

Carbon acquisition and water use in a northern Utah *Juniperus osteosperma* (Utah juniper) population

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Summary Water use and carbon acquisition were examined in a northern Utah population of *Juniperus osteosperma* (Torr.) Little. Leaf-level carbon assimilation, which was greatest in the spring and autumn, was limited by soil water availability. Gas exchange, plant water potential and tissue hydrogen stable isotopic ratio (δD) data suggested that plants responded rapidly to summer rain events. Based on a leaf area index of 1.4, leaf-level water use and carbon acquisition scaled to canopy-level means of 0.59 mm day^{-1} and 0.13 mol m^{-2} ground surface day^{-1} , respectively. Patterns of soil water potential indicated that *J. osteosperma* dries the soil from the surface downward to a depth of about 1 m. Hydraulic redistribution is a significant process in soil water dynamics. Eddy covariance data indicated a mean evapotranspiration rate of 0.85 mm day^{-1} from March to October 2001, during which period the juniper population at the eddy flux site was a net source of CO_2 (3.9 mol m^{-2} ground area). We discuss these results in relation to the rapid range expansion of juniper species during the past century.

Keywords: deuterium, eddy covariance, gas exchange, hydraulic redistribution, soil water potential, stable isotopes.

Introduction

The uplands of arid western North America are largely dominated by piñon–juniper (*Pinus* spp. and *Juniperus* spp.) woodlands (Tausch et al. 1981). Juniper species are highly successful in harsh environments and dominate increasing areas in western North America (Tausch et al. 1981, Soulé and Knapp 1999). The successful range expansion of juniper species throughout western North America may be explained by their physiological adaptation (Owens 1996) to new environmental conditions brought about by changes in land-use such as grazing and fire suppression (Owens 1996). Although carbon acquisition and water use have been studied in several juniper species (see Miller et al. 1992, 1993, Lajtha and Getz 1993, Owens 1996, Moore et al. 1999), research on *Juniperus osteosperma* (Torr.) Little (Utah juniper), one of the most

widespread species in the western USA, has been limited (but see Moore et al. 1999).

Junipers have low stomatal conductance to water vapor (g) and, consequently, low rates of transpiration (E) and carbon assimilation (A). For example, maximum g in juniper species is reported to range from 0.033 to $0.054 \text{ mol m}^{-2} \text{ s}^{-1}$ (Körner et al. 1979, Miller and Shultz 1987), whereas rates two- to four-fold higher have been reported in species of *Pinus*, *Picea* and *Abies* (Körner et al. 1979). Nevertheless, junipers can achieve a high leaf area index (LAI) (Hicks and Dugas 1998), and hence high rates of canopy gas exchange, even on dry sites. Conservative leaf-level water use may enhance drought tolerance, whereas high stand-level water use impedes the establishment of competitors.

Hydrogen stable isotopic composition (δD) of plant tissue and soil water have been used to examine the sources of water for numerous species (White et al. 1985, Flanagan and Ehleringer 1991) including *J. osteosperma*. Donovan and Ehleringer (1994) reported that adult *J. osteosperma* trees did not use summer precipitation at their northern Utah study site. Conversely, Flanagan et al. (1992) and Evans and Ehleringer (1994) observed occasional uptake of summer precipitation by *J. osteosperma* in southern Utah, where summer precipitation is greater. Williams and Ehleringer (2000), working along a summer “monsoon” precipitation gradient, found that summer rains were utilized at sites where summer precipitation is common; at drier sites, summer rains were not utilized even when they were available. Hence, the use of water from different sources depended on the seasonal distribution of precipitation.

The phenomenon of hydraulic redistribution (Burgess et al. 1998, 2001, Ryel et al. 2002), originally termed hydraulic lift (Richards and Caldwell 1987, Caldwell and Richards 1989), which is the transport through roots of water from soil of higher water potential to soil of lower water potential, may play a significant role in the transport, storage and use of soil water. Hydraulic redistribution, both upward and downward, has been described for many species (Burgess et al. 1998, 2001, Caldwell et al. 1998, Smith et al. 1999, Ryel et al. 2002), but its role in the seasonal dynamics of soil water content in ju-

niper stands has not been investigated.

