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Seasonal variations in moisture use in a piñon–juniper woodland

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Abstract In water-limited environments of the intermountain region of North America, summer precipitation may play a role in the structure and function of aridland communities and ecosystems. This study examined the potential reliance on summer precipitation of two widespread, coexisting woody species in the southwestern United States, *Pinus edulis* Englmn. (Colorado piñon) and *Juniperus osteosperma* (Torr) Little (Utah juniper). The current distributions of *P. edulis* and *J. osteosperma* are highly suggestive of different dependencies on summer rainfall. We hypothesized that *P. edulis* was dependent on summer precipitation, utilizing summer precipitation even during extremely dry summers, whereas *J. osteosperma* was not dependent, using summer precipitation only when amounts were above some minimum threshold. Using sap flux and stable isotopic methods to assess seasonal water sources and water use efficiency, we examined the response of these two species to seasonal variations in moisture at a site located near the northern limits of the North American monsoon. Both sap flux and isotopic results indicated that *P. edulis* was responsive to summer rain, while *J. osteosperma* was not. Following summer rain events, sap flux density increased in *P. edulis* for several days, but not in *J. osteosperma*. Isotopic evidence indicated that *P. edulis* took up summer-derived moisture to a greater extent than *J. osteosperma*. Values of the natural abundance stable isotope ratio of carbon of leaf soluble carbohydrates increased over the summer for *P. edulis*, indicative of assimilation at higher water use efficiency, but were invariant for *J. osteosperma*. Our results supported the hypothesis that *P. edulis* and *J. osteosperma* are differentially sensitive to summer precipitation and are discussed in the light of potential changes in the seasonality of precipitation associated with climate change.

Keywords Summer precipitation · *Pinus edulis* · *Juniperus osteosperma* · Transpiration · Water uptake

Introduction

The seasonality of precipitation structures moisture resources in semiarid environments, and impacts plant resource acquisition and survivorship (Schwinning et al. 2004, 2005; Weltzin et al. 2003; Weltzin and McPherson 2003). Understanding the role of the seasonality of precipitation on vegetation is critical if we are to be able to accurately predict the effects of climate change on terrestrial ecosystems, yet relatively little research has been focused on these questions (Weltzin et al. 2003; Weltzin and McPherson 2003). However, recent attempts to model future species distributions under predicted climate scenarios have shown seasonal precipitation to be an important predictive variable in species distributions (Arundel 2005; Cole and Arundel 2007; Guisan and Thuiller 2005; McKenzie et al. 2003; Midgley et al. 2002; Thuiller et al. 2006).

In the Great Basin and Colorado Plateau of the intermountain region of North America, precipitation falling in winter has a markedly different effect on soil moisture than

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that of summer precipitation. Precipitation falling during winter, when there is low evaporative demand and little plant activity, accumulates in the soil and recharges the soil profile, providing a stable moisture resource for the coming growing season (Comstock and Ehleringer 1992). In contrast, precipitation falling during summer, during times of high evaporative demand, readily evaporates from the soil surface, resulting in reduced infiltration and shallower soil moisture resources that are short-lived. These summer precipitation events can be highly variable, and do not necessarily result in plant growth (Ehleringer et al. 1999; Schwinning et al. 2005; Snyder et al. 2004). As a result, winter precipitation is typically more important for annual productivity even though it falls during times of low plant activity (Comstock and Ehleringer 1992; Schwinning et al. 2005).

Summer precipitation may fulfill a variable, but critical role in the structure and function of arid and semiarid communities and ecosystems (Ehleringer et al. 1991, 1999). One of the major challenges facing woody plants in semiarid ecosystems is the discontinuous nature of moisture availability (Loik et al. 2004; Noy-Meir 1973; Schwinning et al. 2004; Williams and Snyder 2003). In these systems, summer precipitation may be critical for breaking an extended summer drought that might otherwise result in plant mortality, with lasting effects on species composition (Schwinning et al. 2005). Years of above-average summer precipitation may also be important for episodic recruitment and growth in long-lived woody species (Grubb 1977; Neilson 1987). In addition, differential use of summer and winter moisture by plants potentially affects a variety of community- and ecosystem-level properties, such as site water balance (Huxman et al. 2005; Neilson 1995), responses to climate change (Ehleringer et al. 1998; Schwinning et al. 2005) and patterns of species coexistence (Chesson et al. 2004; Fowler 1986).

In the intermountain region of North America, summer and winter precipitation are derived from different weather systems (Adang and Gall 1989; Bryson and Hare 1974; Higgins et al. 1997) that are likely to be differentially affected by changes in climate (Loik et al. 2004). Despite uncertainty in current regional model predictions, the southwestern United States seems likely to experience more frequent and severe summer droughts in the future (Cook et al. 2004; Gregory et al. 1997; Houghton et al. 2001). As a result, understanding the importance of summer precipitation in widespread southwestern ecosystems is an important research question.

Piñon–juniper woodlands occupy approximately 223,000 km^2 across the western United States (Mitchell and Roberts 1999) and span a gradient in precipitation, from winter-dominated in the northwest, to summer-dominated in the southwest (West 2006). Within the piñon–juniper woodland species complex, the current distributions of *Pinus edulis* Englmn. and *Juniperus osteosperma* (Torr) Little are highly suggestive of different dependencies on summer precipitation (Neilson 1987). Both species co-occur on the Colorado Plateau where summer precipitation makes up at least 30% of the annual rainfall (West 2006; Fig. 1). However, *J. osteosperma* also extends into the Great Basin, where there can be very limited summer precipitation in some locations. *P. edulis* does not extend into the Great Basin and its distribution appears to be restricted to areas where summer rainfall is frequent (Cole and Arundel 2007).

Despite these differences in distribution, differential sensitivity to summer precipitation between the two species has not been consistently demonstrated. Previous water sourcing studies have indicated that uptake of summer precipitation in *P. edulis* and *J. osteosperma* is variable in space and time (Donovan and Ehleringer 1994; Evans and Ehleringer 1994; Flanagan et al. 1992; Gregg 1991; Leffler et al. 2002; Williams and Ehleringer 2000). However, both species appear capable of taking up summer-derived moisture when it is abundant (Williams and Ehleringer 2000). These previous studies used isotopes within xylem water as tracers of water uptake; however, there has been little work combining isotopic composition of stem water with flux measurements and leaf-level properties in these species in order to verify differences in functional utilization of summer precipitation events. In particular, the recent advances in our understanding of the isotopic signature of soluble carbohydrates (Brugnoli et al. 1988; Gottlicher et al. 2006; Keitel et al. 2003; Scartazza et al.

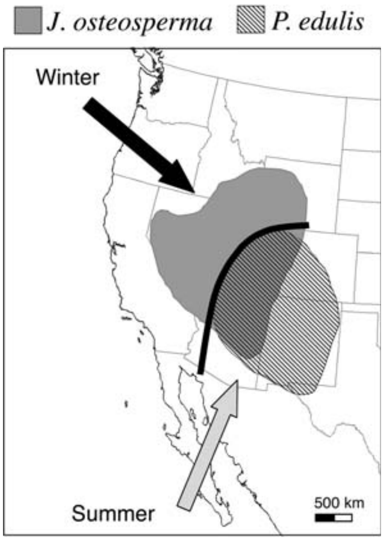


Fig. 1 A map of the western United States showing the simplified current distributions of *Juniperus osteosperma* and *Pinus edulis*, the prevailing seasonal moisture systems and the approximate northern limit of summer precipitation (*solid black line*)

1998) have the potential to add to our understanding of summer precipitation response in these species.

