

TRANSPIRATION AND HYDRAULIC STRATEGIES IN A PIÑON–JUNIPER WOODLAND

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Abstract. Anthropogenic climate change is likely to alter the patterns of moisture availability globally. The consequences of these changes on species distributions and ecosystem function are largely unknown, but possibly predictable based on key ecophysiological differences among currently coexisting species. In this study, we examined the environmental and biological controls on transpiration from a piñon–juniper (*Pinus edulis*–*Juniperus osteosperma*) woodland in southern Utah, USA. The potential for climate-change-associated shifts in moisture inputs could play a critical role in influencing the relative vulnerabilities of piñons and junipers to drought and affecting management decisions regarding the persistence of this dominant landscape type in the Intermountain West. We aimed to assess the sensitivity of this woodland to seasonal variations in moisture and to mechanistically explain the hydraulic strategies of *P. edulis* and *J. osteosperma* through the use of a hydraulic transport model. Transpiration from the woodland was highly sensitive to variations in seasonal moisture inputs. There were two distinct seasonal pulses of transpiration: a reliable spring pulse supplied by winter-derived precipitation, and a highly variable summer pulse supplied by monsoonal precipitation. Transpiration of *P. edulis* and *J. osteosperma* was well predicted by a mechanistic hydraulic transport model ($R^2 = 0.83$ and 0.92 , respectively). Our hydraulic model indicated that isohydric regulation of water potential in *P. edulis* minimized xylem cavitation during drought, which facilitated drought recovery (94% of pre-drought water uptake) but came at the cost of cessation of gas exchange for potentially extended periods. In contrast, the anisohydric *J. osteosperma* was able to maintain gas exchange at lower water potentials than *P. edulis* but experienced greater cavitation over the drought and showed a lesser degree of post-drought recovery (55% of pre-drought uptake). As a result, these species should be differentially affected by shifts in the frequency, duration, and intensity of drought. Our results highlight the sensitivity of this woodland type to potential climate-change-associated shifts in seasonal moisture patterns and demonstrate the utility of mechanistic hydraulic models in explaining differential responses of coexisting species to drought.

Key words: drought; hydraulic transport model; *Juniperus osteosperma*; piñon–juniper woodlands; *Pinus edulis*; plant water use; sap flux; species distributions.

INTRODUCTION

Anthropogenic climate change is likely to alter the patterns of moisture availability globally, through changes to the Earth's energy budget (Houghton et al. 2001). In the southwestern United States, these changes may entail both modifications to seasonal precipitation patterns and increases in evaporative demand causing extended periods of drought (Gregory et al. 1997, Houghton et al. 2001, Cook et al. 2004). The consequences of such changes in moisture availability on species distributions, and thus ecosystem function, are largely unknown but have potentially important implications for land management across the region. While

climate envelope models are often used for exploring potential range changes in species distributions under altered climate, they are limited by the challenge of extrapolating into previously un-encountered environmental conditions and a lack of integration of physiological differences between coexisting species (Hijmans and Graham 2006). A more mechanistic approach, based on an understanding of key ecophysiological differences among currently coexisting species, may improve predictions of the response of species and ecosystems to potential climate change.

The pulsed nature of moisture resources represents a major challenge for woody plants in semiarid ecosystems (Noy-Meir 1973, Williams and Snyder 2003, Loik et al. 2004, Schwinning et al. 2004). In order to persist in semiarid systems, woody plants must utilize periodic inputs of moisture for carbon gain while avoiding mortality during extended periods of drought. Water is the primary resource limiting primary productivity in arid and semiarid environments (Noy-Meir 1973), but it

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is the magnitude and duration of drought periods that influences plant mortality in these systems. The dominant species of arid and semiarid environments may be differentially vulnerable to changes in water resources (Ehleringer et al. 1998, 1999), with alterations in the seasonality and duration of moisture potentially having large consequences for species survival and ecosystem function (Weltzin and McPherson 2003, Weltzin et al. 2003) and vegetation distribution (Neilson 2003).

While total annual precipitation is undoubtedly important in determining primary productivity and vegetation distribution (Le Houerou 1984, Stephenson 1990), there is a growing realization of the importance of seasonality of precipitation in structuring moisture resources and the impact that differential sensitivity to surface moisture availability may have on plant resource acquisition and survivorship in semiarid environments (Neilson 2003, Weltzin et al. 2003, Williams and Snyder 2003, Schwinning et al. 2004, 2005b, Hely et al. 2006). Precipitation falling during times of low evaporative demand (winter) accumulates in the soil and recharges the soil profile. As the evaporative demand increases, the shallow soil layers dry out due to evaporation, but deeper moisture remains due to the high resistance to water vapor diffusion through the dry surface soil layers. Once the lower profile is charged, deeper moisture provides a relatively stable resource for plant uptake. Precipitation falling during times of high evaporative demand (summer) will readily evaporate from the soil surface, resulting in lower infiltration rates and shallower soil moisture resources that are short lived. Accessing this shallow soil moisture requires maintaining roots in surface layers, which then experience high soil temperatures and very low water potentials between moisture pulses. There appear to be strong trade-offs associated with accessing these different water sources in arid and semiarid environments (Schwinning and Ehleringer 2001), with plants tending to specialize in one form vs. another (Sala et al. 1989, Ehleringer et al. 1991, Flanagan et al. 1992, Lin et al. 1996, Schwinning et al. 2002, Snyder et al. 2004, Xu and Li 2006). It is these differential adaptive features that can influence the ability of a species to persist in an area if there are significant shifts in the variability, seasonality, and distribution of moisture inputs.

Piñon–juniper woodlands (see Plate 1) occupy approximately 55–75 million acres (22–30 Mha) in the western United States (Mitchell and Roberts 1999, West 1999b). Previous work has indicated that the co-occurring piñon and juniper species differ in their carbon and water relations, with juniper species having a lower potential for carbon gain, but a higher tolerance to drought, than piñon (Barnes and Cunningham 1987, Miller et al. 1992, Lajtha and Getz 1993, Linton et al. 1998, Nowak et al. 1999, Williams and Ehleringer 2000). These trade-offs result in differential competitive abilities of the two genera, with the proportion of piñon and juniper in a given area being, in part, a function of plant

available moisture (Padien and Lajtha 1992). Piñons dominate more mesic sites and junipers the drier sites (Tausch et al. 1981, Nowak et al. 1999, West 1999a, Martens et al. 2001), with considerable overlap of distributions.

Across the distribution of piñon–juniper woodlands there is a strong climatic gradient in seasonality of precipitation, from predominantly winter precipitation in the Great Basin to predominantly summer precipitation in New Mexico. This seasonality gradient reflects two opposing weather systems: a frontal system from the Pacific Northwest that moves southeast across the interior in the winter months and a monsoonal system moving northwards into the interior from the equatorial Pacific in the summer (Bryson and Hare 1974). The geographic change in species composition in piñon–juniper woodlands (Neilson 1987, West 1999b) appears to be associated with this gradient, yet at present we lack a mechanistic understanding of this biogeography. In the winter-precipitation-dominated Great Basin, *Juniperus osteosperma* (Torr.) Little and *Pinus monophylla* Torr. & Frém. co-occur. As one moves southeast onto the Colorado Plateau, one crosses the northern-most extent of the North American monsoon (Adang and Gall 1989, Higgins et al. 1997), and the proportion of summer rain increases. Across this transition, *P. monophylla* is replaced by *Pinus edulis* Englm., with intervening hybrid zones (Lanner 1974, Lanner and Van Devender 1998). However, there is no corresponding change in *Juniperus* species across this monsoon boundary. *J. osteosperma* and *P. edulis* woodlands continue south on the Colorado Plateau, with an increasing proportion of summer rain, until *J. osteosperma* is eventually replaced by *Juniperus monosperma* (Engelm.) Sarg. on the Mogollon Rim in Arizona and into New Mexico.

Water uptake studies from across this gradient in seasonality have indicated that there is a threshold response in the uptake of summer precipitation (Williams and Ehleringer 2000). *P. edulis* and *J. osteosperma* only took up summer precipitation when it represented a considerable fraction of the annual rainfall (Williams and Ehleringer 2000). Studies from other locations have shown that both *Pinus* and *Juniperus* are capable of taking up shallow soil moisture during the summer (Flanagan et al. 1992, Breshears et al. 1997, Williams and Ehleringer 2000, Leffler et al. 2002). However, these patterns of summer water uptake have not been consistent across field sites and years (Flanagan et al. 1992, Donovan and Ehleringer 1994, Williams and Ehleringer 2000, Leffler et al. 2002). This inconsistency is perhaps unsurprising considering the inherently variable nature of moisture availability in arid and semiarid systems (Loik et al. 2004) and the necessarily sparse temporal replication of the studies in question.