In the present study, the seasonal soil water dynamics of a *J. osteosperma* stand were investigated by monitoring water potential at several soil depths from 1999 to 2001. We quantified winter–spring recharge of soil water, examined water uptake from different soil depths and determined if hydraulic redistribution is a significant factor in soil water dynamics. We also quantified leaf-level water use and carbon acquisition during the 2000 growing season to examine the patterns of gas exchange in relation to water availability. We estimated stand-level gas exchange from leaf-level fluxes, and also monitored ecosystem-level fluxes of CO₂ and water vapor during 2001 using the eddy covariance technique.

Materials and methods

Study site and species

The study was conducted in a *J. osteosperma* woodland in Tooele County, Utah (40°15'37.1" N, 112°28'29.4" W, 1660 m elevation), about 8.5 km from the town of Rush Valley. Climate at this site is typical of Great Basin old deserts (Caldwell 1985), with cold winters and hot summers. Most of the total annual precipitation occurs during the winter and spring; however, deep snowpack is rare. The site is dominated by *J. osteosperma*, with widely scattered *Artemisia tridentata* Nutt. (Big sagebrush) and *Achnatherum hymenoides* (R. & S.) Barkworth (Indian ricegrass) individuals in the understory. Studies indicate that *J. osteosperma* individuals are uniformly distributed within a population (Welden et al. 1990) and we observed an inter-tree distance of about 3 m. Weather data for the study were collected from a weather station (Campbell Scientific, Logan, UT) about 3 km away.

Soil at the site is a fine, loamy, mixed Xerollic Calciorthid of the Taylorsflat series (Tooele County, Utah Soil Survey 1993). The coarse fragment fraction increases with depth; coarse fragment samples range from 0 to 80% in the upper 1 m (Lowe 1999). A petrocalcic layer exists at a depth of 1 to 3 m throughout the study area (Lowe 1999).

Leaf-level measurements

Gas exchange and plant water status measurements were conducted on the same five adult individuals over the course of the study. Measurements were made every 2 weeks from April 11 to September 5, 2000 and then every 3 weeks until October 18, 2000.

Predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential measurements were made with a Scholander pressure chamber (Scholander et al. 1965) (PMS Instruments, Corvallis, OR). Predawn measurements were made between 0400 and 0500 h and were completed before sunrise. Midday measurements were conducted between 1030 and 1230 h. One stem per individual was measured during each sampling period.

Gas exchange measurements were made with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE) on three stems per tree in the morning (0900–1000 h MST) and

afternoon (1300–1400 h MST). All measurements were made on the south side of trees on sunny days; a supplemental Li-Cor light source (LI-6400-02) was used to maintain a constant photosynthetically active radiation (PAR) flux density in the chamber of 1750 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for all measurements. The carbon dioxide concentration ([CO₂]) of air entering the chamber was 400 $\mu\text{l l}^{-1}$. Leaf temperature measurements were made before the gas exchange measurements and the chamber temperature was held at this value (over a range from 14 to 42 °C). Because gas exchange rates of *J. osteosperma* are low, the rate of gas flow through the chamber was kept low (300 $\mu\text{mol s}^{-1}$), resulting in a chamber humidity significantly higher than that of the ambient air. The system measured *A*, *g*, *E*, sub-stomatal [CO₂] (*c_i*) and instantaneous water-use efficiency (WUE = *A/E*). Projected leaf area of foliage within the gas exchange chamber was determined with a Li-Cor LI-3100 leaf area meter. Total leaf surface area was estimated as $\pi \times$ projected leaf area because the foliage was cylindrical (Miller et al. 1987).

We determined leaf area per tree and site leaf area index (LAI) to scale leaf-level gas exchange measurements to canopy-level estimates of water use and carbon acquisition. Measurements were made on 12 trees occurring within the 700-m² study site, but excluding trees used for the gas exchange measurements. Tree height (*h*) was determined with a clinometer. Canopy width was measured in the east–west and north–south directions and canopy circumference was measured at the widest points. Based on the shape of the tree, canopy volume was modeled as a sphere, a cone or a cylinder with the mean radius from canopy diameter and circumference measurements. Additionally, leaves were collected from a known volume of each canopy to determine leaf area density and total tree leaf area. Line transects were used to determine canopy cover at the site, thereby enabling estimation of site leaf area index for *J. osteosperma*.

Total daily carbon gain (*A_d*) and transpiration (*E_d*) at the canopy scale were calculated for each measurement day as the mean of the morning and afternoon leaf gas exchange rates multiplied by LAI and day length (*h*).

