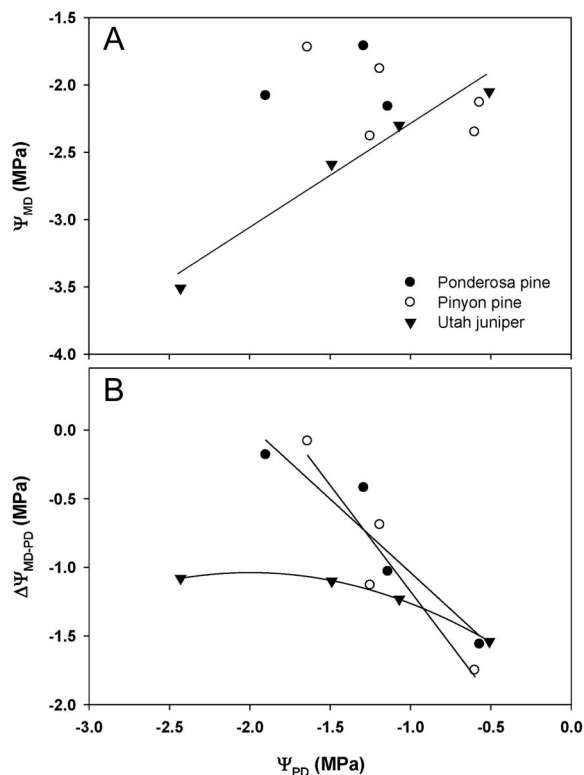


Figure 1. Relationships between mean Ψ_{PD} and Ψ_{MD} (A) and $\Delta\Psi_{MD-PD}$ (B) of ponderosa pine, pinyon pine, and Utah juniper shoots pooled over spring and summer measurements in 2005 and 2006. In A, the relationship is significant and linear for Utah juniper ($r^2 = 0.97$, $P = 0.01$, line shown) but not significant for ponderosa pine ($r^2 = 0.03$, $P = 0.81$) or pinyon pine ($r^2 = 0.50$, $P = 0.29$). In B, the relationship is significant for all species, curvilinear for Utah juniper ($r^2 = 0.99$, $P = 0.01$), and linear for ponderosa pine ($r^2 = 0.89$, $P = 0.05$) and pinyon pine ($r^2 = 0.89$, $P = 0.05$) based on best-fit regressions. Sample size for all means was five plants.

difference for juniper ranged between -1.5 MPa when Ψ_{PD} was -0.6 MPa to -1.0 MPa when Ψ_{PD} was -2.5 MPa.

Diurnal Variation in Water Potential and Leaf Gas Exchange

The Ψ of all species in spring 2006 decreased from early morning values of approximately -1 MPa to midday values between -2.1 and -2.4 MPa and then increased to late

Table 1. Ψ_{PD} and Ψ_{MD} shoot water potentials in spring and summer 2005 and 2006 of pinyon pine, ponderosa pine, and Utah juniper.

Species	2005				2006			
	Spring		Summer		Spring		Summer	
	Ψ_{PD}	Ψ_{MD}	Ψ_{PD}	Ψ_{MD}	Ψ_{PD}	Ψ_{MD}	Ψ_{PD}	Ψ_{MD}
.....(MPa).....								
Pinyon pine	-0.60A (0.05)	-2.35b (0.12)	-1.19B (0.03)	-1.88a (0.07)	-1.25B (0.11)	-2.38b (0.04)	-1.64 C (0.08)	-1.72a (0.04)
Ponderosa pine	-0.57A (0.06)	-2.13b (0.12)	-1.29B (0.16)	-1.71a (0.06)	-1.14B (0.04)	-2.16b (0.06)	-1.90 C (0.06)	-2.08b (0.08)
Utah juniper	-0.51A (0.03)	-2.05a (0.10)	-1.49B (0.13)	-2.59b (0.07)	-1.07B (0.17)	-2.30ab (0.04)	-2.43 C (0.26)	-3.51 c (0.17)

