

Differential summer water use by *Pinus edulis* and *Juniperus osteosperma* reflects contrasting hydraulic characteristics

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Summary Previous studies of pinyon–juniper woodlands show that *Pinus edulis* Engelm. makes better use of soil water from summer precipitation pulses than does co-occurring *Juniperus osteosperma* (Torr.) Little. To investigate the basis of this difference, we examined seasonal variation in cavitation and hydraulic conductance. *Pinus edulis* remained isohydric over the growing season. Minimum water potentials never fell below -2.3 MPa, and the extent of xylem cavitation remained near constant during the dry season. In contrast, *J. osteosperma* was anisohydric, reaching water potentials as low as -6.9 MPa, and experiencing progressively greater xylem cavitation as the dry season progressed despite having more cavitation-resistant xylem than *P. edulis*. We conducted an irrigation experiment to observe the responses of the study species to a summer pulse of water. Although sap flow increased in both species in response to the 25-mm irrigation pulse, only *J. osteosperma* responded to the 10-mm pulse. This was inconsistent with the response of *P. edulis* to light rain events and may have been due to a difference in the distribution of irrigation water and rain water between the under- and between-canopy areas. Whole-plant conductance increased following the 25-mm irrigation in *P. edulis* but remained constant in *J. osteosperma*. We hypothesized that this difference was caused, in part, by differential refilling of embolized xylem. Area specific hydraulic conductivity was 66% higher in roots of irrigated *P. edulis* trees relative to roots of control trees 3 days after the 25-mm irrigation ($t = 2.14$, $P = 0.02$, $df = 16$). There was no change in hydraulic conductivity of the roots of *J. osteosperma* or in the stems of either species. Our results indicate that the response to an irrigation pulse in *P. edulis* depended on cavitation avoidance in stems and the reversal of cavitation in roots, resulting in increased whole-plant conductance and water uptake. In contrast, *J. osteosperma* failed to exploit light summer rain events but was able to extract deep soil water at low water potentials.

Keywords: cavitation, hydraulic conductivity, irrigation, moisture pulse, rain event.

Introduction

Plants in arid and semi-arid areas of the intermountain region of North America are reliant on summer precipitation (Ehleringer et al. 1991, 1999). Summer rains occur in short pulses that wet only the uppermost soil layer (Noy-Meir 1973, Loik et al. 2004, Schwinning et al. 2004). To make use of this water source before it is lost through evaporation, plants must have absorbing roots near the soil surface and high whole-plant conductance.

Between summer rain pulses, superficial soil layers are hot and dry, which can cause root desiccation and root xylem cavitation (Sperry et al. 1998). Plants thus face the challenge of limiting the risk of xylem cavitation, while maintaining high xylem conductance (Tyree et al. 1994, Hacke et al. 2006, Pittermann et al. 2006).

Previous studies showed that *Pinus edulis* Engelm. uses summer precipitation to a greater extent than co-occurring *Juniperus osteosperma* (Torr.) Little (Flanagan et al. 1992, Evans and Ehleringer 1994, Williams and Ehleringer 2000). In pinyon–juniper woodlands in southern Utah, both *P. edulis* and *J. osteosperma* use summer precipitation during above-average rainfall years (West 2006). However, only *P. edulis* uses small precipitation events during dry years (West et al. 2007). In this study we investigated possible mechanisms underlying the difference between these species in their response to rain pulses.

A variety of studies have shown that pinyons and junipers differ in their water relations (Barnes and Cunningham 1987, DeLucia and Schlesinger 1991, Lajtha and Barnes 1991, Lajtha and Getz 1993, Linton et al. 1998, Nowak et al. 1999, Williams and Ehleringer 2000). *Pinus edulis* has higher rates of transpiration than *J. osteosperma* when water availability is high, but is more sensitive to drought and ceases transpiration at shoot water potentials of about -2 MPa versus about -4.5 MPa in *J. osteosperma* (West 2006). *Pinus edulis* is more vulnerable to cavitation than *J. osteosperma* (Linton et al. 1998) and exercises stomatal control to regulate water potential, with stomatal conductance and assimilation declining to zero at about -2 MPa versus -4.5 MPa in *J. osteosperma*.

(Lajtha and Barnes 1991, Williams and Ehleringer 2000). These differences in water relations result, in part, in spatial differences in distribution. Pinyons dominate more mesic sites within pinyon–juniper woodlands, whereas junipers dominate the drier microsites (Tausch et al. 1981, West 1999, Nowak et al. 1999, Martens et al. 2001, Mueller et al. 2005).

Despite being less tolerant to drought, *P. edulis* responds to small precipitation pulses during the driest time of the year, whereas *J. osteosperma* is less responsive to pulses (West et al. 2007), indicating that responsiveness to rain pulses is not necessarily a function of drought tolerance. It appears that *J. osteosperma* is more deeply rooted than *P. edulis* (West et al. 2007), which may account for its lack of response to small summer precipitation pulses. However, this does not explain how *P. edulis* is able to take up superficial soil water following brief summer rain events after a period of drought.

To examine possible mechanisms underlying rain pulse responses, we followed two approaches. First, we modeled naturally occurring seasonal variations in cavitation and plant hydraulic conductance of *P. edulis* and *J. osteosperma* by measuring sap flux, water potential and vulnerability to cavitation. We hypothesized that isohydric control of water potential in *P. edulis* prevents cavitation during drought, thus allowing water uptake following summer rain events. In contrast, we postulated that the anisohydric control of water potential in *J. osteosperma* results in greater cavitation during dry periods, thus limiting the ability of this species to respond to precipitation pulses. Second, we conducted an irrigation experiment to test our hypothesis that both *P. edulis* and *J. osteosperma* respond to heavy irrigation, but only *P. edulis* responds to light irrigation, and that the response of *P. edulis* is facilitated by the refilling of embolized root xylem.