In this paper we examine the differences in functional utilization of summer precipitation of *P. edulis* and *J. osteosperma* by combining several independent lines of evidence including seasonal variations in transpiration (sap flux), source water [natural abundance stable isotopic ratios of hydrogen (δ^2H) and oxygen (δ^{18}O)] and stomatal limitations on photosynthesis [natural abundance stable isotopic ratio of carbon (δ^{13}C) of soluble leaf carbohydrates ($\delta^{13}C_s$)]. We hypothesized that *P. edulis* was dependent on summer precipitation, utilizing summer precipitation even during dry summers, whereas *J. osteosperma* was not dependent, using summer precipitation only when in abundance, but not at low levels. We reasoned that functional differences between the species would be most apparent during times of water stress. If *P. edulis* responded to summer moisture during times of severe water deficit, this would indicate a reliance on summer moisture for survival. Conversely, a lack of response in *J. osteosperma* would suggest no dependence on summer precipitation for survival. Specifically, we hypothesized that: (1) water sources of *P. edulis* and *J. osteosperma* would not differ during the winter, (2) *P. edulis* would be more responsive to summer pulses of moisture in a dry year than *J. osteosperma*, and lastly that (3) carbon isotopes of soluble leaf sugars would indicate a greater degree of stomatal sensitivity to moisture variations over the summer drought for *P. edulis* than *J. osteosperma*.

Materials and methods

Site description

The study site was a mature piñon–juniper woodland near Canyonlands National Park in southern Utah (latitude 38°56′N, longitude 109°82′W), in the northern reaches of the North American monsoon. The site was located at 1,800 m elevation and had a negligible slope. 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. 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. Thirty-year climate data from The Neck, Canyonlands National Park, approximately 11 km from our site, gave 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, http://www.wrcc.dri.edu). During the 2 years of this study, summer precipitation (June–September) was 33 mm (2003) and 46 mm (2004), representing 40% and 55% of the long-term mean, respectively.

Soil and precipitation measurements

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 were scaled to volumetric water content (θ; m^3 m^{-3}) by calibrating with gravimetrically determined soil moisture values taken from adjacent locations under a range of soil moistures. Rainfall was measured with a tipping bucket rain gauge (TE525; Texas Electronics, Dallas, Tex.). All measurements were made at 30-s intervals with 10-min averages stored on a CR23x datalogger (Campbell Scientific, Logan, Utah).

Sap flux measurements

Sap flux was measured with 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 by the empirical equation (Granier 1985; Granier 1987):

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

where J_s is sap flux density of the sapwood (in g cm^{-2} 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 non-uniform sapwood depth, were avoided. When installing the probes, bark and phloem were removed from a 2-cm^2 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 (usually about 50 cm).

Sap flux values reported in this paper represent the average J_s for all individuals of the species ($n \approx 10$). Daily sums were calculated as the total sap flux over the daylight hours (determined from photosynthetically active radiation measurements). Differences in sap flux responses of *P. edulis* and *J. osteosperma* to precipitation events (Fig. 2) were visually determined.

Plant water potential measurements and stomatal conductance

Plant water potential (Ψ) measurements were made predawn (Ψ_{PD}; 1.5 h before sunrise) and midday (Ψ_{MD}; approximately 12:30 p.m.). Distal twigs of *J. osteosperma* and *P. edulis* ($n = 6$ per species) were measured with a Scholander-type pressure chamber (PMS, Corvallis, Oreg.). Twigs subtending well-lit, healthy foliage were excised, using a sharp razor blade, from the south side of trees instrumented with sap flow sensors. Ψ measurements were made in the field immediately after excising the twig. Ψ_{PD} measurements were used to predict stomatal conductance (g_s) for *P. edulis* and *J. osteosperma* using previously derived empirical relationships for these species (Williams and Ehleringer 2000).

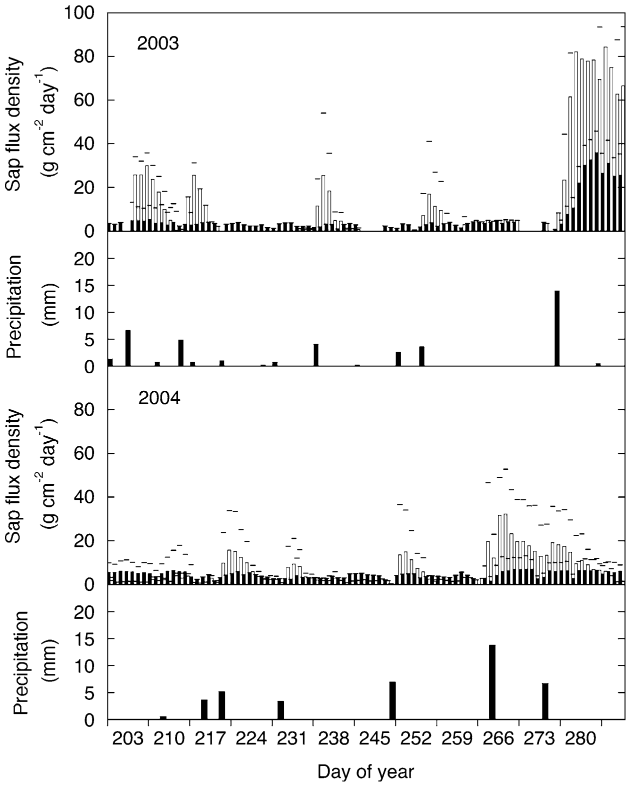


Fig. 2 Sap flow of *P. edulis* (*white bars*) and *J. osteosperma* (*black bars*), and rainfall over two dry summers in southern Utah, showing greater responsiveness to summer precipitation events for *P. edulis*. *Dashes* represent SEs. Sap flow values are the mean of five to ten trees per species. Where no data are shown, sap flux could not be resolved above zero. There were no missing data for this time period

Environmental water sampling

δ^2H and δ^{18}O were measured in waters from a variety of sources. Precipitation was collected at our fieldsite via a funnel connected to a 2-l bottle. The bottle contained 5 mm of mineral oil to prevent evaporative enrichment of the collected precipitation. Once a month, precipitation was sampled from below the mineral oil layer, via Pasteur pipette, and was placed into a 10-ml water-tight glass vial, sealed with Parafilm. The collector was then emptied and reset. Precipitation samples were collected from April 2004 to August 2005.

Soil water samples were obtained, at 5-cm increments, from freshly dug soil pits. Samples were collected immediately after clearing the face to prevent evaporative enrichment. Due to the shallow soils at our site, samples were rarely collected below 40 cm. Each sample consisted of approximately 10 cm^3 of soil and was placed in a water-tight glass vial, sealed with Parafilm, which was then placed in a cooler containing dry ice. Results from the soil water isotopic analyses were combined into two soil layers, 5–20 cm (shallow) and 21–45 cm (deep) for data analysis.

Plant source water samples were obtained by sampling fully suberized twigs of *J. osteosperma* and *P. edulis* that were upstream from any foliage. Stem samples (~60 × 10 mm) were excised from the south side of the tree at midday, and were then immediately placed in water-tight glass vials, sealed with Parafilm and placed in a cooler containing dry ice. Soil and stem samples were collected from August 2003 to July 2004.

Soil and stem samples were kept frozen in the laboratory until ready for water extraction. The methodology for water extraction for isotopic analysis has been previously described (West et al. 2006). Precipitation samples did not require extraction, but were filtered prior to isotopic analysis.