Data are presented as mean (SE). Different letters within rows indicate significant differences among Ψ_{PD} (capital) and Ψ_{MD} (lowercase) within a species based on two-way analysis of variance of season and year followed by Tukey mean comparisons ($P \leq 0.05$). Sample size for all means was five plants.

afternoon values between -1.7 to -2.0 MPa (Figure 2A). Variation in Ψ_{PD} among species was more pronounced in summer than in spring 2006. In summer (Figure 2B), Ψ_{PD} was lower for juniper (-2.5 MPa) than for either pine (-1.5 to -1.8 MPa). The Ψ of both pines in summer changed less than 0.1 MPa during the day, whereas Ψ of juniper decreased during the day by about 0.8 MPa (Figure 2B).

Daily variation in g_s differed among species within a season and between seasons within a species in 2006. In spring, g_s of all species peaked in the early morning and then declined during midday (Figure 2C). In summer, g_s of both pines peaked in early morning, decreased to near zero through midafternoon, and increased slightly in the late afternoon (Figure 2D). Juniper had a pattern of variation in g_s in summer similar to that of the pines, except that g_s stayed above zero during midafternoon. Temporal variation in P_n (Figure 2E and F) was similar to variation in g_s (Figure 2C and D), and P_n was positively ($r \geq 0.70$) and significantly ($P \leq 0.006$) correlated with g_s for all species and seasons.

In spring 2006, g_s was negatively and linearly related to VPD for ponderosa pine ($P < 0.0001$), pinyon pine ($P = 0.0002$), and juniper ($P = 0.0156$) (Figure 3). The slope for the linear regression of g_s on VPD during spring was greatest for ponderosa pine (-21.4 ± 4.7 $\text{mmol m}^{-2} \text{s}^{-1} \text{kPa}^{-1}$; mean $\pm 95\%$ confidence interval), followed by similar slopes of pinyon pine (-14.9 ± 6.7) and

juniper (-14.2 ± 11.1), but overlap of the confidence intervals indicates that these differences were not statistically significant. In summer, g_s of juniper also was linearly related to VPD ($P = 0.044$), whereas for ponderosa and pinyon pines the relationship between g_s and VPD was curvilinear ($P < 0.0001$ and $P = 0.0013$, respectively) (Figure 3). The g_s of ponderosa and pinyon pines in summer was approximately 0 when VPD was 3.5 kPa or greater, whereas the g_s of juniper was approximately 20 $\text{mmol m}^{-2} \text{s}^{-1}$ (Figure 3).

The only significant relationship between g_s and Ψ occurred for juniper in summer ($P < 0.0001$, $r^2 = 0.94$). The slope ($\pm 95\%$ confidence interval) for the linear regression between juniper g_s and Ψ in the summer was $27.2 (\pm 8.7)$ $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ (data not shown).

Xylem Vulnerability to Cavitation

Xylem vulnerability to cavitation was much lower for juniper than for ponderosa and pinyon pines for both shoots and roots. For shoots, PLC of juniper did not increase until Ψ was more negative than -4 MPa, and 100 PLC occurred at Ψ of approximately -12 MPa (Figure 4A). In contrast, PLC of both ponderosa and pinyon pine shoots increased sharply at Ψ of -2 MPa and reached 100% at Ψ of approximately -6 MPa.