Water extracted from *J. osteosperma* branches was analyzed for δD . Branches were collected from the five study trees on five dates between late May and late September. Samples were sealed in the field, frozen and returned to Utah State University. Water was extracted from the samples by the azeotropic distillation protocol (Revesz and Woods 1990). Precipitation samples were collected periodically throughout the year and analyzed for δD . All water samples were analyzed for δD at the New Mexico Institute of Mining and Technology and are expressed in the standard ‰ notation (Craig 1953) relative to the VSMOW standard (Craig 1957).

Belowground measurements

Soil water potential (Ψ_s) data were collected with a psychrometer array consisting of three trenches containing two or three psychrometers (Wescor and J.R.D. Merrill, Logan, UT) at 30, 45, 60, 90, 120, 150, 180, 240 and 300 cm below the soil surface in each trench. Psychrometers were installed ~15 cm

into the trench wall and the trench was refilled subsequent to installation. The psychrometer array was installed in March 1999, beneath a juniper canopy < 15 m from all study trees. Psychrometer readings were recorded hourly with a Campbell Scientific data logger (Model CR7) from June 17 to October 18, 1999, March 15 to November 23, 2000 and January 31 to October 24, 2001. An additional set of psychrometers was installed in a trench beneath bare ground to determine whether changes in Ψ_s resulted primarily from transpiration or evaporation. Soil water potential values were converted to soil volumetric water content (θ) based on an equation from van Genuchten (1980) that was parameterized for our site (D. Or, personal communication):

$$\theta(\Psi_s) = \theta_r + \frac{\theta_s - \theta_r}{(1 + |\alpha\Psi_s|^n)^m}, \quad (1)$$

where $m = 1 - (1/n)$, $\theta(\Psi_s)$ is volumetric water content ($\text{m}^3 \text{m}^{-3}$) for water potential Ψ_s , θ_s is saturated soil water content ($0.5 \text{ m}^3 \text{m}^{-3}$), θ_r is residual soil water content ($0.0 \text{ m}^3 \text{m}^{-3}$), and α and n are fitting parameters equal to 0.2818 m^{-1} and 1.4 (unitless), respectively. Equation 1 assumes that the soil contains no coarse materials. Mean coarse fragment was calculated for different soil zones (Lowe 1999) established around the psychrometers at the five uppermost depths (0–37.5 cm, 12.2%; 37.5–52.5 cm, 21.5%; 52.5–67.5 cm, 23.7%; 67.5–100 cm, 38.6%; 100–135 cm, 54.4%). Coarse fractions were not calculated below 135 cm, because water uptake was not observed below this depth. Volumetric water content (Equation 1) was reduced by the percent rock fragment (R):

$$\theta_c(\Psi_s) = \theta(\Psi_s) \left(1 - \frac{R}{100}\right). \quad (2)$$

Values from Equation 2 suggest that soil water content exceeded 40% during the early season; however, the field capacity of this soil is ~25% (J. Stark, personal communication). Therefore, all values > 25% were recorded as 25%. The discrepancy was likely the result of poor psychrometer resolution at high soil water content (Rundel and Jarrell 1989).

We used changes in θ to calculate evapotranspiration (ET; mm day^{-1}) in this population of *J. osteosperma*. Each psychrometer was assumed to represent the soil water content from one of the soil layers detailed above. The 30-cm psychrometer was assumed to be representative of 0–37.5 cm; psychrometers were not placed at a depth of less than 30 cm because they are sensitive to diurnal temperature variation (Rundel and Jarrell 1989). We modeled ET as:

$$\text{ET} = \sum_i (\theta_{d-1} - \theta_d) z_i, \quad (3)$$

where θ_d is volumetric soil water content ($\text{m}^3 \text{m}^{-3}$) on day d and z_i is the vertical thickness of soil layer i . This method can yield negative E values when there is net movement of water into a soil layer. All positive daily modeled ET values were

summed to obtain a total modeled ET. This estimate utilizes all the psychrometer data available at our site; however, Ψ_s was typically too high to detect changes in θ before early May. The dates on which data were collected differed from year to year, making only monthly comparisons possible.

Root distribution among soil layers was quantified by mapping two of the trench walls when psychrometers were installed. Roots were counted in $10 \times 10 \text{ cm}$ cells within a $60 \times 300 \text{ cm}$ grid on the trench wall.