δ^{13}C and %N of leaf material

We measured $\delta^{13}C_s$ in *P. edulis* and *J. osteosperma* in order to examine the seasonal changes in photosynthetic response of these two species. Recent studies have shown δ^{13}C in soluble carbohydrates to be a useful predictor of short-term plant response to environmental drivers (Brugnoli et al. 1988; Gottlicher et al. 2006; Keitel et al. 2003; Scartazza et al. 1998). Leaves were sampled from new, healthy foliage on the south side of the tree, 1 h before sunset. Once cut from the tree, leaves were immediately immersed in liquid nitrogen and then placed in vials and kept frozen on dry ice for transport back to the laboratory. In the laboratory, samples were kept frozen at –80°C until analyzed. Leaves were sampled over the 2004 growing season.

Soluble carbohydrates were extracted from the leaves using a procedure modified from Brugnoli et al. (1988) and analyzed for δ^{13}C; 150 mg of sample was ground in a ball mill and then placed in a 50-ml centrifuge tube with 35 ml of de-ionized water. The centrifuge tube was boiled in a water bath for 30 min and then left to cool. The sample was centrifuged for 15 min at 12,100 *g* following which the supernatant was collected and passed through a C-18 Sep-Pak cartridge (Waters, Milford, Mass.) to remove large organic molecules. The sample was then passed through an ion-exchange column, consisting of Dowex-50 and Dowex-1 (Sigma-Aldrich, St Louis, Mo.), and filtered. The remaining sample was freeze-dried. Approximately 2 mg of this sample was then weighed out into tin capsules for stable isotope analysis.

A portion of the leaves collected as described above were used to determine the nitrogen content of the bulk leaf tissue (%N). Whole leaf tissue was dried at 70°C for 48 h and then finely ground in a ball mill. Samples were analyzed with a Carlo Erba elemental analyzer (EA 1108) coupled with a Delta-S continuous-flow isotope ratio-mass spectrometer (Thermo-Finnigan, Bremen, Germany). Due to the low nitrogen content of the material, approximately 6 mg was used to obtain reliable estimates of %N.

Isotopic analyses

For water samples, microliter quantities of water were injected directly into a TC/EA coupled to a Delta Plus XL isotope ratio mass spectrometer (Thermo-Finnigan) (Gehre et al. 2004). Both δ^2H and δ^{18}O were obtained from the analysis. Leaf samples were analyzed for δ^{13}C in a Carlo Erba elemental analyzer (EA 1108) coupled with a Delta-S continuous-flow isotope ratio-mass spectrometer (Thermo-Finnigan). Isotope ratios are expressed in ‰ relative to Vienna standard mean ocean water (δ^2H and δ^{18}O) and Peedee belemnite (δ^{13}C). All samples were analyzed at the SIRFER facility (University of Utah, Salt Lake City, Utah). Measurement precision was 1.56 (δ^2H), 0.19 (δ^{18}O), and 0.02‰ (δ^{13}C).

Water source modeling

In order to determine the fractional contribution of water sources to the plants, we used IsoSource, a visual basic program designed to solve for all possible source contributions of a mixture based on a linear mixing models (Phillips and Gregg 2003). We used IsoSource as our two isotopes (δ^2H and δ^{18}O) were strongly correlated (r = 0.97), rendering the use of a traditional three-end-member mixing model impossible (Phillips and Gregg 2001). Two of the source endpoints were derived from the 5- to 20-cm-layer and 21- to 45-cm-layer soil water isotopic measurements. We created a third endpoint to represent a stable, deeper source of moisture available to the plants. The isotopic composition of this moisture source was set to the winter precipitation flux-weighted isotope ratio (δ_{flux}) measured at our site, the rationale being that winter precipitation was most likely to recharge this deep moisture source at our site. The δ_{flux} was calculated as:

$$\delta_{\text{flux}} = \frac{\Sigma(\delta_i p_i)}{\Sigma(p_i)} \quad (2)$$

where δ_i = δ^2H or δ^{18}O of precipitation in the *i*th sample (‰), and p_i = the amount of precipitation comprising that sample (mm). The isotopic composition of this deeper moisture source was kept constant over the course of the year, assuming that it was sufficiently deep not to be subject to evaporation.

The model predictions contained considerable uncertainty for source contributions from the two shallow soil layers, thus we combined these two layers post hoc, following the approach suggested by Phillips et al. (2005), to provide estimates of fractional contributions of surface soil (5–45 cm) and deeper (>45 cm) moisture sources.

Results

Sap flux responses to summer moisture pulses

Following periodic summer precipitation pulses (days 200–273), sap flux increased in *P. edulis*, but not in *J. osteosperma* (Fig. 2). These precipitation events were only sufficient to wet the top 10 cm of the soil as indicated by our soil moisture measurements (data not shown). There was a considerable response from both species to the large, post-summer precipitation event near the end of the growing season in 2003 (day 274). Coincident with this event, soil moisture increased at the 20-cm depth and maximum air temperatures decreased below 20°C for the first time since day 130 (data not shown). The response of *J. osteosperma* to this post-summer event emphasizes the lack of response to the earlier summer events (days 200–273).

Isotopic variation in environmental waters

The δ^2H and δ^{18}O of precipitation plotted close to the global meteoric water line (Fig. 3a) indicating no evaporative enrichment occurred in our precipitation collector. From these samples, we calculated a local meteoric water line (LMWL) of δ^2H = 7.5(δ^{18}O) + 1.8. The δ^2H and δ^{18}O of winter and spring precipitation (collectively labeled ‘‘winter’’ for simplicity) were more negative than that of summer precipitation (Fig. 3a). We calculated the flux-weighted isotopic composition of precipitation falling at our site as δ^{18}O = –12.9‰ and δ^2H = –101‰ (total annual precipitation, April 2004–March 2005). The winter flux-weighed isotope ratio (November 2004–May 2005) was δ^{18}O = –13.9‰ and δ^2H = –103‰.

Soil water samples appeared to be derived from evaporatively enriched winter precipitation. Soil water samples plotted to the right of the LMWL, with a regression line of δ^2H = 2.9(δ^{18}O) – 64 (R^2 = 0.94, $P < 0.0001$) (Fig. 3b). A slope of approximately 3 represents water undergoing evaporation in a low humidity environment, a common scenario for shallow soil layers in arid environments (Clark and Fritz 1999; Gat 1996). The intersection of the soil water regression with the LMWL had co-ordinates of δ^2H = –105‰ and δ^{18}O = –14.3‰, values almost within instrument precision of the winter precipitation flux-weighted isotope ratio which suggested that the soil water in summer was derived primarily from the progressive evaporative enrichment of winter precipitation.

Summer precipitation events should have contributed to soil moisture in the shallow soil layers, resulting in shallow soil water samples close to the summer precipitation values on the LMWL. However, our monthly sampling strategy failed to detect these samples. Several of the shallow soil layers had insufficient moisture to extract for isotopic analysis, probably due to the short-lived nature of the summer moisture pulses. Thus it is likely that these events were under-represented in this dataset.

Plant water sources

Water isotope values from *J. osteosperma* were more tightly clustered than those of *P. edulis*, indicating a more consistent water source for the former (Fig. 3c, d). Stem water isotope values for *J. osteosperma* were constant over the duration of the growing season (Fig. 4). There was a greater degree of variation in the stem samples from *P. edulis*, with summer samples being more enriched than winter samples (Fig. 4).