Methods

Site description

The study area was a mature pinyon–juniper woodland near Canyonlands National Park (38.56° N, 109.82° W) in southern Utah. The area is located at 1800 m a.s.l. and is almost flat. Within this area, one site was selected for long-term monitoring and another for manipulation of soil water content through irrigation. The sites are located within 500 m of each other, and the following description applies to both. Soils are Rizno series fine sandy loam, interspersed with rock outcrops (Grand County Soil Survey, Map 52). Soils are shallow, with depth to sandstone ranging from 0 to 50 cm. Thirty-year climate data from The Neck, Canyonlands National Park, about 11 km from our site, indicate a mean annual precipitation of 232 mm, a mean annual air temperature of 11.5 °C and a mean frost-free period of 150–200 days (1971–2000, Western Regional Climate Center). Woody plants at this site include *Pinus edulis* (Colorado pinyon), *Juniperus osteosperma* (Utah juniper), *Ephedra viridis* Cov. (mormon tea) and *Purshia mexicana* (D. Don) Henrickson (Mexican cliffrose). The understory is sparse with well developed biological crusts indicating minimal grazing pressure.

Seasonal plant hydraulic parameters

Plant water potentials were measured at the field site every 2 weeks from June to November 2003 and every month from April to November 2004. At each measurement period, pre-dawn (Ψ_{PD} , 1.5 h before sunrise) and midday (Ψ_{MD} , about 1230 h) water potentials of distal twigs of *P. edulis* and *J. osteosperma* ($n = 6$ per species) were measured with a Scholander-type pressure chamber (PMS, Corvallis, OR). Twigs subtending well-lit healthy foliage were excised with a sharp razor blade from the south side of the canopy. Water potentials were measured in the field immediately after twig excision.

Seasonal loss of conductivity in *P. edulis* and *J. osteosperma* stem and root xylem was calculated from the vulnerability to cavitation of the xylem (data previously published by Linton et al. 1998) and the in situ xylem pressure potential. We used the mid-point between Ψ_{PD} and Ψ_{MD} (i.e., the water potential at the hydraulic mid-point of the soil to leaf continuum) as the estimate of in situ xylem pressure potential because this is likely a more appropriate estimate of the pressure potential experienced by larger roots and stems, where the vulnerability curves were measured, than either Ψ_{PD} or Ψ_{MD} (Linton et al. 1998).

Whole-plant water conductance (k_p , $\text{kg m}^{-2} \text{MPa}^{-1} \text{s}^{-1}$) was calculated from Darcy's Law for steady-state bulk flow through porous media:

$$k_p = \frac{J_s}{\Delta\Psi} \quad (1)$$

where J_s is midday sap flux ($\text{kg m}^{-2} \text{s}^{-1}$) and $\Delta\Psi$ is the difference between soil water potential (Ψ_{soil}) and Ψ_{MD} (MPa). Calculations of k_p were performed only when $\Delta\Psi$ was greater than 0.25 MPa. We estimated Ψ_{soil} from Ψ_{PD} . Under certain circumstances Ψ_{PD} has been shown to underestimate Ψ_{soil} (Donovan et al. 1999, 2001), and this may be a source of error in our results. For these calculations, J_s was measured with constant heat thermal dissipation gauges (Granier 1987) on the same trees as water potential measurements. A detailed description of the sap flux method is presented in West et al. (2007). Briefly, sensors consisted of a pair of 20-mm-long, 2-mm-thick stainless steel probes, each containing a copper-constantan thermocouple at 10 mm. These probes were inserted radially into the xylem, about 1 m above ground, and axially spaced 100–150 mm apart. The downstream probe contained a constantan heater coil supplied with a constant power source. The upstream probe was an unheated, reference probe. Sap flux density was calculated from the temperature difference between the probes following the empirical equation of Granier (1987). Measurements were made continuously from May 2003 to December 2004 and were replicated on 10 individuals of each species (except $n = 5$ for *P. edulis* in 2003). Concurrent with sap flux density measurements, soil water availability was measured at five depths (10, 200, 300, 400 and 500 mm) with multisensor, annular frequency domain capacitance probes (EnviroSMART SDI-12, Sentek, Adelaide, Australia).

lia). Sensor outputs were scaled to volumetric water content (θ , $\text{m}^3 \text{m}^{-3}$) by calibration with gravimetrically determined soil water values taken from adjacent locations with a range of soil water contents. All depths were averaged to determine mean soil water content for the entire soil profile (θ_{tot}).

Irrigation experiment

At the irrigated site, trees were typically between 2- and 4-m tall. Stand density was low (54 trees per hectare), with a mean distance between nearest neighbors of 8.7 m. Within the site, 16 mature trees each of *P. edulis* and *J. osteosperma* were selected. Closely grouped trees were excluded from the experiment. Selected trees were randomly assigned to no irrigation (control, $n = 6$ per species), 10-mm irrigation ($n = 5$ per species) or 25-mm irrigation ($n = 5$ per species) treatments. The 10- and 25-mm irrigation depths were considered representative of normal and large storms for this ecosystem.

Trees were irrigated between 0300 and 0600 h on August 6, 2004. The irrigation water was labeled with deuterated water so that $\delta^2\text{H} = 11.6\text{‰}$ (relative to Vienna Standard Mean Ocean Water, VSMOW), which was approximately 70‰ enriched relative to previously measured plant water. Water was applied evenly in a 5-m-diameter circle around the base of each tree with a handheld water diffuser. Irrigation amounts were calculated from regularly measured flow rates.