To be able to accurately capture the dynamics of plant water use in these systems, long-term, continuous studies of plant water use are required. Sap flux methodology is

a powerful tool for such studies, as transpiration can be measured continuously from component species of an ecosystem over multiple years, with sufficient frequency to detect responses to environmental conditions (Granger et al. 1996). Such studies have been successfully employed to study the responses of woody species to variable soil moisture conditions (Pataki et al. 2000, Oren and Pataki 2001, Phillips and Oren 2001, Martinez-Vilalta et al. 2003, Wullschleger and Hanson 2006). However, few have done so in arid and semiarid environments that experience severe summer droughts (Martinez-Vilalta et al. 2003).

In this study, we examined the environmental and biological controls on plant water use in a *P. edulis*–*J. osteosperma* woodland on the Colorado Plateau in southern Utah. Here we have a plant community exposed to a strong seasonality gradient. The potential for climate-change-associated shifts in moisture inputs could play a critical role in influencing the relative vulnerabilities of *P. edulis* and *J. osteosperma* to drought and affecting management decisions regarding the persistence of this dominant landscape type in the Intermountain West. Our study aimed to (1) assess the sensitivity of this woodland to soil drought and seasonal variations in moisture by examining the interannual and seasonal variation in transpiration, and (2) mechanistically explain the hydraulic limitations of *P. edulis* and *J. osteosperma*, through the use of a hydraulic transport model, in order to improve our understanding of the influence of seasonal moisture patterns on species distribution in these woodlands.

METHODS

Study site

The study site was a mature piñon–juniper woodland near Canyonlands National Park in southern Utah latitude 38°33'36" N, longitude 109°49'12" W, elevation 1800 m). The site was located near the southern limits of winter frontal precipitation and the northern limits of summer monsoon moisture in the southwestern United States (Ehleringer et al. 1999). Soils were Rizno series fine sandy loam, interspersed with rock outcrops (Grand County Soil Survey, Map 52). Soils were shallow, with depth to sandstone ranging from 0 to 50 cm. The site had a negligible slope. Thirty-year climate data give mean annual precipitation of 232 mm, mean annual air temperature of 11.5°C, and an average freeze-free period of 150–200 days (1971–2000, Western Regional Climate Center, data available online).² Woody plants at this site included *Pinus edulis* Englmn. (Colorado piñon), *Juniperus osteosperma* (Torr) Little (Utah juniper), *Ephedra viridis* Cov. (Mormon tea), and *Purshia mexicana* (D. Don) Henrickson (Mexican cliffrose). The understory was sparse with extremely well-developed biological crusts indicating minimal grazing pressure. The majority

of the biomass was *P. edulis* and *J. osteosperma*. All plant measurements were replicated on 5–10 individuals of both *P. edulis* and *J. osteosperma* located within an 80 m diameter area. Within this area, *J. osteosperma* contributed 88% and *P. edulis* 12% of the basal area. Leaf area index of the plot was calculated to be 0.24, using measured basal sapwood area and the equations of Schuler and Smith (1988).

Soil and atmospheric measurements

Measurements were made continuously on site from May 2003 to December 2005. Soil moisture was measured at five depths (10, 20, 30, 40, 50 cm) with multisensor, annular frequency domain capacitance probes (EnviroSMART SDI-12, Sentek, Adelaide, Australia) installed in a PVC access tube (Paltineanu and Starr 1997). Outputs from these sensors (scaled frequency) were converted to volumetric water content (θ , m³/m³) by calibrating with gravimetrically determined soil moisture values taken from adjacent locations under a range of soil moistures ($\theta = 0.0024[\text{scaled frequency}]$, $R^2 = 0.64$, $P \ll 0.0001$). Micrometeorological measurements were made in the intercanopy at 1.5 m height. Air temperature and relative humidity were measured with a shaded, ventilated CS500 sensor (Campbell Scientific, Logan, Utah, USA). Photosynthetically active radiation (PAR) was measured with a quantum sensor (LI190SB, Campbell Scientific, Logan, Utah, USA). Rainfall was measured with a tipping bucket rain gauge (TE525, Texas Electronics, Dallas, Texas, USA). All measurements were made at 30-s intervals, with 10-min averages stored on a CR23x datalogger (Campbell Scientific, Logan, Utah, USA). The study commenced during May 2003; thus we did not have direct measurements for the beginning of 2003. In order to extend our measurements to the beginning of the 2003 water year, we used the monthly precipitation totals from The Neck, Canyonlands National Park, approximately 11 km from our site (see footnote 2 for data). Overlapping measurement periods from our measurements and those of The Neck indicated that winter precipitation was very similar at these two sites.

Plant water potential measurements

Plant water potential measurements were made every two weeks from June to November in 2003 and every month from April to November 2004 and March to July 2005. At each measurement period the predawn (Ψ_{PD} , 1.5 hours before sunrise) and midday (Ψ_{MD} , approximately 12:30 hours) water potentials of distal twigs of *J. osteosperma* and *P. edulis* ($n = 6$ twigs per species) were measured with a Scholander-type pressure chamber (PMS, Corvallis, Oregon, USA). Twigs subtending well-lit, healthy foliage were excised, using a sharp razor blade, from the south side of trees instrumented with sap flow sensors. Water potential measurements were made in the field immediately after excising the twig.

² (<http://www.wrcc.dri.edu/>)

Sap flux measurements

Sap flux density was measured with Granier-type constant heat thermal dissipation sensors (Granier 1987). The sensors consisted of a pair of 2 cm long, 2 mm thick, stainless steel probes each containing a copper-constantan thermocouple at 1 cm. These probes were inserted radially into the xylem and spaced 10–15 cm axially. The downstream probe contained a constantan heater coil supplied with a constant power source. The upstream probe was an unheated, reference probe. The thermocouples from the two probes were wired together to give a temperature difference between the heated and reference probes. This temperature difference is related to sap flux density by the following empirical equation (Granier 1985, 1987):

$$J_s = 0.0119 \left(\frac{\Delta T_0}{\Delta T} - 1 \right)^{1.23} \quad (1)$$

where J_s is sap flux density (in $\text{g}\cdot\text{cm}^{-2}\cdot\text{s}^{-1}$), ΔT is the temperature difference between the heated and unheated probes, and ΔT_0 is the temperature difference obtained under zero-flow conditions.

Probes were installed in healthy stems approximately 1 m above the ground, although this varied sometimes due to the morphology of the trees (particularly *J. osteosperma*). *J. osteosperma* stems with significant circumferential dieback or convoluted circumferences, indicating nonuniform sapwood depth, were avoided. We selected stems of sufficient diameter to have sapwood at least as deep as the probes. In order to minimize bias due to circumferential variation in sap flow, probes were installed randomly around the circumference of the trees. When installing the probes, bark and phloem were removed from a 2-cm² patch of the stem and the probes were inserted directly into the xylem. The probes were then shielded with plastic covers to divert rainfall and the stem was wrapped in insulation as far above and below the probe as was possible (about 50 cm) in order to minimize passive thermal gradients. Passive thermal gradients were monitored in a set of adjacent unheated sensors in every tree (similar to Goulden and Field 1994). The passive thermal gradients were inconsistent in magnitude and direction and correction of ΔT for these gradients had little effect on the magnitude of the sap flux. Thus we chose not to apply these corrections to our data, instead reporting unmanipulated data from our single heater probes sets and relying on the randomization of sensor placement to even out the effects of passive thermal gradients.

Sap flux measurements were collected continuously from May 2003 to December 2005. Data were recorded at 30-s intervals with 10-min averages stored on a CR23x datalogger. ΔT data were converted to J_s using the program Baseliner (available online).³ Care was taken to select ΔT_0 for each day, but only under

conditions of low vapor pressure deficit (VPD) and constant nighttime ΔT . Where this was not realized, the previous ΔT_0 was used until suitable conditions for determining ΔT_0 occurred again. In order to avoid problems with wounding or infection, data from the probes were checked monthly for signs of signal decay. When necessary, probes were relocated to different stems or different trees. Sample size was maintained at 10 individuals per species except for 2003 ($n = 10$ for *J. osteosperma*, $n = 5$ for *P. edulis*) and occasional periods where equipment failed or trees died.

Sap flux values reported in this paper represent the average J_s for all individuals of the species ($n \approx 10$ individuals). Daily sums (J_{SD}) were calculated as the total sap flux over the daylight hours (determined from PAR measurements).

Scaling

Basal area and stem diameter at sap flux probe height (~ 1 m) were measured for all *P. edulis* and *J. osteosperma* individuals in the plot. A relationship between stem diameter and sapwood area at sap flux probe height (~ 1 m) was obtained in an adjacent plot, so as not to influence the trees being measured for sap flux. Sapwood depth was visually determined as the portion of translucence from a stem core. Sapwood depth never exceeded 3.5 cm and was an average of 2.0 cm for both *J. osteosperma* and *P. edulis* individuals.