Several *P. edulis* summer samples plotted between the LMWL and the soil water regression line (Fig. 3d) indicating some uptake of enriched summer rainfall that persisted in the transpiration stream after it was evaporated from the soil. This was in agreement with our sap flux data (Fig. 2), supporting the hypothesis that *P. edulis* utilized summer precipitation to a greater extent than *J. osteosperma*.

With few exceptions, the soil water at all depths was more enriched than the stem water for both species

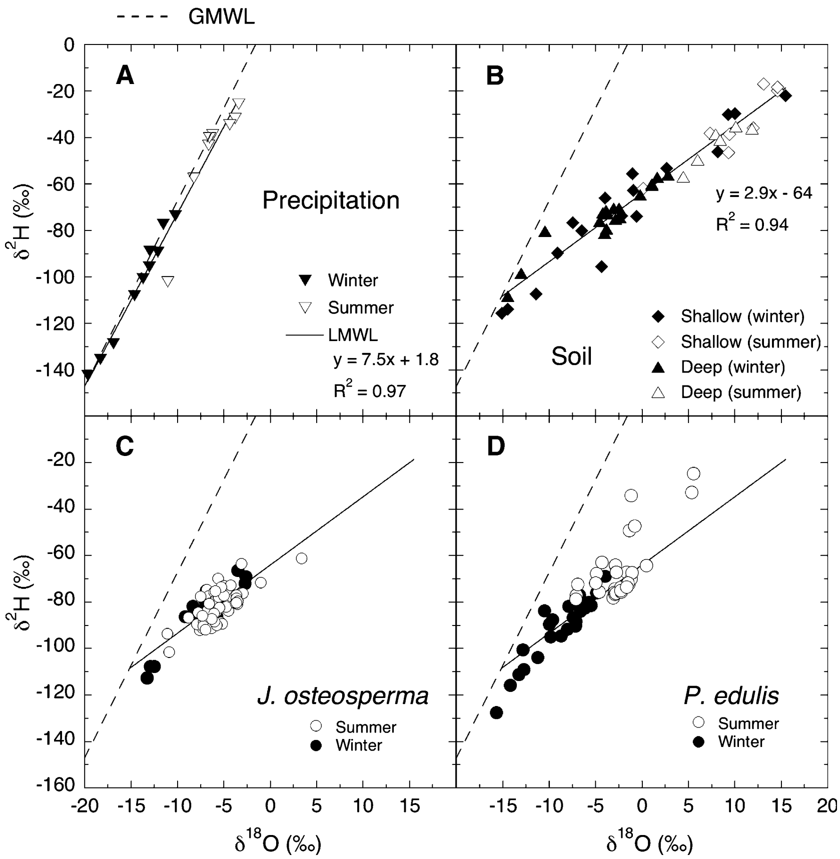


Fig. 3a–d Isotopic composition of environmental and plant water sampled at our fieldsite. **a** Precipitation, **b** soil water from shallow (5–20 cm) and deep (21–45 cm) soil layers, **c** stem water from *J. osteosperma*, **d** stem water from *P. edulis*. Samples were classified into summer (July, August, September, October) and winter. The global meteoric water line (*GMWL*) is plotted in each panel for reference. The regression through soil water samples is plotted in **b**, **c**, **d**. δ^2H Natural abundance stable isotopic ratio of hydrogen, $\delta^{18}O$ natural abundance stable isotopic ratio of oxygen

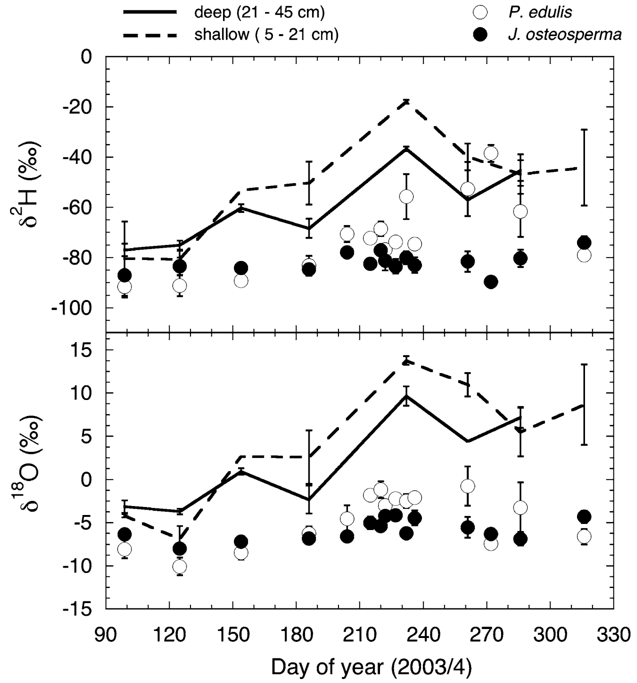


Fig. 4 Mean isotopic composition of soil water and *P. edulis* (*open circle*) and *J. osteosperma* (*filled circle*) stem water, sampled over 2003 and 2004, showing that the measured soil water cannot account for the isotopic composition of stem water

(Fig. 4). In order to test whether a third, deeper source of moisture could account for the isotopic composition of stem water, we used a three-ended mixing model to determine the relative contributions of three potential moisture sources. Adding a deeper moisture source with the isotopic composition of the winter precipitation flux-weighted isotope ratio allowed us to model our measurements with the exception of the late-season *P. edulis* measurements. These measurements did not fall within the three sources defined in the model. We attribute this to the uptake of summer-derived moisture that is depleted in ^{18}O relative to evaporatively enriched soil water (see Fig. 3).

The model predicted a sizeable fraction of uptake from the hypothetical deepest zone for both species (Fig. 5), indicating that both species were functionally dimorphically rooted and may have had access to a deeper water source throughout the growing season. In *J. osteosperma*, uptake seemed to occur predominantly in shallow soil layers early in spring, where soil moisture was highest. As the shallow soils dried, uptake shifted to the deeper moisture source and remained relatively constant over the remainder of the season (Fig. 5). *P. edulis* stem water was best predicted by relatively equal fractions of uptake from shallow soil and deeper moisture sources over the spring and early summer. However, following the arrival of the monsoon (after day 200), the fraction of uptake from the shallow soil layer increased markedly (Fig. 5).

Leaf δ^{13}C and %N

There were distinct differences in the observed seasonal trends of $\delta^{13}C_s$ for *P. edulis* and *J. osteosperma*. Over the course of the 2004 growing season, $\delta^{13}C_s$ for *J. osteosperma* remained constant (slope not significantly different from zero, $P = 0.8$), whereas $\delta^{13}C_s$ varied considerably for *P. edulis* (Fig. 6). $\delta^{13}C_s$ of *P. edulis* and *J. osteosperma* were not significantly different in spring and early summer (days 125–186) when conditions were favorable for transpiration and modeled $g_s > 0$ for both species (Fig. 6). However, as moisture availability declined over the summer, Ψ_{PD} declined so that modeled g_s approached zero for both species (Fig. 6). During this time period, *P. edulis* showed a significant enrichment in $\delta^{13}C_s$, whereas $\delta^{13}C_s$ in *J. osteosperma* remained constant. Modeled g_s values were calculated from periodic Ψ measurements that failed to coincide with periods of increased sap flux following moisture events for *P. edulis* (Fig. 2) and thus may have failed to adequately capture increases in g_s following moisture events. At the end of the growing season, when Ψ_{PD} recovered sufficiently for g_s to be greater than zero, the difference between $\delta^{13}C_s$ of *P. edulis* and *J. osteosperma* declined (Fig. 6).