Plant water potential and isotopic composition of stem water were measured on Days 1, 2, 4, 7, 9, 12, 15 and 18 after irrigation. Water potential was measured as described previously. Stem water was obtained by sampling fully suberized twigs of *J. osteosperma* and *P. edulis* that were upstream of any foliage. Stem samples ($\sim 60 \times 10$ mm) were excised from the south side of the tree at midday and immediately placed in screw-top glass vials, sealed with Parafilm and placed in a cooler containing dry ice.

Isotopic analyses

Water samples extracted from the stem samples by the method of West et al. (2006) were analyzed for isotopic composition by injecting microliter quantities directly into a TC/EA coupled to a Delta Plus XL isotope ratio mass spectrometer (Thermo-Finnigan) (Gehre et al. 2004). Both hydrogen and oxygen isotope ratios were determined. Isotope ratios are expressed in ‰ as:

$$\delta^n E = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) 1000 \quad (2)$$

where n is the heavy isotope of element E and R is the ratio of the heavy to light isotope ($^2\text{H}/\text{H}$ or $^{18}\text{O}/^{16}\text{O}$). Values of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ are reported relative to VSMOW. All samples were analyzed at the SIRFER facility (University of Utah, Salt Lake City). Precision was 1.76‰ for $\delta^2\text{H}$ and 0.14‰ for $\delta^{18}\text{O}$.

We used the $\delta^{18}\text{O}$ and $\delta^2\text{H}$ measurements of stem water to distinguish between post-irrigation enrichment of $\delta^2\text{H}$ caused by evaporation and that caused by uptake of the enriched irrigation water (Brooks et al. 2006). The naturally occurring

variation in $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of plant and soil water at our site, before irrigation, was tightly correlated along a local evaporation line ($\delta^2\text{H} = 3.08\delta^{18}\text{O} - 64.7$, $R^2 = 0.84$, $n = 99$). Natural variation in $\delta^2\text{H}$ was -103.7 to -29.7‰ . However, values deviated by only 12‰ ($\delta^2\text{H}$ maximum residual) above the evaporation line. Thus, plants were assumed to have taken up irrigation water only if they were above the 12‰ range of the evaporation line. By plotting pre- and post-irrigation stem water values on a $\delta^{18}\text{O}$ – $\delta^2\text{H}$ plot, irrigation water uptake could be visualized. Pre-irrigation values were obtained from stems sampled one day before irrigation. Post-irrigation values represented the maximum increase in stem water $\delta^2\text{H}$ measured up to 18 days after irrigation.

Heat-ratio sap flux measurements

During the irrigation experiment, the sap flux of each tree was measured by the heat-ratio method (Burgess et al. 2001). The sensor sets consisted of three 35-mm-long, 1.3-mm-diameter stainless steel needles axially spaced 6 mm apart. The center probe contained a 17 Ω nichrome heater. The upstream and downstream probes contained two copper-constantan thermocouples inserted at 5- and 15-mm depths. Probes were manufactured in the laboratory. Sensor sets were inserted radially into the xylem, at about 1-m height, using a stainless steel drilling guide to achieve the 6-mm axial spacing. After installation, sensors were shielded from direct sunlight and precipitation with aluminum pans. Measurements were recorded at half-hourly intervals with Campbell Scientific AM16/32 multiplexers and CR10X data loggers (Campbell Scientific). Heaters were triggered by a solid-state relay controlled by the data logger to produce a 2-s heat pulse. Temperatures were recorded during the period when the ratios of the upstream and downstream temperatures were most constant (between 70 and 100 s after the heat pulse). Sensors were installed in late June 2004 and were zeroed in late September 2004. Sapwood was severed to a depth of 50 mm around the sensors with a cordless router.

Our interest was in the hydraulic limits of *P. edulis* and *J. osteosperma* following irrigation. Sap flux may be submaximal because of measurement error (e.g., due to insufficient sapwood depth, excessive wounding, needle inserted into nonconductive sapwood) and biological variation. We therefore excluded submaximal sap flux measurements from our analysis and focused solely on the observed maximum sap flux densities. Whole-plant conductance over the course of the irrigation experiment was calculated as described in Equation 1.

Xylem conductivity measurements

Changes in the xylem hydraulic conductivity in *P. edulis* and *J. osteosperma* were measured 3 days after irrigation. Roots and stems were sampled from control (non-irrigated) and irrigated (25-mm irrigation) trees. Roots (~ 2.5 -mm xylem diameter) were sampled at a depth of about 20 cm under the canopy of each tree. Stems were sampled from straight twigs (~ 4 -mm xylem diameter). All samples were wrapped in moist paper towels and aluminum foil, sealed in plastic bags and kept in a

cooler until measured in the laboratory. Conductivity was measured in the laboratory within 36 hours of collection by a modification of the protocol described by Sperry et al. (1988). Stem and root segments were placed in clean distilled water and the ends were cut back at least 20 mm, under water, to remove embolisms. The ends were then trimmed with a new razor blade to clear physical obstructions. One end of the segment was fitted with a rubber gasket and was connected to clear tubing leading to a reservoir of distilled, filtered (0.2 μm) 20 mM KCl with a gravity pressure head of 500 mm. After two minutes, to allow the flow rate to stabilize, water passing through the stem segment was collected for 10 minutes in pre-weighed vials containing cotton wool. The vials were then weighed, the length and cross-sectional area of the xylem were measured and the area specific conductivity was calculated as:

$$k_s = \left(\frac{M_w L}{P t} \right) \left(\frac{1}{A} \right) \quad (3)$$

where k_s is the area-specific conductivity ($\text{mg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$), M_w is the mass of water (mg), L is the length of the segment (m), P is the pressure gradient (MPa), t is the duration of water collection (s) and A is the cross-sectional xylem area (m^2).