Stand level transpiration was calculated as

$$T = \sum_{i=1}^2 J_{s,i} \left(\frac{A_{s,i}}{A_g} \right) \quad (2)$$

where $J_{s,i}$ and $(A_{s,i}/A_g)$ are sap flux density ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and sapwood area to ground area ratio (m^2/m^2) of species i and T is total stand transpiration (mm/d). Our measurement record did not cover the beginning of 2003. Thus, in order to estimate stand transpiration in 2003, a sap flux pattern symmetrical to that seen in 2004 was assumed. This was supported by rainfall records from The Neck, Canyonlands National Park indicating similar conditions in spring of 2003 and 2004.

Modeling

A hydraulic transport model (previously described in Sperry et al. 1998, Hacke et al. 2000) was used to predict how the hydraulic properties of the rhizosphere and plant xylem limited transpiration by each species. The model was used in its simplest form with the hydraulic pathway from the soil to the leaf being represented by three hydraulic conductances in series: a rhizosphere conductance from bulk soil to the root, a root xylem conductance, and a stem xylem conductance. These conductances decline with decreasing water potential according to soil properties and xylem vulnerability curves. The model calculates the steady-state rate of water flow from the soil at a given water potential to the canopy at a lower water potential. When using an

³ (<http://c-h2oecology.env.duke.edu/site/resources.html>)

appropriate soil water potential and a measured midday leaf water potential, the model predicts the midday transpiration rate (E_{pred}). As soil and/or midday water potentials drop during drought, the model calculates the decline in transpiration and the loss of conductivity in soil and xylem conductivity. Similarly, as water potentials moderate following a drought, the recovery of transpiration rate is predicted, assuming the soil conductivity recovers with water potential. The xylem conductivity can be set to recover or not, depending on whether the xylem cavitation is reversible.

We used the model to predict the loss of conductivity and water transport in the hydraulic continuum caused by summer drought, as well as the recovery of water uptake following summer rain in *P. edulis* and *J. osteosperma*. The plant component of the model was parameterized with maximum conductivity (K_{max} , calculated as $E_{\text{MD}}/(\Psi_{\text{PD}} - \Psi_{\text{MD}})$ during the wettest time of spring, where E_{MD} is the midday transpiration rate) and vulnerability curves of roots and shoots to cavitation (data from Linton et al. 1998). The soil was parameterized as one layer, using plant Ψ_{PD} as a surrogate for Ψ_{soil} as we lacked both detailed rooting distribution data and reliable Ψ_{soil} data spanning the entire rooting depth of the plants. As plant Ψ_{PD} represents the integrated Ψ_{soil} over the entire absorbing root length, running the model in this manner does not return any information about rooting depth differences between the species. The “vulnerability curves” for loss of soil conductivity with water potential were calculated from soil texture data and Ψ_{soil} from Ψ_{PD} (Campbell 1985).

Fluxes were expressed on a leaf area basis (based on the equations of Schuler and Smith 1988) with leaf area assumed constant through the season. The model requires an estimate of the root:leaf area ratio ($A_{\text{R}}:A_{\text{L}}$). Instead of measuring this difficult parameter, we solved for it by choosing the value giving the best fit between the model flux (E_{pred}) and the measured flux (E_{meas}). The soil texture varied through the soil profile at our site from sandy loam to loam. We ran model simulations across the range of these soil textures to assess its sensitivity to this parameter. These simulations indicated that by increasing or decreasing $A_{\text{R}}:A_{\text{L}}$ in coarser or finer soils, respectively, nearly identical values for E_{pred} were predicted. Thus, for simplicity, the model results obtained using the average soil texture for the site (sandy loam) are presented here.

With all model parameters in hand, we simulated a drought-recovery cycle in order to explore the affect of drought on soil-plant continuum conductivity, and the post-drought recovery of transpiration in *J. osteosperma* and *P. edulis*. Ψ_{PD} was incrementally decreased from maximum measured values to minimum measured values. Ψ_{MD} was calculated from the relationship between measured Ψ_{PD} and Ψ_{MD} for both species (*J. osteosperma*, $\Psi_{\text{MD}} = (0.82 \times \Psi_{\text{PD}}) - 1.24$, $R^2 = 0.99$, $P \ll 0.001$; *P. edulis*, $\Psi_{\text{MD}} = (0.27 \times \Psi_{\text{PD}}) - 1.74$, $R^2 = 0.57$, $P \ll 0.001$). E_{pred} values were normalized (maximum E_{pred}

= 1.0), to allow for effective comparison between pre- and post-drought responses.

Statistics

All statistical analyses were performed using JMP (Version 5.1, SAS Institute, Cary, North Carolina, USA). Nonlinear curves fitted to (sap flux - D) data (Fig. 3) had the formula $y = a(1 - e^{-bx})$ (Ewers et al. 2001). Model fit was assessed by ANOVA.

RESULTS

Interannual and seasonal variation in environmental conditions

Significant variation in precipitation and available soil moisture was observed over the study. Annual precipitation varied considerably over the three years of this study (Appendix A). The 2003 and 2004 water years (1 October–30 September) had below-average precipitation, especially over the summer. The year 2005 was an above-average water year, with both winter and summer precipitation being about 145% of the normal long-term mean. This variation in precipitation was reflected in the volumetric soil moisture values (θ_{tot} ; Appendix A), with high levels of soil moisture being available for a longer portion of the growing season in 2005 than in 2004. Despite varying precipitation inputs, the annual minimum θ_{tot} was similar during all three years of the study. This is consistent with other arid and semiarid regions, indicating that year-to-year soil water storage in these systems is close to zero (Seyfried et al. 2001, 2005, Schwinning et al. 2005a).

There was a strong seasonal pattern to θ_{tot} at our study site. In general, peak values of $\theta_{\text{tot}} \approx 0.1 \text{ m}^3/\text{m}^3$ (close to field capacity for these soils) were recorded during winter and spring, whereas minimum values of $\theta_{\text{tot}} < 0.032 \text{ m}^3/\text{m}^3$, indicative of extreme soil drought, occurred during the height of the summer (Fig. 1). In all years, there was marked dry down over the course of the growing season, mitigated by periodic increases in soil moisture following rain events (Fig. 1).

Seasonal variation in sap flux

Strong seasonal variation in sap flux was observed for both *P. edulis* and *J. osteosperma* over the three years of the study (Fig. 2). Two distinct seasonal pulses in sap flux were observed at our study site: a spring and a summer pulse. The spring pulse began with the onset of measurable fluxes on day 63 (day 1 is 1 January) in 2004 and day 43 in 2005 (the onset of fluxes in 2003 was not recorded). Following the onset, sap flux increased to a maximum for both species as vapor pressure deficit (D) increased (Fig. 1). The tight correlation between sap flux and D during this period (Fig. 3A) indicated that soil moisture was not limiting. Subsequent to attaining this maximum, sap flux declined in concert with soil moisture (Fig. 3B), indicating the date at which soil moisture became limiting. This date differed between the years (Fig. 2), most likely due to the greater amount of