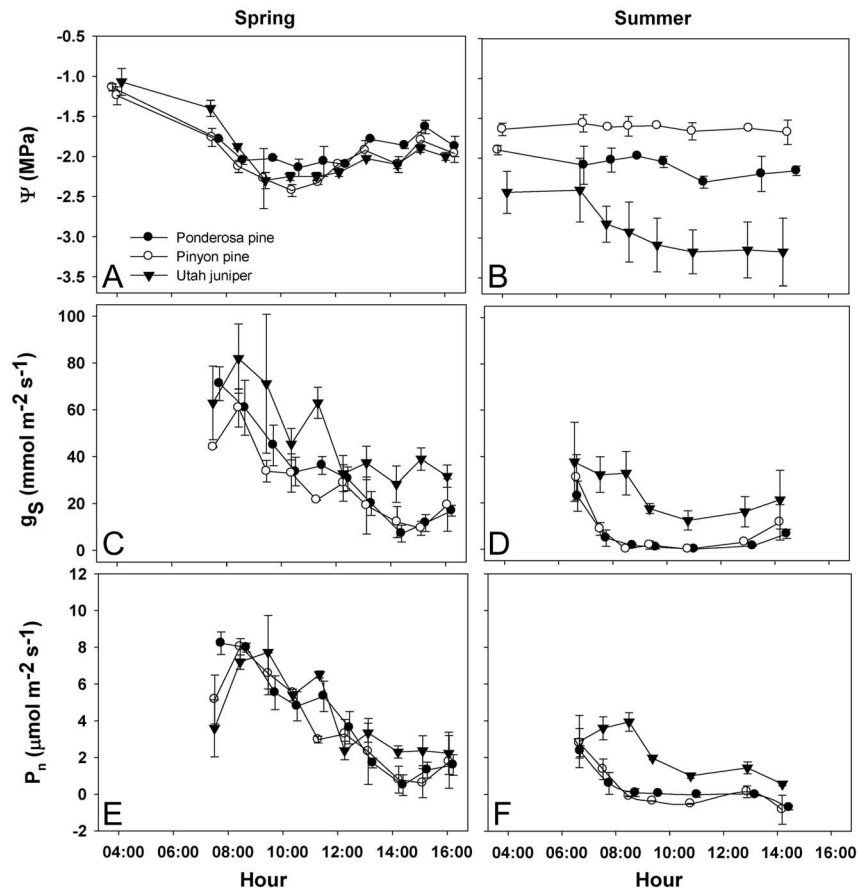


Figure 2. Diurnal variation in mean (± 1 SE) shoot water potential (Ψ ; A and B), stomatal conductance to water vapor (g_s ; C and D), and net photosynthetic rate (P_n ; E and F) of ponderosa pine, pinyon pine, and Utah juniper in spring (A, C, and E) and summer (B, D, and F) 2006. Sample size for all means was two plants. g_s and P_n are expressed on a projected leaf area basis.

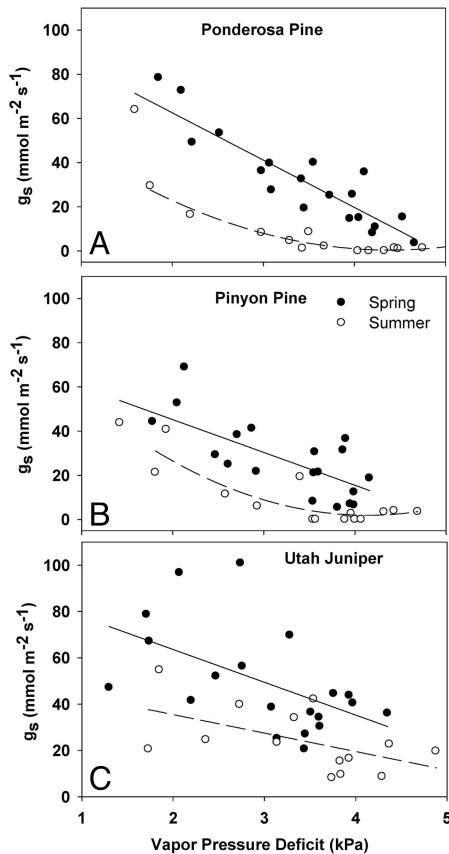


Figure 3. g_s by VPD during spring (● and solid line) and summer (○ and dashed line) in 2006 of ponderosa pine (A), pinyon pine (B), and Utah juniper (C). Lines show the best fit regressions, which were significant for all relationships (ponderosa pine spring $r^2 = 0.83$, $P < 0.0001$, summer $r^2 = 0.95$, $P < 0.0001$; pinyon pine spring $r^2 = 0.55$, $P = 0.0002$, summer $r^2 = 0.70$, $P = 0.0031$; Utah juniper spring $r^2 = 0.28$, $P = 0.0156$, summer $r^2 = 0.30$, $P < 0.0444$). g_s is expressed on a projected leaf area basis.