Results

Seasonal variations in whole-plant conductance

Seasonal trends in Ψ_{MD} and percent loss of conductivity (PLC) (Figure 1) in *Pinus edulis* and *Juniperus osteosperma* highlighted differences in the hydraulic patterns of these species. In *J. osteosperma*, Ψ_{MD} declined over the growing season as the summer drought progressed, reaching a minimum of -6.9 MPa in 2003 and -5.9 MPa in 2004. Based on the Ψ measurements, a progressive loss of conductivity in *J. osteo-*

sperma over the course of the summer drought was calculated, with stems and roots reaching 49% and 66% loss of conductivity by the end of the 2003 summer drought and 26% and 51% loss of conductivity by the end of the 2004 summer drought, respectively.

In contrast to *J. osteosperma*, *P. edulis* maintained a constant minimum Ψ_{MD} during the growing season of about -2.3 MPa (Figure 1). This isohydric behavior resulted in a relatively constant degree of xylem cavitation with a PLC of around 47% over the course of the growing season (Linton et al. 1998; Figure 1).

Calculated k_p differed considerably over the growing season in both species (Figure 2). *Pinus edulis* maintained a higher k_p than *J. osteosperma* during the spring and fall when soil water content was highest. During the summer drought, $\Delta\Psi$ and J_s approached zero for *P. edulis* but were greater than zero for *J. osteosperma*, presumably reflecting differences in stomatal control (Linton et al. 1998, Williams and Ehleringer 2000). This prevented the calculation of k_p for *P. edulis* during the summer drought. Measurement of $\Delta\Psi$, sampled one day after a 7.8-mm summer precipitation pulse (Day 203, 2003), showed that k_p increased sharply in *P. edulis* but not in *J. osteosperma*, consistent with the hypothesis that high conductances allow *P. edulis* to use water from summer precipitation more fully than *J. osteosperma*.

Irrigation experiment

In both species, Ψ_{PD} increased markedly following the 25-mm irrigation (Figure 3), with the highest increase in Ψ_{PD} after the irrigation in *J. osteosperma* (Table 1). Contrary to our hypothesis, there was a significant increase in Ψ_{PD} in *J. osteosperma* trees that received the 10-mm irrigation, but Ψ_{PD} of the 10-mm-irrigated *P. edulis* trees did not differ significantly from that of the control trees (Table 1).

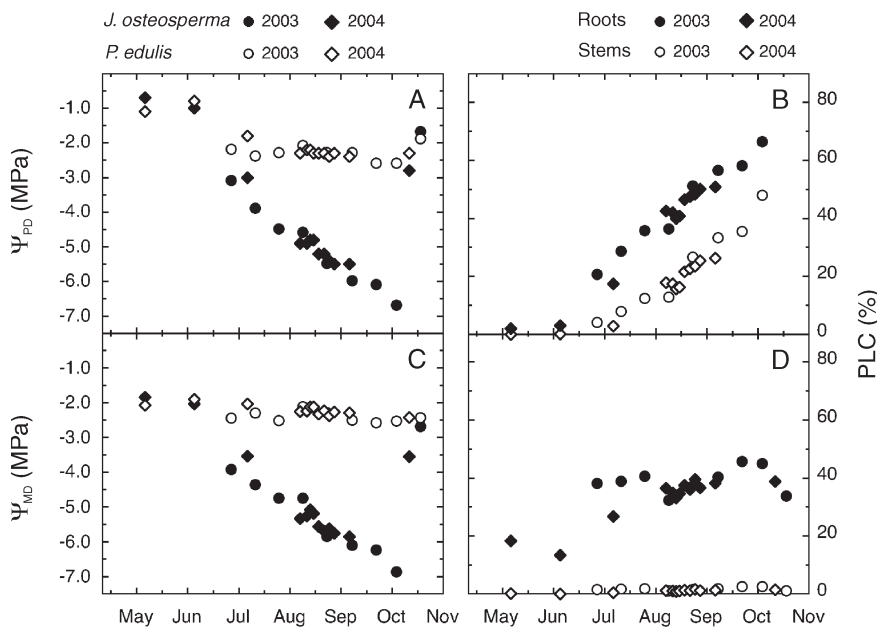


Figure 1. Seasonal courses of (A) predawn (Ψ_{PD}) and (C) midday (Ψ_{MD}) stem water potentials and estimated percent loss conductivity (PLC) of (B) *Juniperus osteosperma* and (D) *Pinus edulis* roots and stems. Percent loss of conductivity was estimated from the midpoint between Ψ_{PD} and Ψ_{MD} and the vulnerability curves of Linton et al. (1998). Water potential measurements were collected over 2 years ($n = 6$ for each measurement). Errors bars are contained within the size of the symbols.

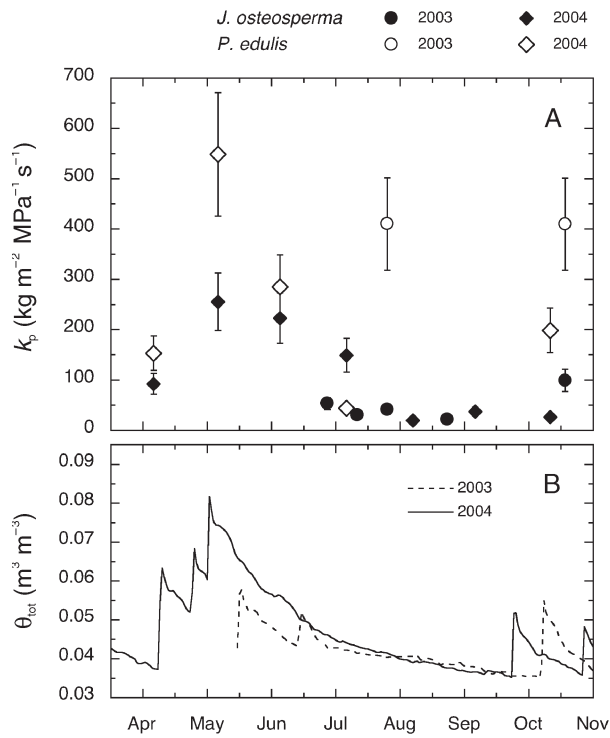


Figure 2. Seasonal changes in (A) calculated whole-plant water conductance (k_p) in *Juniperus osteosperma* and *Pinus edulis* over 2 years and (B) total volumetric soil water (θ_{tot}) for the 50 cm soil profile. Calculations of k_p were based on Darcy's Law.