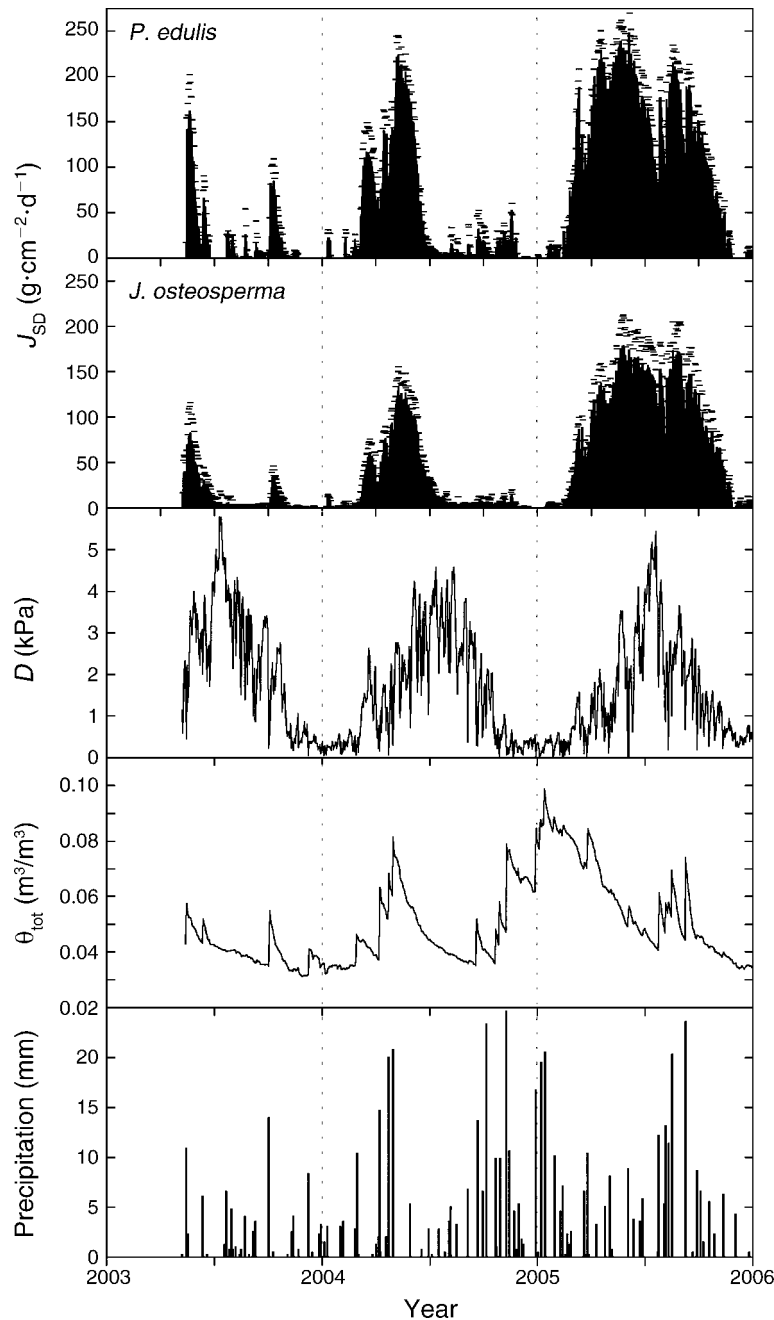


FIG. 1. Daily sap flux (J_{SD}) of *Pinus edulis* and *Juniperus osteosperma*, vapor pressure deficit (D), volumetric soil moisture (θ), and precipitation over the course of three years in southern Utah, USA.

moisture available from winter and spring precipitation in 2005 than in 2004 (Appendix A). During this time period there was no relationship between sap flux and D (data not shown).

The summer pulse was highly variable over the three years of study, highlighting the sensitivity of the system to summer rain. In the two below average precipitation years (2003, 2004), there was minimal summer rain and effectively no summer sap flux, apart from periodic

increases following rain events for *P. edulis* (Fig. 2). Sap flux increased again following large rain events late in the growing season that infiltrated to 20 cm in the soil (Fig. 2). In the wet year (2005), the pattern was quite different. The declining trend in sap flux was reversed by the arrival of the monsoon on day 204. The heavy monsoon rains (145% of normal) extended the summer pulse through to the end of the growing season (Fig. 2).

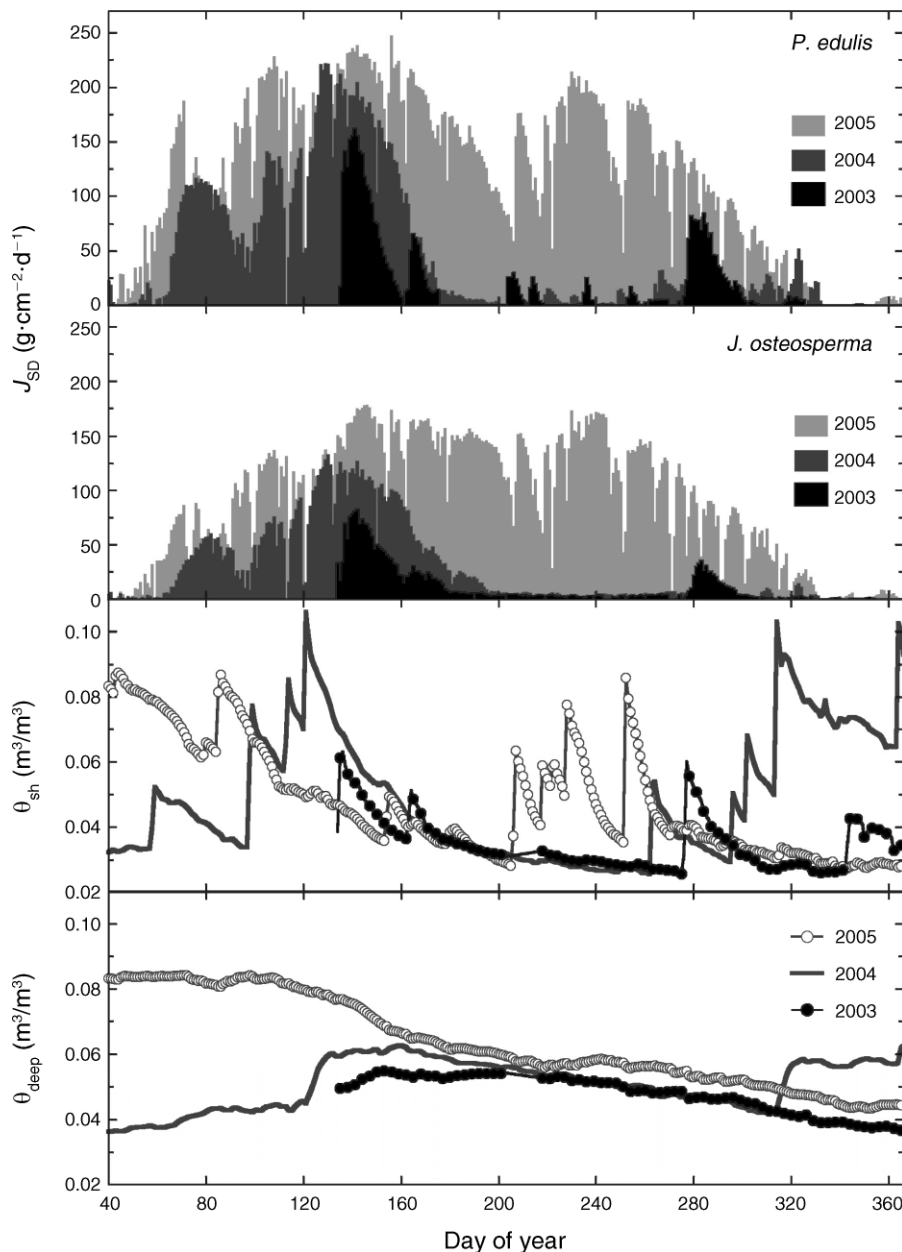


FIG. 2. Seasonal courses of daily sap flux (J_{SD}) of *P. edulis* and *J. osteosperma* and volumetric soil moisture in the shallow (θ_{sh} , 5–35 cm) and deep soil layers (θ_{deep} , 35–55 cm) for the three years of study. Note that there are no data before day 128 in 2003. On the x -axis, day 1 is 1 January.

Species responses to environmental drivers

While seasonal patterns of sap flux described above apply to both species in general, there were marked differences in the response of the two species to environmental drivers. Water potential data indicated that *P. edulis* and *J. osteosperma* employed different strategies in response to summer drought periods. During the early part of the growing season, Ψ_{PD} and Ψ_{MD} values were comparable for *P. edulis* and *J. osteosperma* (Fig. 4). However, during the summer

drought these values diverged. *P. edulis* remained isohydric, tightly regulating Ψ_{MD} so as not to exceed -2.6 MPa (Fig. 4). In contrast, *J. osteosperma* was anisohydric, allowing Ψ_{MD} to reach -6.9 MPa during the dry summers of 2003 and 2004. Paired t tests showed that there was a significant difference between Ψ_{PD} and Ψ_{MD} for *J. osteosperma* during the summer, indicating some degree of water loss over the course of the day. This was not the case for *P. edulis*.