Confidence intervals for Ψ_{50} calculated from means and standard errors in Table 2 show that shoot vulnerability to cavitation was slightly greater for pinyon pine (−2.6 to −2.9 MPa) than for ponderosa pine (−3.3 to −3.6 MPa) and was lowest for juniper (−8.1 to −8.4 MPa).

For roots (Figure 4B), PLC of juniper increased linearly for changes in Ψ between 0 and −5 MPa and increased sharply for Ψ more negative than −5 MPa. The PLC of juniper roots reached 100% at Ψ of −8 MPa. The PLC of ponderosa and pinyon pine roots also increased linearly as Ψ became more negative and reached 100% when Ψ was approximately −3 MPa. Confidence intervals of Ψ_{50} calculated from the means and SEs in Table 2 showed that root vulnerability to cavitation was similar for pinyon pine (−1.4 to −1.9 MPa) and ponderosa pine (−1.8 to −2.2 MPa) and was lowest for juniper (−5.4 to −7.1 MPa). Maximum specific xylem hydraulic conductivity was significantly ($P \leq 0.05$) greater for roots than for shoots for all species (Table 2).

Discussion

We report the first direct comparison of water relations characteristics, including xylem vulnerability to cavitation

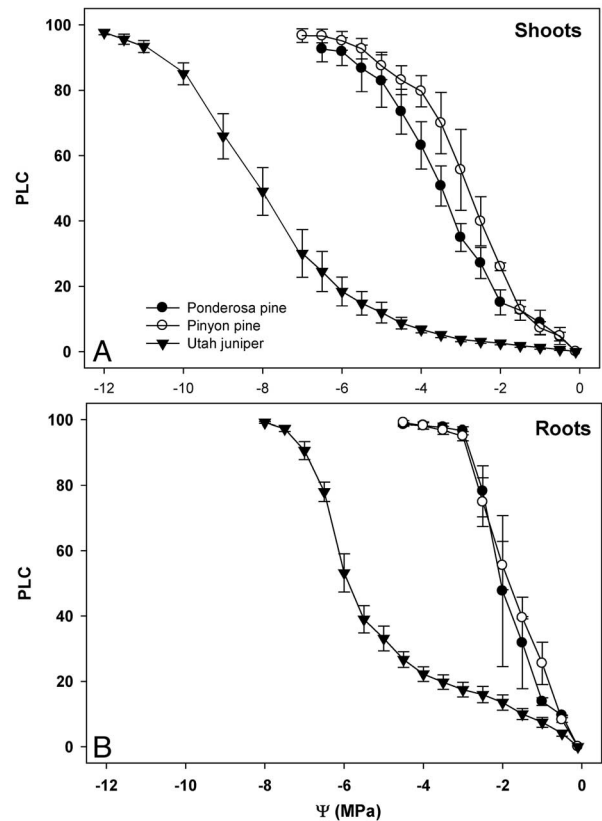


Figure 4. Mean (± 1 SE) percentage loss of hydraulic conductivity (PLC) versus Ψ for ponderosa pine, pinyon pine, and Utah juniper shoots (A) and roots (B). Sample size for all means was five plants. The centrifuge method was used for all measurements of ponderosa pine and pinyon pine and measurements of Utah juniper at Ψ between 0 and −6.5 MPa. The air-injection method was used for measurements of Utah juniper at Ψ more negative than −6.5 MPa.