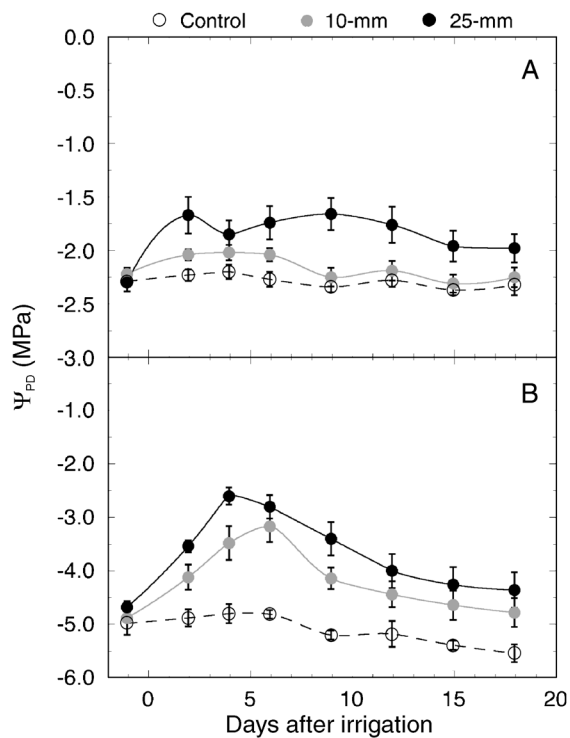


Figure 3. Changes in predawn stem water potential (Ψ_{PD}) in (A) *Juniperus osteosperma* and (B) *Pinus edulis* following irrigation. Treatments were a 25-mm irrigation ($n = 5$ per species), a 10-mm irrigation ($n = 5$) and a control ($n = 6$, no irrigation).

Table 1. Mean maximum increase in predawn stem water potential (MPa \pm 1 SE) in *Juniperus osteosperma* and *Pinus edulis* within 9 days following irrigation. Irrigation treatments of 25 mm and 10 mm were applied within a 5-m-diameter circle around the base of each tree. Controls received no irrigation. Results from ANOVA ($df = 16$) are shown. Significant differences within a species are shown with different letters (post-hoc Tukey HSD test).

	25 mm	10 mm	Control	F	P
<i>J. osteosperma</i>	2.1 \pm 0.1 a	1.8 \pm 0.5 a	0.3 \pm 0.1 b	13.4	< 0.001
<i>P. edulis</i>	0.7 \pm 0.2 a	0.3 \pm 0.1 b	0.3 \pm 0.1 b	6.1	0.01

Uptake of irrigation water was assessed by analyzing the isotopic content of post-irrigation xylem water against the local evaporation line (short-dashed line in Figure 4). Post-irrigation values for control trees and all 10-mm-irrigated *P. edulis* trees were contained within the 12‰ threshold above the

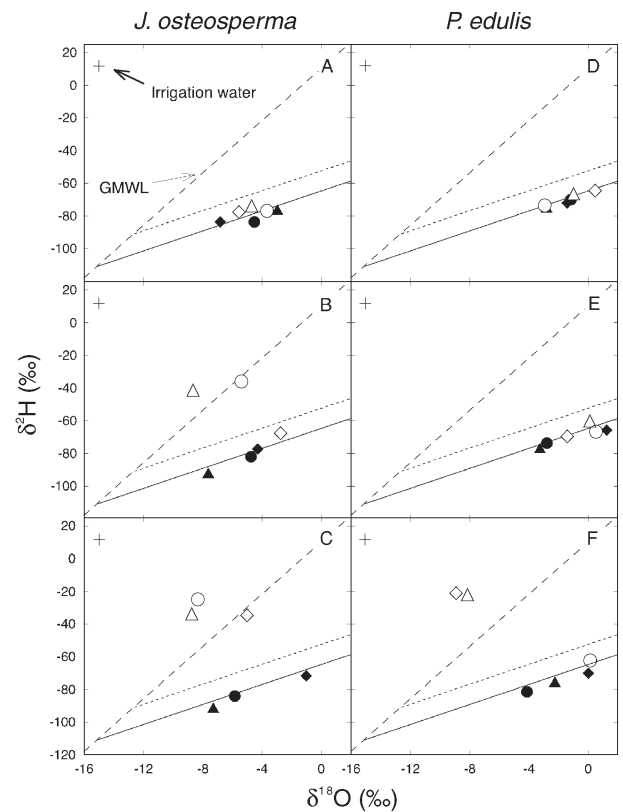


Figure 4. Plots of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of stem water in *Juniperus osteosperma* and *Pinus edulis* for the various irrigation treatments: control (A and D), 10-mm irrigation (B and E) and 25-mm irrigation (C and F). Symbols represent pre-irrigation (closed) and maximum post-irrigation (open) values for individual trees. The solid line represents the evaporation line for all pre-irrigation soil and plant samples at the site in 2004. The short-dashed line represents the maximum pre-irrigation residuals observed from this regression. All samples above the dashed line are interpreted as having taken up some fraction of the irrigation water (+). The global meteoric water line ($y = 8x + 10$) is plotted for reference (long-dashed line).