P. edulis showed a greater sensitivity to moisture limitation than *J. osteosperma* (Fig. 5). In general, when

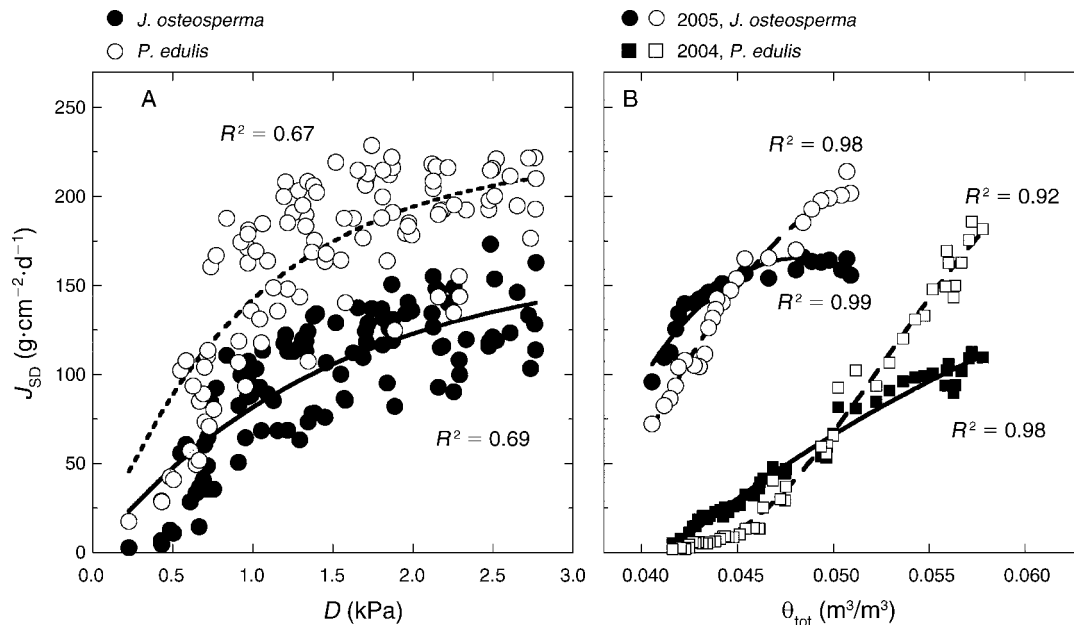


FIG. 3. Response curves of daily sap flux (J_{SD}) of *P. edulis* and *J. osteosperma* to vapor pressure deficit (D) and total soil moisture (θ_{tot}). (A) Sap flux data, when $\theta_{tot} > 0.06 \text{ m}^3/\text{m}^3$, plotted against D . Nonlinear relationships plotted are $y = 224(1 - e^{-1.01x})$ for *P. edulis* and $y = 165(1 - e^{-0.68x})$ for *J. osteosperma*. (B) Sap flux from two distinct summer dry-down periods, where $\theta_{tot} < 0.06 \text{ m}^3/\text{m}^3$, plotted against θ_{tot} . R^2 values are reported from second-order polynomial fits for all curves except for *P. edulis*, 2004 (third-order).

soil moisture was not a limiting factor due to conditions of high θ_{tot} and low D , *P. edulis* had significantly higher sap flux than *J. osteosperma* (Fig. 5, day 128). D , but not θ_{tot} (relationship nonsignificant, not shown), appeared to be the primary driver on J_s during such time periods (Fig. 3A, $\theta_{tot} \geq 0.06 \text{ m}^3/\text{m}^3$). However, when θ_{tot} declined to below $0.06 \text{ m}^3/\text{m}^3$ and D increased, sap flux in *P. edulis* declined to levels equal to and then below *J. osteosperma* (Fig. 5, days 165, 179), and *P. edulis* showed a much sharper decline in sap flux compared to *J. osteosperma* (Fig. 3B). The relative responses of *P. edulis* and *J. osteosperma* to soil drying were the same in a dry year (2004) as for a wet year (2005), although the magnitudes of the fluxes differed (Fig. 3B). Ultimately, sap flux ceased at -2.3 MPa for *P. edulis* and approached zero at approximately -4.0 MPa for *J. osteosperma* (Fig. 6).

Model results

We solved for above- and belowground plant allocation ($A_R:A_L$) at our site by comparing measured transpiration data (E_{meas}) with model predictions (E_{pred}). Transpiration measurements were well predicted when using a $A_R:A_L$ of 1 for *J. osteosperma* and 0.3 for *P. edulis* (Appendices B and C).

Post-drought fluxes in *J. osteosperma* were better predicted by assuming no recovery in xylem embolism, consistent with experimental evidence (West et al. 2007b). The model was less informative on this point for *P. edulis*, probably because with so much less xylem

embolism, the consequences of its reversal were not as significant. The good fit between E_{pred} and E_{meas} indicated that the variation in transpiration fluxes of *P. edulis* and *J. osteosperma* could be explained by changes in xylem and soil conductivities and the differences in vulnerability to cavitation and $A_R:A_L$ of the two species.

The predicted loss of conductivity caused by the summer drought was considerable in both species. For the entire soil-plant pathway, *J. osteosperma* averaged $93.7\% \pm 0.7\%$ (mean \pm SD) loss of conductivity (PLC) relative to spring conditions, and *P. edulis* averaged 83.8 ± 3.3 PLC (2003, 2004 droughts pooled). Most of this loss occurred within the soil, or rhizosphere, component (Fig. 7, "rhizosphere" datum). The two species showed important differences in the amount of drought-induced xylem cavitation. Despite *J. osteosperma* having much greater resistance to xylem cavitation than *P. edulis* (Linton et al. 1998), the model predicted that *J. osteosperma* experienced a greater loss of conductivity (60 and 40 PLC in roots and shoots, respectively) than *P. edulis* (40 and 5 PLC in roots and shoots) at the height of the drought (Fig. 7). This was due to much lower minimum Ψ_{MD} experienced by the anisohydric *J. osteosperma* compared to the isohydric *P. edulis* (Fig. 4).

Using the model to simulate water uptake through a drought cycle quantified the importance of the difference in xylem embolism between the two species for their post-drought water uptake (Fig. 8). We assumed the large loss of conductivity in the rhizosphere was readily

refilled with the advent of moisture, thus the differences in the drought recovery of the two species were due to the percentage loss of conductivity in the xylem. Following increasing water potential back to spring time values, the model predicted a persistent 45 ± 4 PLC in the soil–leaf pathway for *J. osteosperma* because of irreversible xylem cavitation, as opposed to only 6 ± 3 PLC in *P. edulis* (Fig. 8). Experimental evidence has indicated that *J. osteosperma* does not refill embolized xylem following drought, whereas *P. edulis* is capable of refilling embolized root xylem (West et al. 2007b). Thus, the persistent PLC for *P. edulis* following drought may be further reduced by the refilling of embolized xylem.

Stand level transpiration

The study site had a total basal area density of $18.4 \text{ cm}^2/\text{m}^2$ and was dominated by *J. osteosperma* (88% of the total basal area; Appendix D). Sapwood (y) and stem diameter (x) relationships were the same for *J. osteosperma* and *P. edulis* (*J. osteosperma*, $y = 0.54x - 24$, $R^2 = 0.72$, $P \ll 0.0001$; *P. edulis*, $y = 0.53x - 15$, $R^2 = 0.85$, $P \ll 0.0001$). Due to a greater total sapwood area, *J. osteosperma* contributed more to the stand-level flux than *P. edulis* (Fig. 9). The maximum daily canopy transpiration (T) at our study site was 0.34 mm/d .

Annual totals for T ranged between 10 and 50 mm/yr (Fig. 9). This represented between 6.5% and 14.5% of the total annual rainfall. At our site, the understory was negligible and *P. edulis* and *J. osteosperma* dominated the plant biomass, thus T approximates total ecosystem transpiration. Total transpiration was correlated to total annual precipitation, with a greater fraction of precipitation lost as transpiration (T/PR) during wet years (Fig. 9), indicating that the vegetation had the capacity to increase transpiration in response to wet cycles.

DISCUSSION

While year-to-year variations in soil moisture availability influence transpiration activities of *P. edulis* and *J. osteosperma*, it is the differential responses of these species to seasonal moisture and to summer drought that may have the greatest influence on the ability of these two species to persist as a dominant woodland type in the Intermountain West. Piñon disappear from piñon–juniper woodlands at lower, drier elevations (Tausch et al. 1981, Nowak et al. 1999, West 1999a, Martens et al. 2001), presumably because of their greater sensitivity to summer drought. In the piñon–juniper woodlands of the Four Corners region (southeastern Utah, southwestern Colorado, northeastern Arizona, and northwestern New Mexico), recent extended droughts have contributed to extensive mortality of *P. edulis* across broad landscape scales (Breshears et al. 2005). These massive mortality events will greatly influence community structure with cascading effects through different trophic systems (Brown et al. 2001, Mueller et al. 2005). Our detailed examination of hydraulic differences between *P. edulis* and *J. osteosperma*