of shoots and roots, among ponderosa pine, pinyon pine, and Utah juniper growing at the same site, which reduced the influence of many potential environmental effects on inherent species differences. This approach, however, did not control for potential differences among species in all factors, such as rooting depth and microsite-level variation in soil. Our prediction that juniper would be less vulnerable to water stress-induced xylem cavitation and show less isohydric behavior than ponderosa and pinyon pines was supported. Compared with both pines, juniper had lower xylem vulnerability to cavitation of shoots and roots (Table 2; Figure 4), larger seasonal (Table 1) and diurnal variations in shoot Ψ (Figure 2), a stronger relationship between Ψ_{MD} and Ψ_{PD} (Figure 1), and greater maintenance of midday g_s and P_n during drought (Figure 2). In contrast, both pines exhibited muted seasonal and diurnal variation in Ψ during drought, no relationship between Ψ_{MD} and Ψ_{PD} , and complete midday stomatal closure and 0 P_n during drought. Our finding of greater vulnerability of ponderosa and pinyon pines to xylem cavitation than Utah juniper is consistent with previously reported differences between the Pinaceae and Cupressaceae families for data pooled over sites and studies (Martínez-Vilalta et al. 2004). Our finding of stronger isohydric behavior of pinyon pine than Utah juniper is

Table 2. Xylem Ψ_{50} and maximum specific xylem K_x of ponderosa pine, pinyon pine, and Utah juniper shoots and roots.

Species	Shoot Ψ_{50}	Root Ψ_{50}	Shoot K_x	Root K_x
(MPa)(kg s ⁻¹ m ⁻¹ MPa ⁻¹)	
Pinyon pine	-2.71 (0.05)	-1.69 (0.09)	0.2 (0.02)	8.4 (1.7)
Ponderosa pine	-3.42 (0.06)	-1.98 (0.07)	0.4 (0.06)	6.7 (1.5)
Utah juniper	-8.24 (0.06)	-6.23 (0.34)	0.3 (0.03)	4.4 (0.70)

Data are presented as mean (SE). Sample size for all means was five plants.

consistent with previous reports (Linton et al. 1998, Williams and Ehleringer 2000, West et al. 2007).

Stomatal regulation of transpiration and xylem water potential has been described by two categories (Tardieu and Simmonneau 1998): isohydric (strong regulation) and anisohydric (weak regulation). Junipers often have been described as being more anisohydric than pinyon and ponderosa pines (McDowell et al. 2008, Koepke et al. 2010, McDowell 2011). Our results support previous descriptions with the caveat that the hydraulic differences between Utah juniper and the pines occur along a gradient of isohydry, rather than being in distinctly different categories. Utah juniper was less isohydric than ponderosa and pinyon pines in our study, but it did partly regulate water loss during drought. For example, the slope of the temporal relationship between Ψ_{MD} and Ψ_{PD} for juniper in Figure 1A was 0.78, indicating that each 1 MPa decrease in Ψ_{PD} was accompanied by a 0.78 MPa decrease in Ψ_{MD} . An indirect measure of stomatal regulation, the relationship between $\Delta\Psi_{MD-PD}$ and Ψ_{PD} , also suggested weaker regulation for juniper than for the pines (Figure 1B). This interpretation is consistent with our direct measurements of the response of g_s to drought and VPD, in which juniper's responses were more muted than those of the pines. Juniper also was the only species that had a significant relationship between g_s and shoot Ψ , suggesting direct hydraulic control of the stomatal aperture (Buckley 2005). The lack of a relationship between g_s and shoot Ψ for ponderosa and pinyon pines in our study may have resulted from the narrow range in Ψ included in our daytime measurements (-1 to -2 MPa), because this relationship is most pronounced at Ψ between 0 and -1 MPa for those species (e.g., Barnes 1986, Kolb and Stone 2000). This lack of relationship for the pines also might be due to regulation of g_s by chemical signals, such as abscisic acid (e.g., Sturm et al. 1998, Perks et al. 2002).