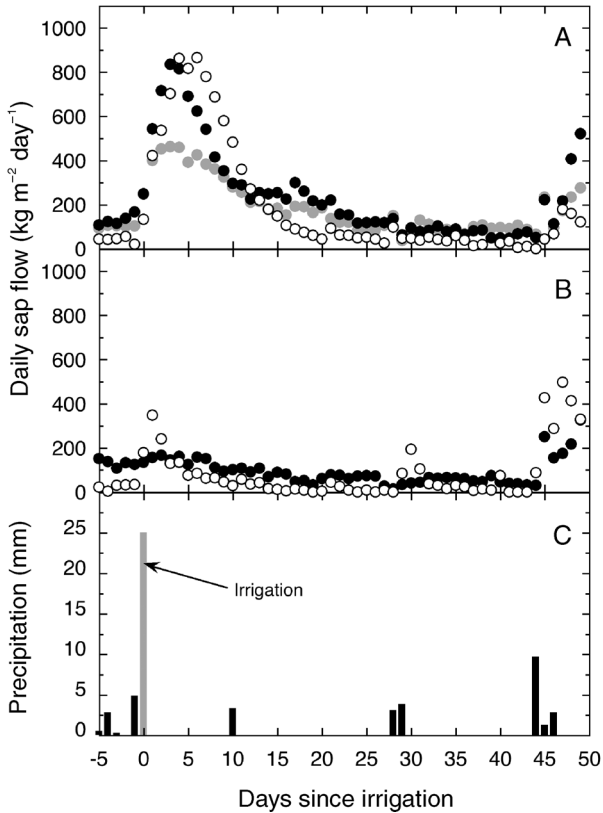


Figure 5. Maximum sap flow responses of (A) 25- (●) and 10-mm (○) irrigated *Juniperus osteosperma* and 10-mm irrigated *Pinus edulis* (○) trees and (B) control *J. osteosperma* (●) and *P. edulis* (○) trees. (C) Natural precipitation events (black bars) and the maximum irrigation treatment (gray bar).

local evaporation line, indicating no uptake of irrigation water (Figures 4A, 4D and 4E). Post-irrigation values fell well outside of the 12‰ threshold for two 10-mm and three 25-mm *J. osteosperma* trees and two 25-mm *P. edulis* trees (Figures 4B, 4C and 4F), indicating uptake of irrigation water by these individuals. *Juniperus osteosperma* was more sensitive to the irrigation treatments than *P. edulis*, with two out of three trees responding to the 10-mm irrigation (versus zero for *P. edulis*) and all three trees responding to the 25-mm irrigation (versus two for *P. edulis*).

The responses seen in the Ψ_{PD} and stem water isotope data were supported by the sap flux density measurements (Figure 5). Sap flux increased in both species following the 25-mm irrigation, but only in *J. osteosperma* following the 10-mm irrigation (Figure 5). The sap flux response to the 25-mm irrigation was indistinguishable in magnitude between species and was greater than that of the 10-mm-irrigated *J. osteosperma* (Figure 5). Equipment failure resulted in loss of data for three of five *P. edulis* trees that received the 10-mm irrigation; however, as there was no response seen in Ψ_{PD} or δ^2H for these trees, it is unlikely that they would have exhibited a marked increase in sap flux following irrigation. The *J. osteosperma* control showed no change in sap flux during the experiment; however, sap flux increased following a rain event on Day 44 after irrigation, indicating that the sensor was placed in func-

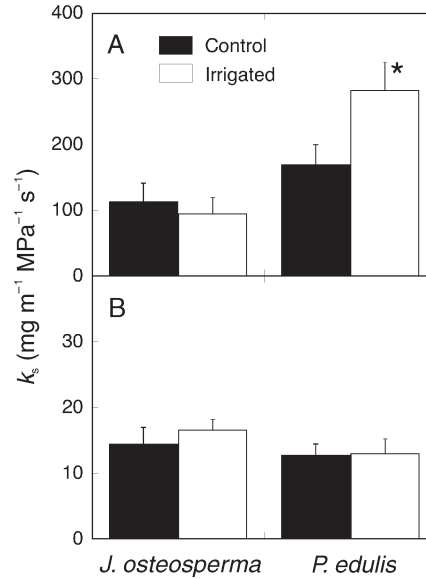


Figure 6. Area specific conductivity (k_s) of (A) roots and (B) stems of *Juniperus osteosperma* and *Pinus edulis* 3 days after a 25-mm irrigation event. Note the difference in scales between the panels. An asterisk (*) indicates a statistically significant treatment effect within a species (t -test, $P < 0.05$).

tional sapwood. The *P. edulis* control trees showed no large increase in sap flux during the experiment; however, sap flux increased following natural rain events on Days 1, 28 and 44 after irrigation (Figure 5), indicating that *P. edulis* responded to small natural rain events over the summer, thus indicating that the lack of response of *P. edulis* to the 10-mm irrigation was anomalous.

Plant hydraulic conductance following irrigation

Based on the patterns of PLC calculated for *P. edulis* (Figure 1), we hypothesized that the response of this species to rain pulses may be due, in part, to the refilling of embolized xylem in roots. A comparison of k_s for irrigated and non-irrigated plants showed that *P. edulis* roots had a 66% greater k_s than control plants (t -test, $t = 2.14$, $P = 0.02$, $df = 16$) 3 days after receiving a 25-mm irrigation (Figure 6). There were no significant differences in k_s for *J. osteosperma* roots ($P = 0.31$) or *J. osteosperma* ($P = 0.24$) or *P. edulis* ($P = 0.47$) stems.