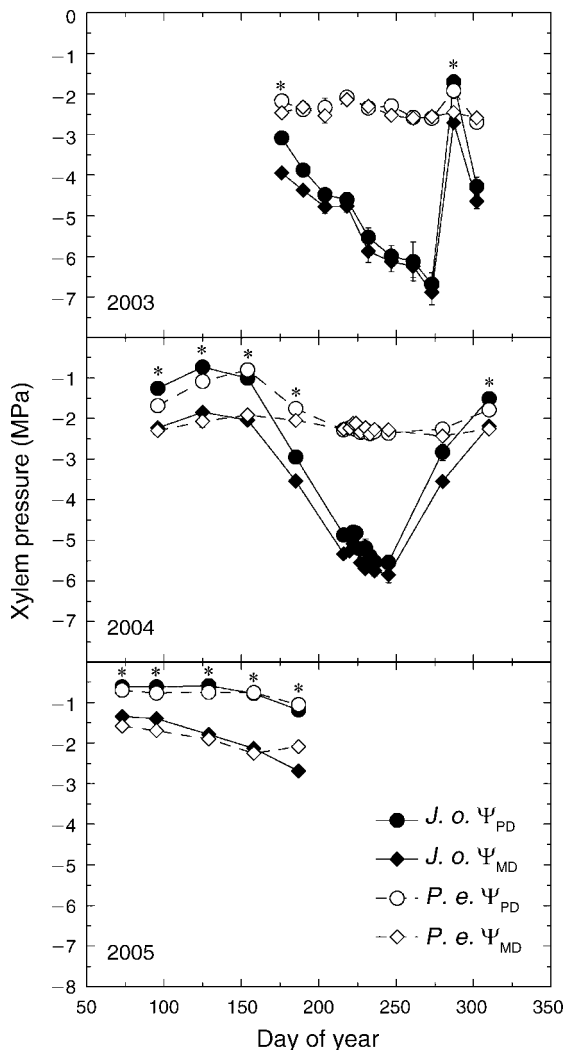


FIG. 4. Predawn (Ψ_{PD} , circles) and midday (Ψ_{MD} , diamonds) xylem water potentials for *P. edulis* (open symbols, *P. e.*) and *J. osteosperma* (solid symbols, *J. o.*) over three years. There was a significant difference between Ψ_{PD} and Ψ_{MD} for all sampling periods for *J. osteosperma* (paired t test, $P < 0.05$). Significant differences ($P < 0.05$) for *P. edulis* are denoted with asterisks.

may contribute to understanding of the mechanisms that lead to differential tree mortality in piñon–juniper woodlands and the sensitivity of these systems to climate change.

Species differences in hydraulic strategies

P. edulis and *J. osteosperma* had remarkably different water relations. *P. edulis* was capable of higher fluxes, but was more sensitive to drought than *J. osteosperma* (Figs. 3 and 5). Our model simulations indicated that isohydric *P. edulis* operated with much less xylem cavitation during drought relative to anisohydric *J. osteosperma* (Figs. 4 and 8). These species represent two contrasting strategies of water use. *P. edulis*

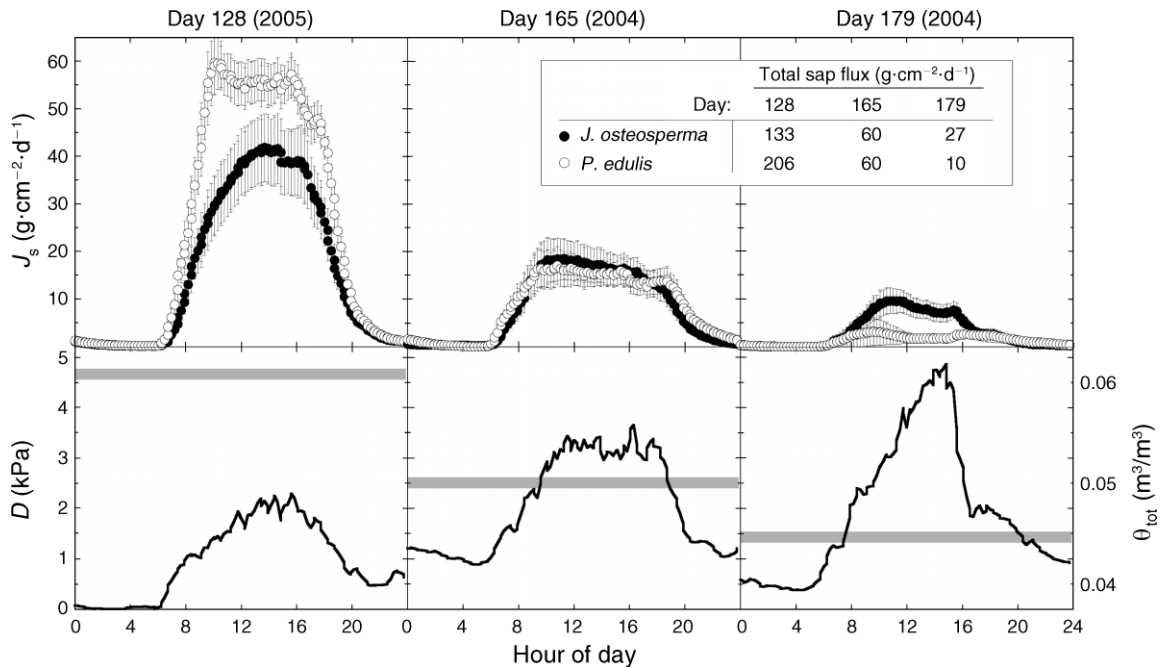


FIG. 5. Diurnal courses of instantaneous sap flux (J_s) of *P. edulis* and *J. osteosperma* over three days of varying soil moisture (θ_{tot} , gray line) and vapor pressure deficit (D , black line). The inset shows daily totals of sap flux for the three days.

sacrifices cavitation resistance and drought tolerance for maximizing water uptake under favorable conditions. More cavitation-resistant xylem tends to have a lower maximum conductivity under favorable conditions when there is no cavitation. In conifers, this trade-off appears to result from mechanical constraints (Pittermann et al. 2006). Tracheids that are resistant to cavitation and can hold water under lower negative pressure must have stronger walls to maintain a comfortable margin of safety from implosion while still functioning to hold up the tree (Hacke et al. 2001). Stronger walls require narrower lumens (Pittermann et al. 2006), which have the disadvantage of offering more resistance to water flow. Thus, the higher fluxes of *P. edulis*, when conditions are favorable, may come at the cost of lower tolerance of negative pressures. *P. edulis* uses isohydric stomatal control (Figs. 4 and 6) to avoid low negative pressure and, consequently, cavitation during the summer drought. In this way it can not only use water effectively during the spring, but by protecting itself from excessive cavitation, together with the ability to refill embolized root xylem (West et al. 2007b), it can also use water almost as effectively after the summer drought has broken. The cost of this strategy is a complete shutdown of gas exchange over potentially many weeks during the growing season.

In contrast, *J. osteosperma* sacrifices high xylem conductivity and springtime fluxes for greater resistance to cavitation. It couples this with anisohydric stomatal regulation that extends its gas exchange much farther into the drought than *P. edulis*, mining as much soil water as possible in spite of suffering considerable

cavitation. Our model results supported the experimental finding that *J. osteosperma* does not refill embolized xylem (West et al. 2007b). Thus, as a result of this cavitation, *J. osteosperma* also sacrifices the ability to effectively use late summer rainfall.

As a consequence of these different strategies, the competitive success of the two species should depend on the relative frequency and duration of periods where Ψ_{PD} is either above or below -2 MPa. Piñon appears to have higher photosynthetic rates than juniper (Lajtha and Getz 1993, Nowak et al. 1999). *P. edulis* has higher leaf area to sapwood area ratios than *J. osteosperma*

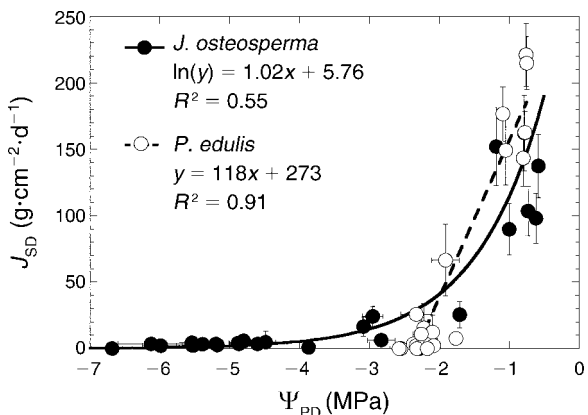


FIG. 6. Daily sap flux (J_{SD}) vs. predawn xylem water potential (Ψ_{PD}) for *P. edulis* and *J. osteosperma*. Sap flux declines to zero at -2.3 MPa for *P. edulis* and approaches zero at -4.5 MPa for *J. osteosperma*.