Eddy covariance

From March 26 to October 27, 2001, ecosystem-level carbon and water flux was measured by the eddy covariance technique (Baldocchi et al. 1988). The flux tower, located 500 m from the experimental site, held a 3-D sonic anemometer (Campbell Scientific, Model CSAT3) and an open-path $\text{CO}_2/\text{H}_2\text{O}$ IRGA (Li-Cor, Model LI-7500) located about 4 m above an approximately 3-m-tall canopy. Corrections for density effects were made as described by Webb et al. (1980).

Data analysis

Relationships between gas exchange variables and environmental variables were examined by stepwise multiple regression analyses. Stomatal conductance explained a large fraction of variation in A , which was, therefore, not examined. Variation in stomatal conductance, however, could be explained by Ψ_{pd} , Ψ_{md} and VPD and a multiple regression analysis was performed with these variables. Transpiration can also be explained in part by g , Ψ_{pd} , Ψ_{md} and VPD. The variation in E explained by g was removed with a bivariate regression and the residual E values used in a multiple regression with Ψ_{pd} , Ψ_{md} and VPD. Morning and afternoon measurements for all dependent variables were analyzed separately. Variables were transformed as necessary to ensure compliance with regression assumptions.

Results

Climate data

The climate of Rush Valley is typical of the Great Basin (Caldwell 1985). Winters are cool with minimum and maximum temperatures of about $-15 \text{ }^\circ\text{C}$ and about $35 \text{ }^\circ\text{C}$, respectively. The growing season usually begins in late May or early June and ends in late September or early October. Vapor pressure deficit during summer afternoons can approach 4 kPa.

In 1999, spring rains continued into June, whereas in 2000 and 2001 little rain fell between May and July. Mean summer temperatures (June–September) were lowest in 1999 ($17.1 \text{ }^\circ\text{C}$), intermediate in 2000 ($18.1 \text{ }^\circ\text{C}$) and highest in 2001 ($21 \text{ }^\circ\text{C}$). Summer precipitation was 28.7 mm in 1999, 112.9 mm in 2000 and 56.6 mm in 2001. Total annual precipitation at Vernon, Utah, ~25 km from our site, was 212, 290 and 239 mm in 1999, 2000 and 2001, respectively. Long-term (1980–2000) annual precipitation at Vernon is 299 mm and long-term summer precipitation (1980–2000) is 93 mm.

Leaf-level gas exchange and water status

Growing season patterns of A , g and c_i were similar and typical of areas with arid summers. Values were high in the spring and autumn and low during the summer (Figure 1). As expected for a species with long-lived foliage, maximum A and g values were observed in the mid-spring and autumn. Carbon assimilation was maintained throughout the growing season, although there was almost complete stomatal closure on the afternoon of Day 214 (August 1), when midday A was greatly