Following irrigation, k_p differed between *J. osteosperma* and *P. edulis* (Figure 7). *Juniperus osteosperma* maintained a constant k_p over the course of the irrigation experiment (Figure 7), whereas, in *P. edulis*, k_p changed substantially during the experiment (Figure 7). Initially, k_p of *P. edulis* was approximately twice that of *J. osteosperma*, but declined to a similar value by the end of the experiment.

Discussion

Plant hydraulic conductivity and pulse response

Pinus edulis is sufficiently shallow rooted to take up water from superficial soil layers wetted by summer rain pulses

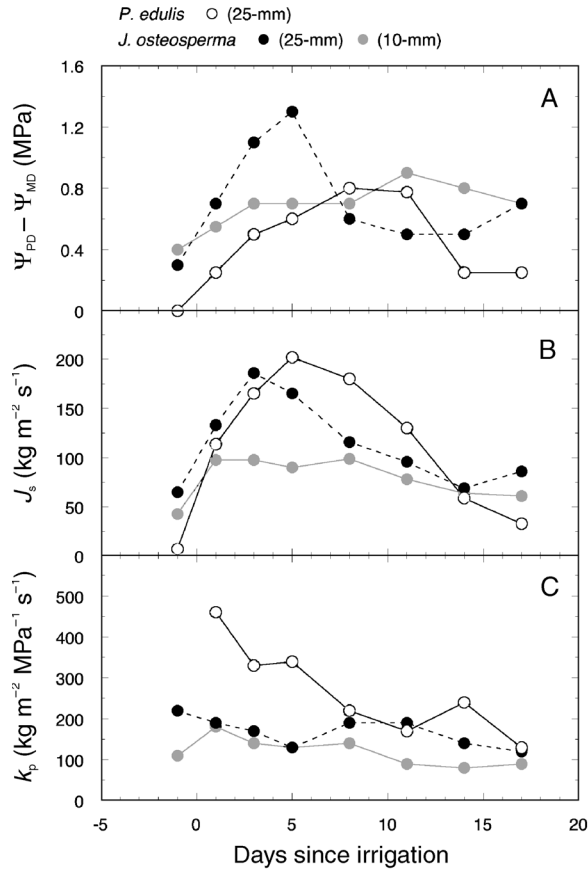


Figure 7. Changes in the (A) stem water potential gradient ($\Delta\Psi = \Psi_{PD} - \Psi_{MD}$), (B) maximum midday sap flux density (J_s) and (C) calculated whole-plant conductance (k_p) for irrigated *Juniperus osteosperma* (25-mm and 10-mm treatments) and *Pinus edulis* (25-mm treatment) trees over the course of the irrigation experiment.

(West et al. 2007). Our results indicate that uptake of summer rainfall by *P. edulis* is achieved through the rapid attainment of high k_p after rain events (Figures 2 and 7). *Pinus edulis* maintained a higher k_p during mesic periods than *Juniperus osteosperma* (Figure 2), which it may do through a combination of cavitation avoidance in stem xylem and reversal of embolism in root xylem following rain events.

Pinus edulis regulates Ψ_{MD} through tight stomatal control (Lajtha and Barnes 1991, Williams and Ehleringer 2000), which prevents extensive stem xylem cavitation. Instead, cavitation is localized in the repairable root xylem.

Root xylem is more vulnerable to cavitation than stem xylem in many species (Alder et al. 1996, Linton et al. 1998, Kolb and Sperry 1999, Ewers et al. 2000, Hacke et al. 2000a, 2000b) and may act as a “hydraulic fuse” protecting those parts of the hydraulic continuum that are less able to recover from cavitation (Sperry et al. 2002). Cavitation of root xylem in shallow soil layers may help isolate the plant from areas of low soil water potential, thereby maintaining high Ψ_{MD} .

Following a rain event, *P. edulis* increases root conductivity through embolism reversal (Figure 6). Cavitation is minimal in stem xylem (Figure 1); thus, refilling root xylem should re-

store a cavitation-free hydraulic pathway. Therefore, the response of *P. edulis* to rain pulses appears to result from the isohydric regulation of Ψ_{MD} , which prevents extensive stem cavitation, and an ability to refill embolized roots. These factors maximize hydraulic conductance following rain events, enabling the rapid uptake of transiently available soil water. These processes may maintain k_p during drought; however, in *P. edulis*, gas exchange ceases when Ψ_{soil} is less than about -2 MPa (Lajtha and Barnes 1991, Williams and Ehleringer 2000). Thus, we predict that *P. edulis* is competitively successful only in environments where the benefits of increased conductance during mesic periods (Ψ_{soil} greater than about -2 MPa) outweigh the costs during xeric periods (Ψ_{soil} less than about -2 MPa). Consistent with this inference, *P. edulis* is more competitive than *J. osteosperma* in more mesic locations (Tausch et al. 1981, Nowak et al. 1999, West 1999, Martens et al. 2001, Mueller et al. 2005).

In contrast to *P. edulis*, *J. osteosperma* does not homeostatically regulate Ψ_{MD} , with the result that PLC increases over the course of the summer (Figure 1). Neither root conductivity nor k_p increased in *J. osteosperma* following rain events (Figure 6). However, xylem of *J. osteosperma* is significantly more resistant to cavitation than that of *P. edulis* (Linton et al. 1998), allowing this species to maintain steep soil-to-leaf water potential gradients and thus the capacity to respond to rain events. This pattern allows gas exchange during periods of low Ψ_{soil} (Williams and Ehleringer 2000), but unlike the pattern observed in *P. edulis*, which prevents severe desiccation during drought through stomatal control, it creates a risk of severe xylem cavitation. This may explain why *J. osteosperma* often displays crown dieback, something not seen in *P. edulis* (authors’ observation). The absence of mechanisms preventing xylem cavitation in *J. osteosperma*, together with its greater rooting depth (West et al. 2007), may explain the lack of response to small rainfall events in *J. osteosperma* during dry summers (2003 and 2004).