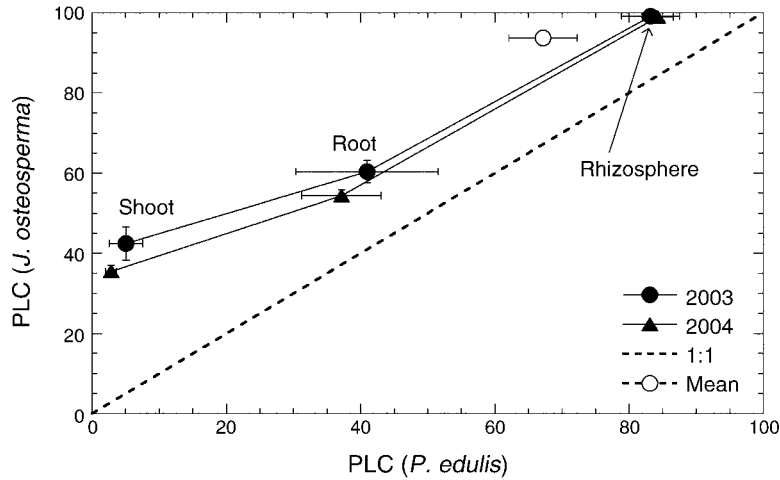


FIG. 7. Predicted percentage loss of conductivity (PLC) at the peak of the drought in 2003 and in 2004 for the shoot, root, and rhizosphere of *J. osteosperma* and *P. edulis*. The mean represents the overall loss of conductivity for the whole soil–plant hydraulic pathway. *J. osteosperma* experienced a greater degree of PLC than *P. edulis*, particularly in the shoot. The majority of the PLC occurred in the rhizosphere for both species, but particularly for *P. edulis*.

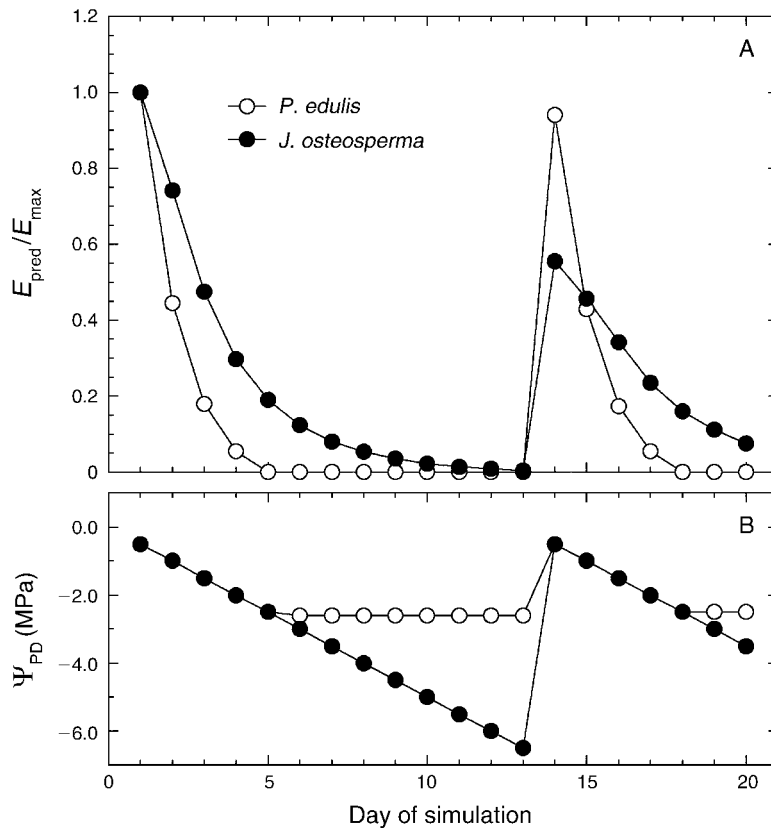


FIG. 8. Simulated drought recovery for *J. osteosperma* and *P. edulis* showing (A) normalized predicted transpiration (E_{pred}/E_{max}) and (B) Ψ_{PD} used for the simulation. The simulation consisted of a drying period from maximum to minimum observed Ψ_{PD} (days 1–13 of the simulation). Ψ_{PD} was reset to maximum observed values on day 14, followed by another drying period (days 15–20). Drought recovery differed between the species: *P. edulis* had 94% recovery, and *J. osteosperma* had 55% following rewetting.

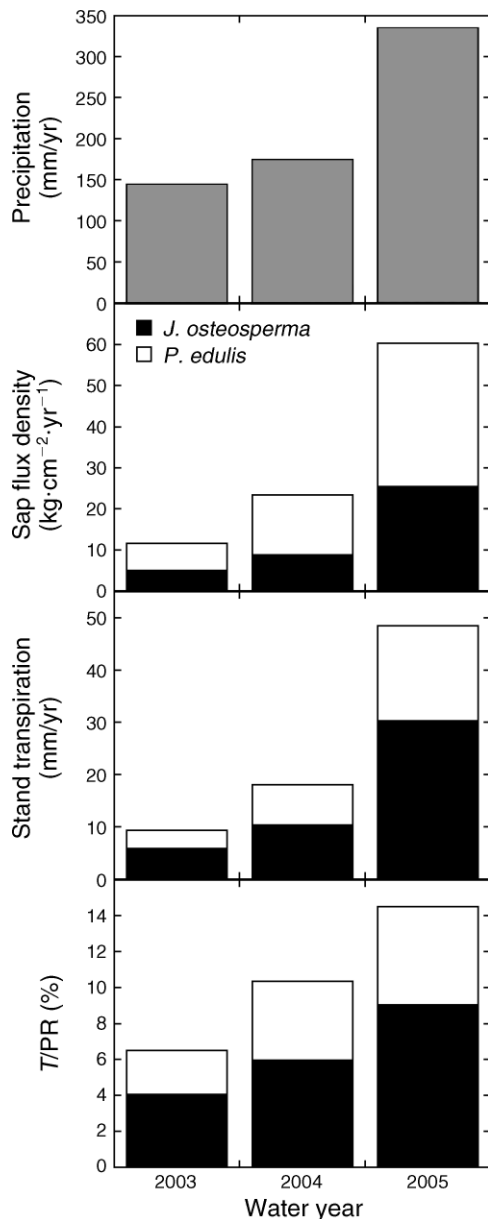


FIG. 9. Total annual rainfall (PR), total annual stand transpiration per sapwood area (sap flux density), total annual stand transpiration per ground area (T), and T/PR over the three years of study. Contributions of *J. osteosperma* and *P. edulis* to the annual total are shown as black and white portions of bars, respectively.

(Schuler and Smith 1988). Thus when sap flux in *P. edulis* is equal to or higher than *J. osteosperma* (i.e., $\Psi_{PD} > -2$ MPa), *P. edulis* should outperform *J. osteosperma*. However, if $\Psi_{PD} < -2$ MPa for prolonged periods, this may lead to mortality in *P. edulis*. Mortality in *P. edulis* is not well understood, but it is likely that the effects of prolonged water stress and consequent depletion of carbon reserves makes *P. edulis* susceptible to beetle attack, leading to mortality (Allen

and Breshears 1998). *J. osteosperma* avoids this fate through an anisohydric strategy, but at the cost of potentially severe cavitation in above ground tissues. *J. osteosperma* trees often contain significant dieback in their canopies, possibly from segmented hydraulic failure following drought. This is not seen in *P. edulis*, where trees are usually entirely alive or entirely dead, as would result from the isohydric strategy described above. These differences in standing architecture appear to reflect the different hydraulic strategies and thus possibly different causes of mortality for these species.

An interesting result of our model simulations was that both species appeared to have low $A_R:A_L$ that shifted hydraulic failure to the rhizosphere (Fig. 7). Concentrating hydraulic failure in the rhizosphere may help to isolate the plant from low water potentials in the soil and prevent excessive, irreversible cavitation from occurring in the xylem. As the rhizosphere is a readily repairable component of the hydraulic continuum, having a low $A_R:A_L$ may aid post-drought recovery of water transport in species subjected to a variable soil moisture regime. The relative differences in the $A_R:A_L$ estimate for the two species ($P. edulis < J. osteosperma$) were consistent with our understanding of optimum water transport and the xylem properties of these two species. Optimum water transport occurs when the rhizosphere and xylem are co-limiting (Sperry et al. 2002). A higher allocation to root biomass reduces the rate of water uptake per root surface area (rhizosphere flux density) thereby reducing the chance of hydraulic failure in the soils surrounding the roots (Sperry et al. 1998, 2002). Species with a higher resistance to cavitation (e.g., *J. osteosperma*) require a greater $A_R:A_L$ in order to avoid rhizosphere failure before xylem becomes co-limiting, whereas for species with a lower resistance to cavitation (e.g., *P. edulis*) optimum $A_R:A_L$ is much lower. In a common soil type, we would predict that *P. edulis* would become xylem limited at lower $A_R:A_L$ than *J. osteosperma*.

Previous work has examined the differences between these species in their capacity to utilize summer rain (Ehleringer et al. 1991, Evans and Ehleringer 1994, Williams and Ehleringer 2000, Leffler et al. 2002). Clearly, both *P. edulis* and *J. osteosperma* have the capacity to use summer moisture when abundant summer moisture is available (2005; Fig. 2). However, it appears as if *P. edulis* is more responsive to small summer rain events in dry years than *J. osteosperma* (West et al. 2007a). Response to summer moisture pulses by *P. edulis* may be important in compensating for the loss of carbon gain during periods when $\Psi_{PD} < -2$ MPa.