Water relations were surprisingly similar for ponderosa pine and pinyon pine in our study. Because pinyon pine is presumed to be more drought resistant than ponderosa pine based on its greater abundance in low-elevation dry environments (Brown 1982, Burns and Honkala 1990, Niinemets and Valladares 2006), we expected pinyon pine to have lower xylem vulnerability to cavitation and less pronounced isohydric behavior than ponderosa pine. Inconsistent with our expectation, pinyon pine vulnerability to cavitation was either slightly greater than (shoots) or similar to (roots) that of ponderosa pine (Table 2; Figure 4), and seasonal and interannual variation in shoot Ψ (Figure 1; Table 1) and diurnal variation of g_s and P_n during drought and in response to VPD (Figures 2 and 3) were similar for the two species. Our finding of slightly greater shoot vulnerability to water stress-induced cavitation for pinyon pine ($\Psi_{50} = -2.7$) than ponderosa pine (Ψ_{50}

$= -3.4$) differs from a recent comparison between ponderosa pine sampled in Montana and pinyon pine sampled in Utah in which shoot Ψ_{50} of both species was approximately -4 MPa (Delzon et al. 2010) and from an earlier compilation over studies and locations (Martínez-Vilalta et al. 2004) that reported greater vulnerability of ponderosa pine (Ψ_{50} range of -2.6 to -3.4 MPa over studies) than pinyon pine (Ψ_{50} mean = -4.5 MPa for one study). Our finding of similar root Ψ_{50} for these species, however, is consistent with a report of similar percent mortality of ponderosa pine and pinyon pine during severe drought at ecotonal sites in northern Arizona where they co-occurred (Koepke et al. 2010). We suggest that the presumed greater drought resistance of pinyon pine than ponderosa pine in the southwestern United States cannot be explained adequately by xylem vulnerability to cavitation or stomatal regulation of water loss. Rather, differences between these species in other characteristics of water use, such as leaf area/sapwood area ratio (Martínez-Vilalta et al. 2004) and total leaf area, probably are more important. For example, the lower stature and smaller canopy of pinyon pine than ponderosa pine (Burns and Honkala 1990) strongly suggest less whole-plant water use by pinyon pine for survival. Alternatively, it is possible that the greater abundance of pinyon pine than ponderosa pine at hot, dry sites is due to traits other than drought resistance, such as temperature sensitivity.

Our finding of greater vulnerability to water stress-induced cavitation of roots than shoots is consistent with previous reports for ponderosa pine (Stout and Sala 2003, Domec et al. 2009) and pinyon pine (Linton et al. 1998), but not with all reports for Utah juniper. Similar vulnerability to cavitation was reported for shoots and roots of Utah juniper sampled in northern Utah (Linton et al. 1998, Pittermann et al. 2006) and Arizona (Willson et al. 2008), whereas, similar to our results, roots were more vulnerable than shoots in samples collected in southern Utah (Pittermann et al. 2006). Our finding of greater cavitation vulnerability of roots than shoots for Utah juniper is supported by greater maximum hydraulic conductivity of roots than shoots (Table 2), consistent with most reports for trees (Sperry and Saliendra 1994, Alder et al. 1996, Sperry and Ikeda 1997, Jackson et al. 2000, Sperry and Hacke 2002, Stout and Sala 2003, McElrone et al. 2004, Hultine et al. 2006). Differences in xylem vulnerability to cavitation between roots and shoots in gymnosperms have been attributed to differences in the ratio of the torus to the pit aperture, thickness of the torus, depth of the pit chamber (Choat and Pittermann 2009, Hacke and Jansen 2009), hydraulic diameter, wood density, and tracheid thickness/span ratio (Domec et al. 2009).