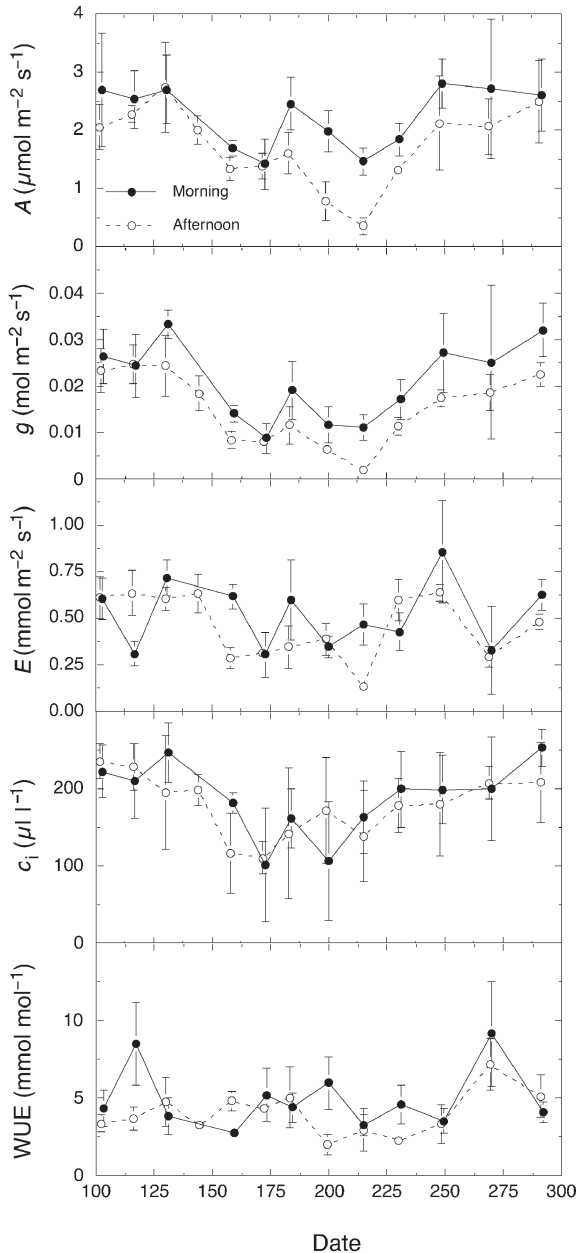


Figure 1. Leaf-level photosynthesis (A), stomatal conductance (g), transpiration (E), sub-stomatal $[CO_2]$ (c_i) and water-use efficiency (WUE). Measurements were made throughout the growing season (April–October 2000). Values are mean \pm standard error of five individuals.

reduced. Following a rain event (15.7 mm) on Day 182 (June 30), morning values of A were similar to those in the spring and fall, whereas g more than doubled and c_i also increased.

Similar daily values of E and water-use efficiency (WUE) were observed throughout the growing season, except on the morning of Day 117 (April 26) and the morning and afternoon of Days 269–270 (September 25–26) when WUE peaked (Figure 1). Suppression of E by reduced g was apparent in the afternoon of Day 214 (August 1), but this had little effect on WUE. The rain event of June 30 (Day 182) was associated with a significant increase in morning E on Day 184 (July 2). The rain event of June 30 had no effect on WUE.

Predawn and midday leaf water potentials declined from spring to summer and recovered following the rain event of June 30 and rains in the autumn (Figure 2).

Carbon assimilation (A) was highly correlated with g in both the morning ($r^2 = 0.823$, $P < 0.001$) and afternoon ($r^2 = 0.901$, $P < 0.001$). Because variation in g can explain a large fraction of the variation in A , we attempted to explain the variation in g and E using a stepwise multiple regression with g and E as independent variables and Ψ_{pd} , Ψ_{md} and VPD as predictors. The variation in g was explained primarily by variation in Ψ_{pd} , both in the morning and afternoon (Table 1). Conversely, when the effect of g on E was removed, morning E values were primarily explained by variation in VPD. None of the predictors examined significantly explained the variation in mid-day E .

Water uptake and hydraulic redistribution

In 1999 and 2000, water uptake by *J. osteosperma* was observed only between 30 and 90 cm below the soil surface, although there was abundant soil water below 1 m (Figure 3). In 2001, water uptake was observed from as deep as 120 cm. Soil water potential for all depths was close to 0.0 MPa in the spring, corresponding to a field capacity θ of about $0.25 \text{ m}^3 \text{ m}^{-3}$. Between 1999 and 2001 the soil became progressively drier. In 1999, the mean minimum soil water potential, Ψ_s , between 30 and 90 cm corresponded to a θ of $0.081 \text{ m}^3 \text{ m}^{-3}$; in 2000 and 2001 Ψ_s corresponded to θ values of 0.073 and $0.059 \text{ m}^3 \text{ m}^{-3}$, respectively.

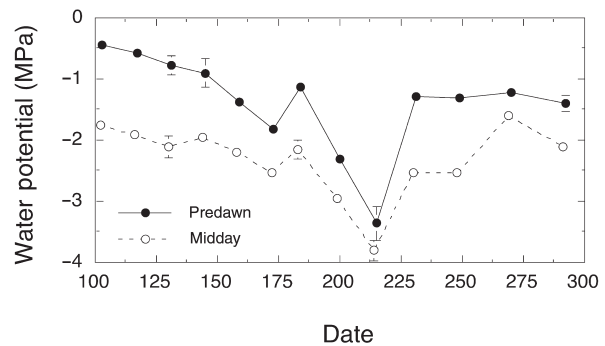


Figure 2. Plant water potential measured throughout the growing season (April–October 2000). Values are the mean \pm standard error of five individuals.

Table 1. Stepwise multiple regression analysis of the relationships between morning and afternoon stomatal conductance (g) and transpiration (E) and predawn water potential (Ψ_{pd}), midday water potential (Ψ_{md}) and vapor pressure deficit (VPD) during the summer of 2000.

Dependent variable	Independent variable	Morning			Afternoon		
		r^2	F	P	r^2	F	P
g	Ψ_{pd}	0.451	8.23	0.017	0.712	27.2	0.001
	VPD	0.139	3.07	0.114	0.142	9.70	0.011
E	VPD	0.476	9.09	0.013	None		

Removal of water from these soil layers proceeded sequentially from shallower to deeper layers (Figure 3). Water uptake was defined as a clear negative trend in Ψ_s and typically began in April for the 30-cm and 45-cm depths but not until May at greater depths.