The change in $\delta^{13}C_s$ of *P. edulis* was related to the water status of the plants, rather than changes in photosynthetic capacity, as $\delta^{13}C_s$ of *P. edulis* was correlated with both Ψ_{PD} ($y = -1.44x - 23.8$, $R^2 = 0.78$, $P < 0.001$; Fig. 7) and g_s ($y = -0.31 \ln(x) - 23.2$, $R^2 = 0.82$, $P < 0.001$; Fig. 7), and %N did not vary considerably over the season (Fig. 6). There was also no change in %N for *J. osteosperma* over the season, suggesting that neither species significantly down-regulated photosynthetic enzymes over the summer drought (Field and Mooney 1986). *P. edulis* maintained higher levels of %N throughout the season, consistent with *P. edulis* having higher photosynthetic rates than *J. osteosperma* (Nowak et al. 1999).

$\delta^{13}C_s$ for *P. edulis* was correlated with % soluble carbohydrate in the leaf ($y = 0.74x + 19$, $R^2 = 0.60$, $P < 0.01$; Fig. 8), which suggested that reduced assimilation in *P. edulis* was associated with a modification in the internal leaf carbon dioxide to ambient carbon dioxide ratio (c_i/c_a) ratio. This was not the case for *J. osteosperma.*

Discussion

Strategies of resource use of *P. edulis* and *J. osteosperma*

P. edulis and *J. osteosperma* showed different sensitivities to seasonal variations in moisture, supporting the hypothesis that *P. edulis* was dependent on summer precipitation,

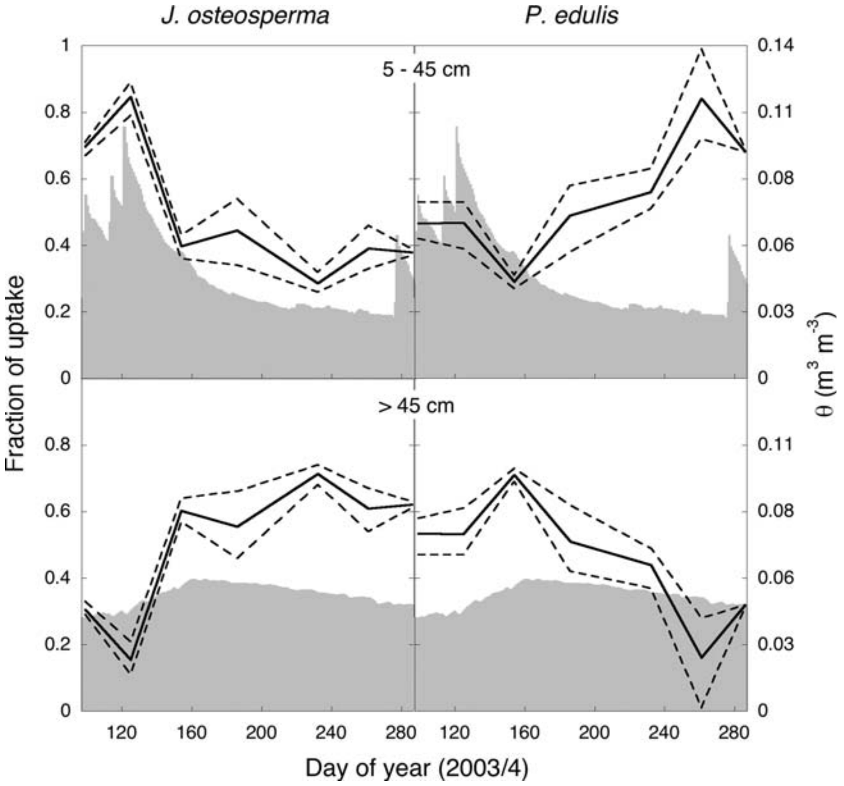


Fig. 5 Fraction of water uptake from measured soil layers (5–45 cm) and a hypothetical deeper moisture source (>45 cm), for *P. edulis* and *J. osteosperma*, produced from the mixing model IsoSource. The *solid line* represents the mean model solution, the *dashed lines* show the range of model solutions. Volumetric soil moisture (*θ*) from these layers is plotted in *gray* for reference. The *θ* for the >45-cm layer represents measurements made from 45–55 cm, and may not be wholly representative of this layer

whereas *J. osteosperma* was not. Water sources did not differ greatly between the species during the spring or early summer, when the plants were utilizing a large fraction of shallow, winter-derived moisture (Fig. 4). Utilizing shallow soil moisture early in the growing season may be adaptive for both species for two reasons. Firstly, this behavior maximizes the extraction of water from the soil, by using shallow resources before they are lost to evaporation. Secondly, nutrient concentrations are highest in the shallow layers of the soil (Evans and Ehleringer 1994; Gebauer and Ehleringer 2000), and the presence of shallow soil moisture may provide the opportunity for uptake of nutrients that are not available later in the growing season. Thus it appears that both *P. edulis* and *J. osteosperma* were reliant on similar moisture sources during the most productive part of the growing season, and might be in direct competition for these resources.

Both species appeared to obtain a considerable fraction of water from below the shallow soil layers at our site (Fig. 5). Soils were rarely deeper than 45 cm, over sandstone bedrock. It is likely that both *P. edulis* and *J. osteosperma* extend roots into cracks in the bedrock and are able to extract water from these locations. *P. edulis* and *Juniperus monosperma* (Engelm.) Sarg. have been shown to exploit cracks in rock and root successfully down to 6 m in New Mexico (Foxx and Tierney 1987). *J. osteosperma* has been shown to extract water from 1 m in the great Basin (Leffler et al. 2002). *J. osteosperma* and *P. edulis* can often be seen growing on rock outcrops without any significant soil development (Harper et al. 2003). In the vicinity of our study site, exposed roots of these species in stream bank cutaways indicated that they were able to extend roots through cracks in the rock (personal observation). This deeper moisture source did not appear to greatly influence transpiration over the course of the dry summers, as transpiration was almost negligible for *J. osteosperma* and was tightly coupled to surface moisture for *P. edulis* (Fig. 2). This may have been due to the below average rainfall during, and for several years preceding, our measurements (Utah Division of Water Resources, http://www.water.utah.gov) that reduced deep soil moisture to levels insufficient to maintain a measurable transpiration flux. Flux from these deeper soil layers may be more significant following above average rainfall years, when moisture infiltrates to sufficient depth and provides recharge for these deeper layers (Seyfried et al. 2005). Nevertheless, the small amount of water derived from the deeper soil layers during droughts may be important for the survival of these trees.