Irrigation versus natural precipitation events

Contrary to our prediction, *J. osteosperma* showed a greater response to irrigation than *P. edulis*, particularly following the 10-mm irrigation treatment (Figure 4). Our irrigation results contrast with results collected following natural summer precipitation events, which indicated that *P. edulis* was more responsive than *J. osteosperma* to summer rains (West et al. 2007). This discrepancy may indicate that our irrigation method did not realistically mimic natural rainfall.

During natural rain events, precipitation falls on both the inter-canopy soil surface and the plant canopies. For conifers, a large proportion of precipitation falling on the canopy is intercepted and evaporated back to the atmosphere (Silva and Rodriguez 2001, Carlyle-Moses 2004, Owens et al. 2006). The remaining precipitation either falls through the canopy or is channeled down the stem. Small rain events result in high interception losses (Laio et al. 2001, Porporato et al. 2002), so that only large storms result in significant throughfall or stem flow. Once on the surface, precipitation either infiltrates the

soil, where it becomes available for plant uptake, or is held in the litter layer, where it eventually evaporates. As a result of these processes, inter-canopy areas receive larger precipitation inputs than areas beneath the canopy (Breshears et al. 1997a, 1997b).

Our irrigation method involved applying water directly to the litter layer and soil surface in a 5-m diameter circle centered around the trunk. This mimicked the effects under the canopy of a large storm (i.e., high throughfall and stem flow), but underrepresented inter-canopy effects.

During the irrigation treatments, there was greater water infiltration through the litter of *J. osteosperma* than of *P. edulis* (authors' observation), which, like some other pine species (Doerr et al. 1998, Scott 2000, Huffman et al. 2001, Mataix-Solera and Doerr 2004), may produce hydrophobic litter. Although infiltration rates may be reduced by *J. osteosperma* litter (Gifford 1970, Scholl 1971), litter interception losses may be small. Litter interception in *Juniperus ashei* (Buchholz) woodlands is estimated to be only 5% of incoming precipitation (Owens et al. 2006). Additionally, hydraulic conductivity of the soil beneath the litter layer is higher below juniper canopies than below pinyon canopies, primarily because of the presence of root macro-channels and macro-pores (Wilcox et al. 2003). Thus, it is likely that litter interception was lower, and infiltration rates higher, below *J. osteosperma* canopies than below *P. edulis* canopies.

Pinus edulis takes up water from inter-canopy locations (Breshears et al. 1997a). This is consistent with the response of *P. edulis* to small rain events (West et al. 2007), with water uptake most likely having occurred in the inter-canopy zone where interception losses were minimal. It is possible that *P. edulis* allocates greater root biomass than *J. osteosperma* to inter-canopy areas, thereby mitigating the effects of litter interception and enabling it to capitalize on small rain events. In contrast, *J. osteosperma* appeared to take up no water from small rain events during the summer (West et al. 2007). This difference could be associated with a greater rooting depth or greater allocation to roots beneath the canopy that are well placed to take up water from throughfall or stem flow, which only occur following larger rain events. Stem flow in *J. ashei* greatly increases water content near the stem to five times that of the surrounding soil (Slaughter 1997), thereby promoting transpiration relative to trees without stem flow (Owens 2004). Our irrigation method would have favored uptake through this pathway.

In previous irrigation experiments in pinyon–juniper woodlands conducted with the irrigation method used here, Williams and Ehleringer (2000) found that *J. osteosperma* took up more irrigation water than *P. edulis* during the summer because, as these authors suggested, high soil temperatures suppressed root activity in *P. edulis* but not in *J. osteosperma*. However, the response of *P. edulis* to natural rain events over two dry summers (West et al. 2007) indicates that high soil temperatures do not prohibit uptake of summer rain by this species. We suggest that our irrigation method favored uptake in *J. osteosperma* but not in *P. edulis*, because of species differences in litter interception, subsurface hydraulic conductivity

and the proportion of roots concentrated beneath the canopy.

Hydraulic patterns and species distributions

This study supported our hypothesis that the response of *P. edulis* to rain pulses is associated with cavitation avoidance in stems and the elimination of root xylem embolisms following precipitation, allowing maintenance of a high whole-plant conductance. This pattern appears to be adaptive in environments with regular precipitation inputs, allowing *P. edulis* to respond rapidly to rain events, but results in restricted assimilation if soil water potentials are below about -2 MPa for extended periods. This may explain the limitation of *P. edulis* to summer rainfall areas (Pendall et al. 1999, Thompson et al. 1999).

Unlike *P. edulis*, *J. osteosperma* underwent progressive xylem cavitation as the summer drought progressed. The lack of response by *J. osteosperma* to small summer rain pulses may be associated with decreased whole-plant conductance and greater rooting depth in the inter-canopy that preclude uptake of summer rain. This resource acquisition pattern appears to be unadaptive for environments where summer precipitation is limited to infrequent pulses. Consistent with this interpretation, *J. osteosperma* is replaced by *Juniperus monosperma* (Engelm.) Sarg. as the fraction of annual precipitation that falls in the summer increases (West 2006). *Juniperus osteosperma* exploits shallow soil water resources (Breshears et al. 1997a). The resource acquisition pattern of *J. osteosperma* may be the product of adaptation to environments where precipitation occurs mainly in winter, and water uptake at low water potentials in the summer is adaptive. Such conditions exist in the Great Basin, where *J. osteosperma* has been prevalent for at least 30,000 years (Nowak et al. 1994).

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