In the study plot free of vegetation, Ψ_s at 30 cm remained above -0.5 MPa until mid-July and only declined to a minimum of about -0.9 MPa by late September. Thus, evaporation from the soil had little effect on removal of water at the 30-cm depth. In contrast, under the juniper stand, Ψ_s at 30 cm was about -3.5 MPa in mid-July and about -5.5 MPa by late September.

Over the three years of Ψ_s data, hydraulic redistribution was

observed following several summer rain events. In 1999, on Day 232 (August 20) a 6-mm rain event was evident at 30, 45 and 60 cm (Figure 3). The increase in θ at these depths corresponded to 0.010 , 0.014 and 0.022 $\text{m}^3 \text{m}^{-3}$, respectively. No water was redistributed as deep as 90 cm. In 2000, from Day 228 to 236 (August 15–23), rain events totaling 10.4 mm were evident at 30, 45, 60 and 90 cm (Figure 3). The increase in θ at these depths corresponded to 0.012 , 0.010 , 0.014 and 0.005 $\text{m}^3 \text{m}^{-3}$, respectively. No water was redistributed by roots deeper than 90 cm. In 2001, between Days 232 and 233 (August 20–21), rain events totaling 15.7 mm were evident at 30, 45, 60 and 90 cm (Figure 3). The increase in θ at these depths corresponded to 0.004 , 0.003 , 0.004 and 0.002 $\text{m}^3 \text{m}^{-3}$, respectively. No water was redistributed deeper than 90 cm.

Significant soil water recharge began in all years following extensive autumn rains (Figure 3). Recharge following snowmelt and spring rains returned all layers from which water had been extracted during the previous growing season to field capacity.

Root distribution was determined when psychrometers were installed in March 1999. More than 50% of all roots were less than 30 cm deep and 75% less than 50 cm deep (Figure 4). Few roots were found below 100 cm.

Soil water sources determined with δD

Winter and summer δD values of precipitation were different in 2000 (Figure 5). Precipitation samples taken before early June were similar (mean = -105‰) but δD of the precipitation increased once monsoon rains began (mean δD between July 5

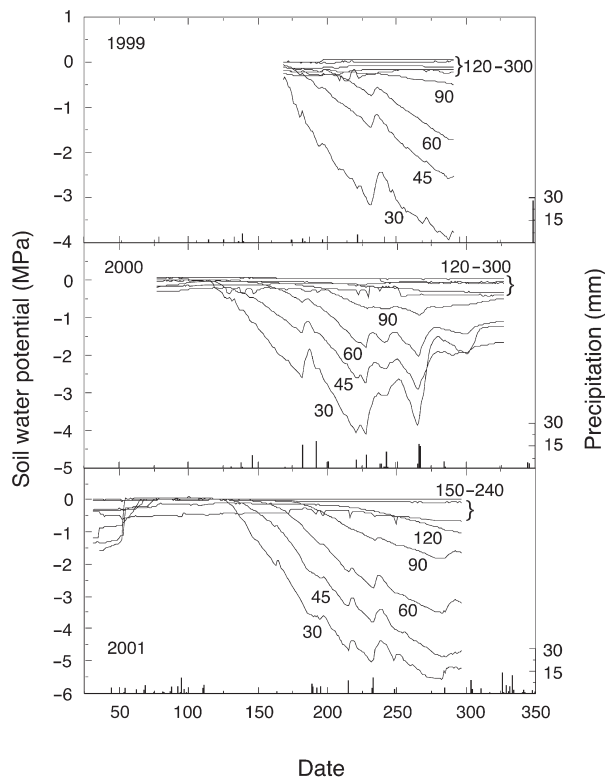


Figure 3. Soil water potential measured with psychrometers at depths from 30 to 300 cm, and daily precipitation (mm). Psychrometers at the 300-cm depth did not function in 2001.

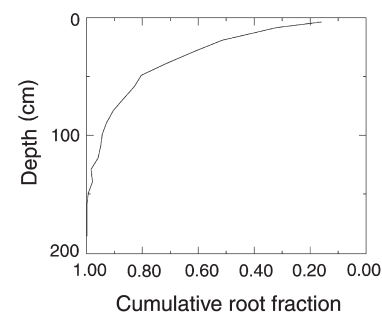


Figure 4. Cumulative root fraction as a function of depth in *J. osteosperma*.