One of the key factors in responding to summer rain is undoubtedly allocation of roots to shallow layers, and the maintenance of metabolic activity in these roots (Ehleringer et al. 1999; Schwinning and Ehleringer 2001). *P. edulis* appeared to have greater uptake from shallower soil layers than *J. osteosperma* during the summer (Fig. 5). Typically, *P. edulis* has been shown to have a greater sensitivity to

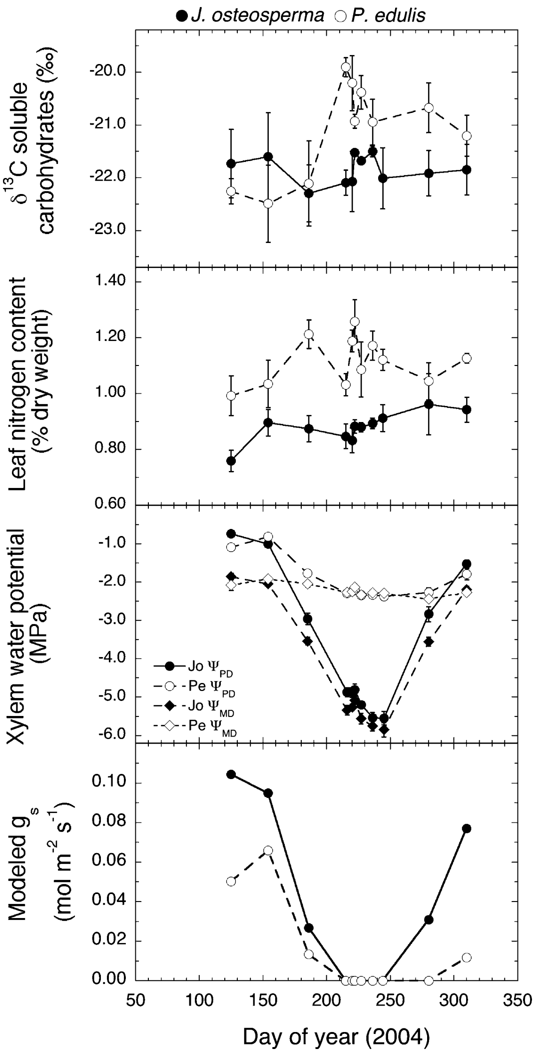


Fig. 6 Natural abundance stable isotopic ratio of carbon ($\delta^{13}C$) of leaf soluble carbohydrates ($\delta^{13}C_s$), leaf nitrogen content, xylem water potential and modeled stomatal conductance (g_s) for *P. edulis* (*open circle*) and *J. osteosperma* (*filled circle*) over the course of a growing season

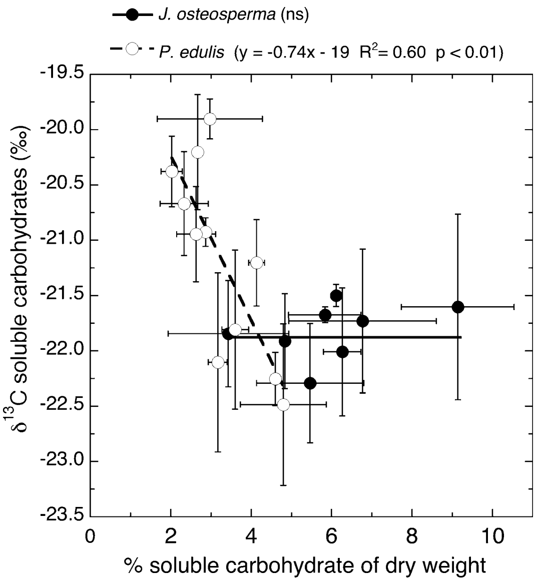
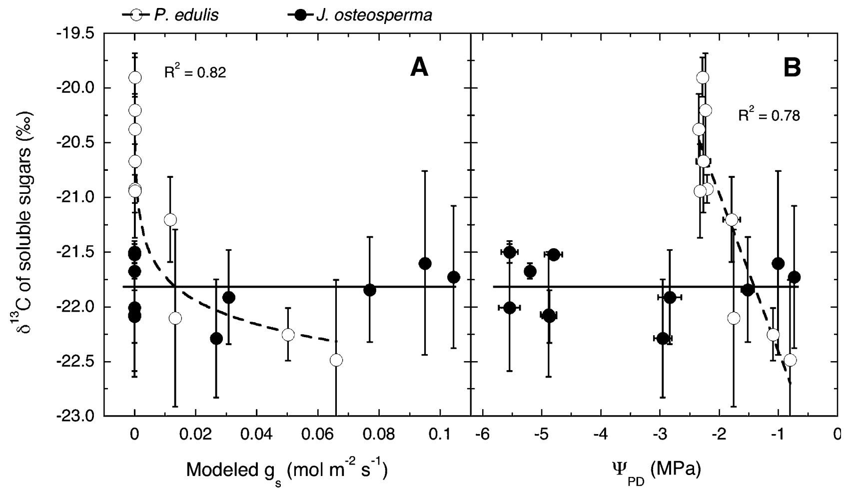


Fig. 8 $\delta^{13}C_s$ versus soluble carbohydrate content of leaves for *P. edulis* (*open circle*) and *J. osteosperma* (*filled circle*). There was a significant linear relationship for *P. edulis*, but not for *J. osteosperma*

summer moisture than *J. osteosperma* (Flanagan et al. 1992; Williams and Ehleringer 2000). It has recently been shown that *P. edulis* is able to increase shallow root conductivity following a moisture pulse (West et al., in press), which may in part explain the ability of *P. edulis* to take up summer moisture pulses. However in manipulative irrigations in southern Utah, *J. osteosperma* appeared to be more responsive to summer irrigation than *P. edulis* (Williams and Ehleringer 2000). This was attributed to high soil temperatures inhibiting fine roots of *P. edulis* (Williams and Ehleringer 2000), although it seems likely that there were artifacts associated with the irrigation methodology (West et al., in press). Our data indicated that *P. edulis* maintained active roots shallower than *J. osteosperma*. A

Fig. 7a, b The relationship of $\delta^{13}C_s$ with water status of *P. edulis* (*open circle*) and *J. osteosperma* (*filled circle*). **a** $\delta^{13}C_s$ versus modeled g_s for *P. edulis* [$y = -0.31 \ln(x) - 23.2$] and *J. osteosperma* (no significant relationship, slope of line = 0). **b** $\delta^{13}C_s$ versus predawn water potential (Ψ_{PD}) for *P. edulis* ($y = -1.44x - 23.8$) and *J. osteosperma* (no significant relationship, slope of line = 0)



difference in rooting distribution could account for the differential inhibition of fine roots suggested by Williams and Ehleringer (2000), as shallower roots should experience greater temperature extremes. Greater sensitivity to soil temperatures may play a role in limiting the distribution of *P. edulis* to summer precipitation areas. Possibly summer soil temperatures may become lethal for *P. edulis* roots in areas that do not have periodic summer precipitation events. This remains to be tested.

There were distinct differences in the observed seasonal trends of $\delta^{13}C_s$ for *P. edulis* and *J. osteosperma* (Fig. 6). The constant $\delta^{13}C_s$ values of *J. osteosperma* may have resulted from *J. osteosperma* maintaining a constant c_i/c_a ratio over the length of the growing season, or from negligible assimilation occurring over the summer, or possibly both. Sap flux data indicated that there were, at best, extremely low levels of transpiration in *J. osteosperma* over the summer (Fig. 2). If low levels of assimilation did in fact occur, the $\delta^{13}C_s$ data indicate that this happened at a near constant c_i/c_a ratio as $\delta^{13}C_s$ was not correlated with g_s, Ψ_{PD} or % soluble carbohydrates for *J. osteosperma* (Fig. 8). A conservative c_i/c_a set point for *Juniperus* species is consistent with other studies (e.g. Ward et al. 2005).