To more broadly compare our estimates of xylem vulnerability to water stress-induced cavitation with previous reports, we calculated 95% confidence intervals of shoot

and root Ψ_{50} measured in mature plants of ponderosa pine, pinyon pine, and Utah juniper in our and previous studies (Table 3). The estimates include samples collected over different years and sites from Arizona and Utah for pinyon pine and Utah juniper and from Arizona, California, Montana, and Oregon for ponderosa pine. Estimates were produced by the air injection and centrifuge techniques for all species; the dehydration technique also was used for Utah juniper in one study. There are more estimates for shoots than roots and for ponderosa pine and Utah juniper than for pinyon pine despite recent interest in mechanisms of drought-induced mortality of pinyon pine (e.g., McDowell et al. 2008, Adams et al. 2009, Breshears et al. 2009).

Based on Table 3, we caution against using xylem vulnerability curves or estimates of Ψ_{50} developed for samples from a specific geographic location to broadly estimate hydraulic behavior of species with wide geographic ranges. Unusually low and high Ψ_{50} have been reported for all species. For example, for pinyon pine our estimates of shoot and root Ψ_{50} for samples from a high-elevation northern Arizona population are significantly higher than estimates for a low-elevation Arizona population (Koepke 2011) and both estimates from Utah (Linton et al. 1998, Delzon et al. 2010). For ponderosa pine, our estimate of shoot Ψ_{50} for a low-elevation northern Arizona population is similar to estimates for a high-elevation Arizona population (Koepke 2011), the eastern Sierra Nevada Mountains in California (Maherali and DeLucia 2000), and one estimate from Montana (Stout and Sala 2003), whereas other estimates from Montana are significantly higher (Piñol and Sala 2000) or lower (Delzon et al. 2010). Root Ψ_{50} of ponderosa pine also varies significantly between Montana and Arizona studies, with lower vulnerability for Arizona samples. Shoot and root Ψ_{50} are more consistent over different studies of Utah juniper, but unusually high (Linton et al. 1998) and low (Willson et al. 2008) values have been reported (Table 3). Consistent with previous reports that the air injection and

centrifuge methods produce similar xylem vulnerability curves and estimates of Ψ_{50} (Pockman et al. 1995, Linton and Nobel 1999), we found no consistent trend in Ψ_{50} among methods for the studies we reviewed, but the sample size is small. Another potential explanation for the differences in Table 3 is intraspecific genetic variation in xylem vulnerability to cavitation, which has been shown in common garden comparisons for some (Kavanagh et al. 1999, Kolb and Sperry 1999, Cochard et al. 2007) but not all (Lamy et al. 2011) woody species. Clearly, more information is needed on sources of variation in xylem vulnerability to cavitation, especially for mature trees.

Our results provide insight into the response of ponderosa pine, pinyon pine, and Utah juniper to the increase in temperature and drought predicted in the future for the southwestern United States (e.g., Seager et al. 2007, Overpeck and Udall 2010). Strong stomatal control of transpiration and xylem water potential by the pines reduces xylem tensions during drought to prevent massive hydraulic failure. By avoiding hydraulic failure, however, prolonged stomatal closure during drought reduces photosynthesis (e.g., Flexas et al. 2006, Adams et al. 2009, Atkin and Macherel 2009, Breshears et al. 2009), which could reduce tree carbon reserves. Plant mortality may follow because of metabolic failure (McDowell et al. 2008, Adams et al. 2009, McDowell and Sevanto 2010), inadequate transport of carbohydrates to sinks (Sala et al. 2010), or inadequate supply of carbon for defenses against lethal biotic agents, such as bark beetles (McDowell et al. 2008, Raffa et al. 2008, Kane and Kolb 2010). Utah juniper experiences high xylem tensions during drought with little apparent cavitation and still maintains positive g_s and P_n , thereby maintaining carbon uptake (Linton et al. 1998, West et al. 2007, McDowell et al. 2008). However, extreme water stress, such as the Ψ_{PD} of -6.6 MPa and Ψ_{MD} of -6.9 MPa reported for Utah juniper in 2003 in southern Utah (West et al. 2007), may substantially reduce hydraulic conductivity, especially for roots, and

Table 3. Confidence intervals (95%) of xylem Ψ_{50} of ponderosa pine, pinyon pine, and Utah juniper shoots and roots estimated from means, SEs, and sample sizes in our (present) and previous studies.