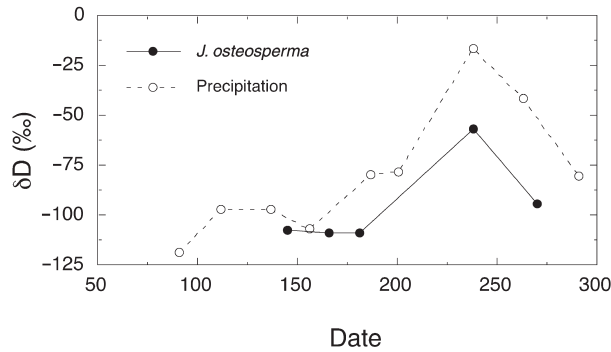


Figure 5. The δD of precipitation and water extracted from *J. osteosperma* stems throughout the 2000 growing season. Values for juniper are the means of five individuals (different from the five selected for gas exchange measurements); standard errors are too small to display on the scale of this graph. Precipitation was collected from one rain gauge and there was no standard error associated with these data.

and August 25 = -58‰). Tissues samples taken before late June were similar (mean = -109‰), but tissue δD increased in late August (-57‰), and declined again by late September (-95‰).

Canopy- and ecosystem-level water use

Total daily A (A_d) was approximated from the leaf-level gas exchange data and stand leaf area index (LAI). Total tree leaf area ranged from 3.7 to 126 m² with a mean (\pm SD) of 63 ± 36 m². We found a mean LAI of 9.3 ± 6.4 (mean \pm SD) for the canopy projection of the trees and a canopy cover of 15% for the stand, yielding a stand LAI of 1.4. On a ground area basis, values of A_d ranged from 0.07 mol m⁻² day⁻¹ on August 3 to 0.20 mol m⁻² day⁻¹ on May 11. Mean A_d across all measurement days was 0.13 ± 0.03 mol m⁻² day⁻¹. Total daily E (E_d) was estimated from the leaf gas exchange data and stand LAI. Values ranged from 0.33 mm day⁻¹ on September 26 to 0.87 mm day⁻¹ on 5 September. Mean E_d was 0.59 ± 0.16 mm day⁻¹.

Daily changes in θ were used to model daily ET from each soil layer (Table 2). It is impossible to obtain a minimum daily

ET with this method because small amounts of water are likely lost even when there is net water movement into the soil. Comparisons among years were also impossible because the available data were for different time periods during each year. With few exceptions, however, monthly modeled ET values were similar among years (Figure 6).

Eddy covariance data for the period from March 26 through October 27, 2001 showed a declining trend in water flux with a mean daily value of 0.85 mm (Figure 6). The CO₂ flux during this period ranged from positive to negative, typically being negative under wetter conditions. Overall the ecosystem was a net source of CO₂ during 2001 with a total CO₂ flux of 3.9 mol m⁻² ground area.

Discussion

We showed for a *Juniperus osteosperma* ecosystem that: (1) carbon assimilation and water use was controlled primarily by soil water supply; (2) during the summer of 2000 (ie., the only year in which δD was measured) *Juniperus osteosperma* plants used summer precipitation; (3) hydraulic redistribution was an important process in soil water dynamics; and (4) ET and transpiration estimates from leaf-level gas exchange, changes in soil water content and eddy covariance are similar in magnitude. These results cast light on the physiological mechanisms enabling *J. osteosperma* to compete successfully in harsh environments.

The observed values of g and A are consistent with reports on other juniper species (Körner et al. 1979, Miller et al. 1992, 1993, Lajtha and Getz 1993, Owens 1996, Moore et al. 1999). Compared with other conifers, g but not A of juniper is relatively low (Körner et al. 1979, Miller and Shultz 1987, Miller et al. 1992, Lajtha and Getz 1993).

Gas exchange in *J. osteosperma* appeared to be limited by soil water supply, not g . Predawn water potential had an apparently greater effect on g than did VPD (Table 1). The small influence of VPD on g is likely related to the dry warm-season atmosphere in Utah that provides sufficient evaporative demand during daylight hours to ensure that VPD seldom limits E (Ryel et al. 2002). Similar close relationships between carbon acquisition, water use and soil water availability were re-

Table 2. Total (mm), maximum (mm day⁻¹) and mean daily transpiration (ET; mm day⁻¹) calculated from changes in soil water content in five soil layers.