The summer pulse response of *P. edulis* (Fig. 2) appeared to allow brief opportunities for carbon assimilation at a high water use efficiency, as indicated by the enrichment in ^{13}C of *P. edulis* soluble carbohydrates over the summer drought (Fig. 6). *P. edulis* has been shown to exert strong stomatal control to maintain its Ψ and prevent cavitation (Linton et al. 1998), with g_s declining to zero at ~–2 MPa (Williams and Ehleringer 2000). As a result, the c_i/c_a ratio, and thus the $\delta^{13}C_s$, might be expected to vary with water status. This was supported by the significant correlation between $\delta^{13}C_s$ and Ψ_{PD} and g_s for *P. edulis* (Fig. 7).

A consequence of strong stomatal control, *P. edulis* has reduced opportunities for gas exchange under drought conditions. *P. edulis* leaves had higher levels of nitrogen than *J. osteosperma* leaves (Fig. 6), indicating a higher photosynthetic capacity in *P. edulis* (Field and Mooney 1986). This is consistent with other data for piñon and juniper species (Lajtha and Barnes 1991; Nowak et al. 1999). Maintaining high photosynthetic capacity would allow *P. edulis* to capitalize on opportunities for carbon gain, but may come at the cost of higher maintenance respiration rates over the summer drought (Reich et al. 1998). This strategy may be beneficial in wet summers, when there is an extended opportunity for carbon gain, but may be detrimental over extended summer droughts. Response to periodic moisture pulses, as shown in this study, may serve to mitigate these costs. As such, we suggest that the allocation of resources to utilize summer rain in the extremely dry years of this study is evidence of a dependence on summer rain for *P. edulis*.

The role of seasonality in piñon–juniper woodlands

The distributions of piñon and juniper species provide evidence for a role of seasonality of precipitation in piñon–juniper woodland composition (e.g., Fig. 1). Paleoecological studies have indicated that the distributions of piñon and juniper species have been dynamic over the last 10,000 years, undergoing considerable northwards expansion during the Holocene, to approximately their modern distributions (Betancourt 1987; Betancourt et al. 1990; Lanner and Van Devender 1998; van Devender 1987). There is some evidence to suggest that this was associated with a shift in the North American monsoon (Neilson and Wullstein 1983) and changes in temperature that allowed establishment of plants on the Colorado Plateau (Betancourt 1987; Malusa 1992). Furthermore, isotopic evidence from *P. edulis* needles from the last 40,000 years indicates that *P. edulis* persistence is tightly coupled to the presence of summer rain (Pendall et al. 1999).

Currently, species boundaries of piñon and juniper appear to be correlated with seasonal precipitation gradients (Malusa 1992; Neilson 1987), suggesting that the distributions of these taxa are sensitive to this climate variable. This is supported by this study, in which we demonstrate the differential sensitivity to summer precipitation for *P. edulis* and *J. osteosperma*.

Predicted future increases in potential evapotranspiration and decreases in summer moisture (Cook et al. 2004; Gregory et al. 1997; Houghton et al. 2001) would increase the severity and extent of summer drought. Extended summer drought would negatively affect *P. edulis* to a greater extent than *J. osteosperma*, potentially resulting in differential mortality of these species. Such differential mortality (piñon > juniper) has been recently documented in piñon–juniper woodlands following a severe drought (Breshears et al. 2005; Mueller et al. 2005). The legacy of such mortality events may be long-lasting and may play an important role in structuring current species distributions (Gray et al. 2006). Together with the paleoecological evidence, our study suggests that the composition of piñon–juniper woodlands is likely to be highly sensitive to changes in seasonality of precipitation, which may in turn affect water balance and productivity (West 2006) and biodiversity (Mueller et al. 2005) over extensive areas in the southwestern United States.

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References

Adang TC, Gall RL (1989) Structure and dynamics of the Arizona monsoon boundary. Month Weath Rev 117:1423–1438

Arundel ST (2005) Using spatial models to establish climatic limiters of plant species' distributions. Ecol Modell 182:159–181

Betancourt JL (1987) Paleoecology of pinyon–juniper woodlands: summary. In: Everett RL (ed) Proceedings—pinyon–juniper conference. General technical report INT-215. US Department of Agriculture, Forest Service, Intermountain Research Station, Reno, Nev., pp 129–139

Betancourt JL, Van Devender TR, Martin PS (eds) (1990) Packrat middens: the last 40,000 years of biotic change. University of Arizona, Tucson, Ariz.

Breshears DD, et al. (2005) Regional vegetation die-off in response to global-change-type drought. Proc Natl Acad Sci USA 102:15144–15148

Brugnoli E, Hubick KT, von Caemmerer S, Wong SC, Farquhar GD (1988) Correlation between the carbon isotope discrimination in leaf starch and sugars of C3 plants and the ratio of intercellular and atmospheric partial pressures of carbon dioxide. Plant Physiol 88:1418–1424

Bryson RA, Hare FK (eds) (1974) Climates of North America. Elsevier, Amsterdam

Chesson P, et al. (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253

Clark IC, Fritz P (1999) Environmental isotopes in hydrogeology. Lewis, New York

Cole KL, Arundel ST (2007) Modeling the climatic requirements for southwestern plant species. In: Starratt S, Bloomquist N (eds) Twenty-first annual Pacific climate workshop. State of California Department of Water Resources (in press)

Comstock JP, Ehleringer JR (1992) Plant adaptation in the Great-Basin and Colorado plateau. Great Basin Nat 52:195–215

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes in the western United States. Science 306:1015–1018

Donovan LA, Ehleringer JR (1994) Water-stress and use of summer precipitation in a Great-Basin shrub community. Funct Ecol 8:289–297

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR (1991) Differential utilization of summer rains by desert plants. Oecologia 88:430–434

Ehleringer JR, Evans RD, Williams DG (1998) Assessing sensitivity to change in desert ecosystems—a stable isotope approach. In: Griffiths H (ed) Stable isotopes: integration of biological, ecological and geochemical processes. BIOS Scientific, Oxford

Ehleringer JR, Schwinning S, Gebauer R (1999) Water use in arid land ecosystems. In: Press MC, Scholes JD, Barker MG (eds) Physiological plant ecology. Blackwell, Oxford, p 480

Evans RD, Ehleringer JR (1994) Water and nitrogen dynamics in an arid woodland. Oecologia 99:233–242

Field CB, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University, Cambridge

Flanagan LB, Ehleringer JR, Marshall JD (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon–juniper woodland. Plant Cell Environ 15:831–836

Fowler N (1986) The role of competition in plant communities in arid and semi-arid regions. Annu Rev Ecol Syst 17:89–110

Foxx TS, Tierney GD (1987) Rooting patterns in the pinyon–juniper woodland. In: Everett RL (ed) Proceedings—pinyon–juniper conference, vol general technical report INT-215. US Department of Agriculture, Forest Service, Intermountain Research Station, Reno, Nev., pp 69–79

Gat JR (1996) Oxygen and hydrogen isotopes in the hydrologic cycle. Annu Rev Earth Planet Sci 24:225–262

Gebauer RLE, Ehleringer JR (2000) Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81:1415–1424

Gehre M, Geilmann H, Richter J, Werner RA, Brand WA (2004) Continuous flow ^{2}H/^{1}H and ^{18}O/^{16}O analysis of water samples with dual inlet precision. Rapid Commun Mass Spectrom 18:2650–2660

Gottlicher S, Knohl A, Wanek W, Buchmann N, Richter A (2006) Short-term changes in carbon isotope composition of soluble carbohydrates and starch: from canopy leaves to the root system. Rapid Commun Mass Spectrom 20:653–660

Granier A (1985) A new method of sap flow measurement in tree stems. Ann Sci For 42:193–200