Interannual and seasonal variation in transpiration

The considerable year-to-year variation in water fluxes at our site is consistent with our understanding of the variability in moisture availability in arid and semiarid systems (Noy-Meir 1973, Loik et al. 2004, Schwinning and Sala 2004) and emphasizes the need for



PLATE 1. Piñon-juniper woodland near the southern Utah (USA) field site, with the La Sal Mountains in the background. Photo credit: A. West.

long-term, continuous measurements of water use in order to accurately capture the dynamics of these systems. Across the three years of this study, annual transpiration was positively correlated with annual precipitation (Fig. 9), a common observation for arid and semiarid regions (Ehleringer et al. 1999), where plants are adapted to take advantage of pulses of moisture (Ehleringer 1994, Schwinning et al. 2004). In addition, the fraction of precipitation lost as transpiration (T/PR) also increased with increasing precipitation (Fig. 9). An increasing T/PR may be due to a combination of physical and biological factors that affect plant uptake of moisture. Simplistically, an increase in annual rainfall should result in moisture penetrating deeper into the soil profile, reducing surface evaporative losses and allowing a greater fraction to be taken up by plants and transpired (Loik et al. 2004). However, the seasonality of precipitation complicates this picture. Wet years can be caused by an increase in winter or summer precipitation, or both. Winter precipitation falls at low intensity during times of low evaporative demand and thus percolates deeper into the soil than a similar amount of rainfall falling in summer, at high intensity, and during times of higher evaporative

demand (Caldwell 1985, Comstock and Ehleringer 1992, Ehleringer et al. 1998, 1999, Williams and Snyder 2003). Thus one would expect T/PR to be higher for winter-derived precipitation than summer (Ehleringer et al. 1999). It has been demonstrated that piñon-juniper stands in Arizona were less productive than stands in the Great Basin despite wetter summers in Arizona (Grier et al. 1992), possibly due to the relative inputs of winter precipitation in these regions. In this study, the fraction of summer rain increased with increasing annual precipitation (Appendix A) and thus changes in seasonal rainfall distribution alone cannot account for the observed changes in T/PR . However, an increase in deep moisture, from winter precipitation, resulting in an increase in T/PR is supported by our data. In the spring of 2005, transpiration remained high, despite the drying of shallow soil layers, due to the presence of deeper moisture (Fig. 2). This was not the case in 2004, when the absence of deeper moisture left transpiration fluxes closely coupled to shallow soil moisture. Additionally, during the summer, transpiration fluxes were higher in a wet year (2005) relative to a dry year (2004) at the same θ_{tot} (Fig. 3B). This could indicate that the plants had access to deeper moisture below the range of our sensors

(50 cm) in the wet year that increased T/PR . While the soils at our site were shallow, it is likely that these plants have roots that penetrate cracks in the rock and extend deeper than 50 cm (Foxy and Tierney 1987, Leffler et al. 2002). This is supported by isotopic evidence of deeper water uptake by *P. edulis* and *J. osteosperma* at this site (West et al. 2007a). Potentially, deeper soil moisture is an important resource following more mesic climate cycles and plants may shift allocation in absorbing root areas accordingly (Schwinning and Sala 2004).

Seasonal variation in moisture had a large effect on transpiration. Over the course of this study, winter and spring precipitation provided the majority of the moisture for transpiration over the growing season, a finding similar to that for other species on the Colorado Plateau (Schwinning et al. 2005b). Winter and spring precipitation provided the moisture for the spring pulse in transpiration, which in the two dry years (2003, 2004) was effectively the only period of transpiration (Fig. 1). However, it is apparent that monsoonal inputs have a significant impact on this system. Below-average winter precipitation and the absence of significant summer rain in 2003 and 2004 reduced transpiration to close to zero over the summer (Fig. 2). This placed considerable drought stress on the plants as indicated by the negative water potentials measured in *J. osteosperma* (Fig. 4) and the mortality of several *P. edulis* at the study site over the summers of 2003 and 2004 (A. West, *personal observation*). When monsoon rains were heavy, as in 2005, the system had a large capacity for response (Fig. 2). The monsoon rains of 2005 extended the growing season by ~100 days (Fig. 2). The wet winter preceding the 2005 monsoon may have created conditions that favored the response of plants to this summer moisture, as the history of moisture conditions modulates the response of plants to moisture events (Schwinning et al. 2005a). Such a large response to monsoonal moisture may not have occurred if the preceding conditions had been dry. Nevertheless, it is likely that these wet years significantly affect the ecology of these woodlands, by being the years of increased productivity, recruitment, and establishment (Gottfried 1987).

Estimates of transpiration based on scaling of sap flux measurements are subject to a number of potential errors. These include inadequate representation of radial variation in flow rates (Clearwater et al. 1999), tree-to-tree variation (Cermak et al. 2004), or stand level sapwood area. In some cases, sap flux can underestimate transpiration when compared with other methods (Wullschlegel and Hanson 2006) and thus the absolute magnitude of our estimates should be viewed accordingly. Our estimates of T (Fig. 9) are comparable with other estimates for piñon–juniper woodlands derived from different methods. Estimates in the literature include 0.09–0.21 mm/d for *J. occidentalis* woodlands (leaf level model [Miller et al. 1987]), 0.19–0.99 mm/d for a piñon–juniper woodland in New Mexico (canopy diffusion model [Lane and Barnes 1987]) and 0.33–0.87

mm/d for a *J. osteosperma* woodland in Northern Utah (scaled-up leaf-level fluxes [Leffler et al. 2002]). The percentage of precipitation leaving our site as transpiration (T/PR , Fig. 9) is at the low end of the 15–80% range calculated by Lane and Barnes (1987) for piñon–juniper woodlands. This is not unreasonable, however, considering the low leaf area index, shallow soils, and exposed rocks of our site, all of which would favor increased evaporation and runoff.

Sensitivity of P. edulis and J. osteosperma to changes in precipitation patterns

Our detailed examination of hydraulic differences between *P. edulis* and *J. osteosperma* illustrates the importance of considering differences in key ecophysiological parameters when attempting to predict the consequences of climate change on species distributions. The current distributions of *P. edulis* and *J. osteosperma* are highly suggestive of different dependencies on summer rainfall (West et al. 2007a). *P. edulis* appears limited to areas receiving a sizeable fraction of annual precipitation in the summer, whereas *J. osteosperma* occurs in areas with a higher proportion of winter precipitation. Our hydraulic transport model shed light on a potential mechanistic basis for these distribution differences. The characteristics of isohydric regulation of water potential, low $A_R:A_L$ and efficient water transport under mesic conditions of *P. edulis* seem adaptive for utilizing frequent inputs of moisture over the growing season. In contrast, the characteristics of anisohydric regulation of water potential, cavitation resistant xylem, and higher $A_R:A_L$ of *J. osteosperma* seem adaptive for maximally extracting moisture from the soil under conditions of drought. Considering that summer precipitation environments tend to be more pulsed than winter environments (Loik et al. 2004), these two patterns would seem to be adaptive for summer and winter dominated precipitation environments respectively. As a result shifts in seasonal rainfall patterns across the range of these woodlands would likely impact the ability of these two species to persist as a dominant woodland type in the Intermountain West.

Our mechanistic approach to understanding the differential response of these species to seasonal moisture availability should improve our ability to predict the consequences of change in seasonal precipitation patterns on *P. edulis* and *J. osteosperma* distributions. Future climate conditions in the southwestern United States are expected to be warmer with an increase in frequency and variability of droughts due to the combined effects of increased potential evapotranspiration and decreased summer moisture (Gregory et al. 1997, Houghton et al. 2001, Cook et al. 2004). Extended summer drought could push *P. edulis*, and to a lesser extent *J. osteosperma*, across a mortality threshold with consequences for the whole ecosystem (Breshears et al. 2005, Mueller et al. 2005). It remains a significant future

challenge to determine best practices for land management agencies to mitigate these potential consequences.

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APPENDIX A

Climate variables at our field site over the course of this study showing the variation in precipitation, volumetric soil moisture, and temperature (*Ecological Archives* A018-031-A1).

APPENDIX B

Regression parameters for modeled vs. measured transpiration values across the range of root:leaf area ratios run in our simulations (*Ecological Archives* A018-031-A2).

APPENDIX C

A figure showing measured leaf-level transpiration and predicted transpiration for *Pinus edulis* and *Juniperus osteosperma* over the course of the study (*Ecological Archives* A018-031-A3).

APPENDIX D

Allometric parameters used to scale sap flux measurements to stand transpiration (*Ecological Archives* A018-031-A4).