Species	Study	Sample location	Technique	Shoot Ψ_{50}	Root Ψ_{50}
			(MPa).....	
Pinyon pine	Present	Arizona: high elevation	C	-2.6 to -2.9	-1.4 to -1.9
	Koepke 2011	Arizona: low elevation	C	-3.6 to -4.1	-3.0 to -3.1
	Linton et al. 1998	Utah	AI	-4.0 to -5.0	-2.5 to -3.5
	Delzon et al. 2010	Utah	C	-3.7 to -4.3	
Ponderosa pine	Present	Arizona: low elevation	C	-3.3 to -3.6	-1.8 to -2.2
	Koepke 2011	Arizona: high elevation	C	-3.5 to -3.7	-2.0 to -2.1
	Maherali and DeLucia 2000	California	AI	-1.9 to -3.3	
	Piñol and Sala 2000	Montana	AI	-2.4 to -3.0	
	Stout and Sala 2003	Montana	AI	-2.3 to -3.9	-0.6 to -1.4
	Delzon et al. 2010	Montana	C	-3.7 to -4.3	
	Domec et al. 2009	Oregon	AI	-4.0 to -5.6	-1.3 to -2.5
Utah juniper	Present	Arizona	AI/C	-8.1 to -8.4	-5.4 to -7.1
	Willson and Jackson 2006	Arizona	D	-7.3 to -8.7	
	Willson et al. 2008	Arizona	C	Mean = -11.9^a	Mean = -10.4^a
	Linton et al. 1998	Utah	AI	-5.8 to -7.4	-3.8 to -8.2
	Pittermann et al. 2006	Utah	C	Mean = -7.8^a	Mean = -7.0^a
	Delzon et al. 2010	Utah	C	-8.2 to -8.8	

The location of the sampled population and technique for measuring xylem vulnerability to cavitation (AI, air injection; C, centrifuge; D, dehydration) are listed for each study.

^a Confidence interval could not be calculated because SE is not reported.

probably causes partial canopy dieback of surviving plants (Koepeke et al. 2010) via hydraulic failure. Areas in need of further investigation regarding drought resistance mechanisms of isohydric and anisohydric species include the potential adaptive role of cavitation in releasing stored water from stem capacitance to the canopy and the magnitude and frequency of refilling or repair of xylem embolisms (Sperry et al. 2008, Meinzer et al. 2009).

In summary, our study of three common trees growing at the same ecotonal forest-woodland site in the drought-prone southwestern United States produced six important findings. First, estimates of xylem vulnerability to cavitation vary over different studies of pinyon and ponderosa pines but are more consistent for Utah juniper. Second, roots of all species we studied were more vulnerable to water stress-induced cavitation than shoots and probably are important in drought resistance. Third, shoot and root xylem of Utah juniper was less vulnerable to water stress-induced cavitation than ponderosa and pinyon pines, consistent with the greater drought resistance of Utah juniper. Fourth, xylem vulnerability to cavitation does not explain the greater drought resistance of pinyon pine than ponderosa pine. Fifth, Utah juniper shoots partly regulated water potential during drought via stomatal closure, but regulation was weaker than that for ponderosa and pinyon pine shoots, which had similar leaf-level water relations and gas exchange responses to drought. Sixth, Utah juniper's greater maintenance of stomatal conductance and photosynthesis under hot, dry conditions than co-occurring ponderosa and pinyon pines suggests enhanced performance of juniper over the pines in the climate forecasted for the future in the southwestern United States.

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