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol 3:309–320

Gray ST, Betancourt JL, Jackson ST, Eddy RG (2006) Role of multidecadal climate variability in a range extension of pinyon pine. Ecology 87:1124–1130

Gregg J (1991) The differential occurence of the mistletoe, *Phoradendron juniperinum*, on its host, *Juniperus osteosperma*, in the Western United States. MSc thesis, University of Utah, Salt Lake City, Utah

Gregory JM, Mitchell JFB, Brady AJ (1997) Summer drought in northern midlatitudes in a time-dependent CO$_2$ climate experiment. J Clim 10:662–686

Grubb PJ (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol Rev Camb Philos Soc 52:107–145

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecology Lett 8:993–1009

Harper KT, Sanderson SC, McArthur ED (2003) Pinyon–juniper woodlands in Zion National Park, Utah. West N Am Nat 63:189–202

Higgins RW, Yao Y, Wang XL (1997) Influence of the North American monsoon system on the US summer precipitation regime. J Clim 10:2600–2622

Houghton JT, et al. (2001) Climate change 2001: the scientific basis. Cambridge University, Cambridge

Huxman TE, et al. (2005) Ecohydrological implications of woody plant encroachment. Ecology 86:308–319

Keitel C, et al. (2003) Carbon and oxygen isotope composition of organic compounds in the phloem sap provides a short-term measure for stomatal conductance of European beech (*Fagus sylvatica* L.). Plant Cell Environ 26:1157–1168

Lajtha K, Barnes FJ (1991) Carbon gain and water use in pinyon pine-juniper woodlands in northern New Mexico: field versus phytotron chamber measurements. Tree Physiol 9:59–68

Lanner RM, Van Devender TR (1998) The recent history of pinyon pines in the American southwest. In: Richardson DM (ed) Ecology and biogeography of *Pinus*. Cambridge University, Cambridge, pp 171–182

Leffler AJ, Ryel RJ, Hipps L, Ivans S, Caldwell MM (2002) Carbon acquisition and water use in a northern Utah *Juniperus osteosperma* (Utah juniper) population. Tree Physiol 22:1221–1230

Linton MJ, Sperry JS, Williams DG (1998) Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. Funct Ecol 12:906–911

Loik ME, Breshears DD, Lauenroth WK, Belnap J (2004) A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia 141:269–281

Malusa J (1992) Phylogeny and biogeography of the pinyon pines *Pinus* subsect. Cembroides. Syst Bot 17:42–66

McKenzie D, Peterson DW, Peterson DL, Thornton PE (2003) Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. J Biogeogr 30:1093–1108

Midgley GF, Hannah L, Millar D, Rutherford MC, Powrie LW (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Glob Ecol Biogeogr 11:445–451

Mitchell JE, Roberts TC (1999) Distribution of pinyon–juniper in the Western United States. In: Monsen SB, Stevens R (eds) Proceedings: Ecology and Management of Pinyon–Juniper Communities within the Interior West, 15–18 September 1997, Provo Utah. RMRS-P-9. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, pp 146–154

Mueller RC, Scudder CM, Porter ME, Talbot Trotter R, Gehring CA, Whitham TG (2005) Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J Ecol 93:1085–1093

Neilson RP (1987) On the interface between current ecological studies and the paleobotany of pinyon–juniper woodlands. In: Everett RL (ed) Proceedings of the Pinyon–Juniper Conference. General technical report INT-215. US Department of Agriculture, Forest Service, Intermountain Research station, Reno, Nev., pp 93–98

Neilson RP (1995) A model for predicting continental-scale vegetation distribution and water balance. Ecol Appl 5:362–385

Neilson RP, Wullstein LH (1983) Biogeography of two southwest American oaks in relation to atmospheric dynamics. J Biogeor 10:275–297

Nowak RS, Moore DJ, Tausch RJ (1999) Ecophysiological patterns of pinyon and juniper. In: Monsen SB, Stevens R (eds) Proceedings: Ecology and Management of Pinyon–Juniper Communities within the Interior West, 15–18 September 1997, Provo Utah. RMRS-P-9. US Department of Agriculture, Forest Service, Rock Mountain Research Station, Ogden, pp 35–46

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4:25–51

Paltineanu IC, Starr JL (1997) Real-time soil water dynamics using multisensor capacitance probes: laboratory calibration. Soil Sci Soc Am J 61:1576–1585

Pendall E, Betancourt JL, Leavitt SW (1999) Paleoclimatic significance of delta D and delta C-13 values in pinon pine needles from packrat middens spanning the last 40,000 years. Palaeogeogr Palaeoclimatol Palaeoecol 147:53–72

Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–179

Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–269

Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. Oecologia 144:520–527

Reich PB, et al. (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. Oecologia 114:471–482

Scartazza A, Lauteri M, Guido MC, Brugnoli E (1998) Carbon isotope discrimination in leaf and stem sugars, water-use efficiency and mesophyll conductance during different developmental stages in rice subjected to drought. Aust J Plant Physiol 25:489–498

Schwinning S, Ehleringer JR (2001) Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. J Ecol 89:464–480

Schwinning S, Sala OE, Loik ME, Ehleringer JR (2004) Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. Oecologia 141:191–193

Schwinning S, Starr BI, Ehleringer JR (2005) Summer and winter drought in a cold desert ecosystem (Colorado Plateau). Part II. Effects on plant carbon assimilation and growth. J Arid Environ 61:61–78

Seyfried MS, et al. (2005) Ecohydrological control of deep drainage in arid and semiarid regions. Ecology 86:277–287

Snyder KA, Donovan LA, James JJ, Tiller RL, Richards JH (2004) Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. Oecologia 141:325–334

Thuiller W, Lavorel S, Sykes MT, Araujo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Divers Distrib 12:49–60

Van Devender TR (1987) Late Quaternary history of pinyon–juniper–oak woodlands dominated by *Pinus remota* and *Pinus edulis*. In: Everett RL (ed) Proceedings of the Pinyon–Juniper conference. General technical report INT-215. US Department of Agriculture, Forest Service, Intermountain Research station, Reno, pp 99–103

Ward JK, et al. (2005) Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California. Proc Natl Acad Sci USA 102:690–694

Weltzin JF, McPherson GR (2003) Predicting the response of terrestrial ecosystems to potential changes in precipitation regimes. In: Weltzin JF, McPherson GR (eds) Changing precipitation regimes and terrestrial ecosystems. University of Arizona, Tucson, Ariz.

Weltzin JF, et al. (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53:941–952

West AG (2006) The influence of seasonality of precipitation on transpiration in piñon–juniper woodlands. PhD thesis, Department of Biology, University of Utah, Salt Lake City, Utah

West AG, Patrickson SJ, Ehleringer JR (2006) Water extraction times for plant and soil materials used in stable isotope analysis. Rapid Commun Mass Spectrom 20:1317–1321

West AG, Hultine KR, Jackson TL, Ehleringer JR (in press) Contrasting hydraulic strategies explain differential summer moisture use of *Pinus edulis* and *Juniperus osteosperma*. Tree Physiol

Williams DG, Ehleringer JR (2000) Intra- and interspecific variation for summer precipitation use in pinyon–juniper woodlands. Ecol Monogr 70:517–537

Williams DG, Snyder KA (2003) Responses of woody plants to heterogeneity of soil water in arid and semiarid environments. In: Weltzin JF, McPherson GR (eds) Changing precipitation regimes and terrestrial ecosystems: a North American perspective. University of Arizona, Tucson, Ariz., pp 28–46