Year	Evapotranspiration	0–37.5 cm	37.5–52.5 cm	52.5–67.5 cm	67.5–100 cm	100–135 cm
1999	Total	46.5	29.1	27.6	24.8	0
	Maximum	4.3	2.0	0.82	1.0	0
	Mean	0.51	0.28	0.26	0.26	0
2000	Total	59.3	27.3	30.0	56.3	0
	Maximum	4.3	2.1	1.2	2.2	0
	Mean	0.45	0.21	0.25	0.50	0
2001	Total	76.2	30.7	30.2	64.4	63.1
	Maximum	9.2	2.6	2.6	9.0	2.4
	Mean	0.60	0.24	0.24	0.52	0.38

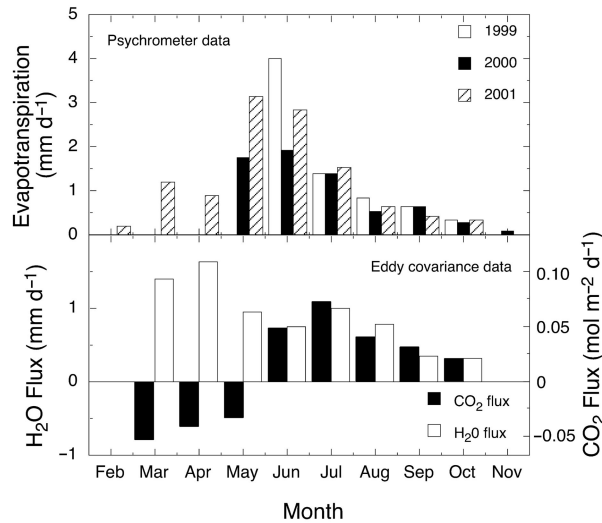


Figure 6. Mean daily evapotranspiration for each month calculated from the change in soil water content measured with soil psychrometers (top panel) and mean daily water and CO₂ flux for each month from a *J. osteosperma* community as measured by the eddy covariance system between March 26 and October 27, 2001 (bottom panel). Note that there is no evapotranspiration value calculated from the psychrometers for March or April 2000; no change in soil water content was observed until May 2000. Positive flux values indicate gas release from the community and negative values indicate uptake.

ported for a *Juniperus occidentalis* Hook. stand in central Oregon, USA (Miller et al. 1993). Moreover, Williams and Ehleringer (1996) found similar $\delta^{13}\text{C}$ values among *J. osteosperma* populations at different sites in Utah even though VPD varied among these sites, suggesting that VPD had little influence on gas exchange of the juniper populations in their survey.

In August 2000, stem tissue δD increased sharply, suggesting that summer precipitation was being absorbed (Figure 5). Using a two-end-member mixing model (White et al. 1985) with winter (-105.33‰ prior to early June) and summer (-16.85‰ between July 19 and August 25) precipitation, we calculated that stem water sampled on August 25 contained 54% summer precipitation. Both gas exchange and stem water potential also responded to summer precipitation (Figures 1 and 2). Following the June 30, 2000 rain event, A , g , E , c_i , Ψ_{pd} and Ψ_{md} all increased, suggesting that *J. osteosperma* maintained active roots in the upper soil layers that were capable of rapidly using water and nutrient pulses during the summer. Moreover, the high Ψ_{pd} , Ψ_{md} and gas exchange observed in late summer and early autumn resulted from numerous small rain events that neither penetrated nor were redistributed as deep as 30 cm. In contrast to our findings, no uptake of summer precipitation was observed in another northern Utah study with *J. osteosperma*, though conditions were similar (Donovan and Ehleringer 1994). Donovan and Ehleringer (1994) also reported a shallow petrocalcic layer at their site, hence the root distribution at their site is likely similar to the root distribution at our site. Moreover, summer precipitation during the

years these studies were conducted was similar. These studies suggest that use of summer precipitation by *J. osteosperma* in northern Utah is highly variable and may be related to subtle interactions of root distribution and the amount and timing of rain events. Use of summer precipitation by *J. osteosperma* has been observed at other sites in Southern Utah and Arizona where summer rains are generally more prominent (Flanagan et al. 1992, Williams and Ehleringer 2000).

The shallow root distribution of *J. osteosperma* may be partly responsible for the gas exchange patterns we observed. Most roots were found within the upper 50 cm of soil and virtually no roots were found below 100 cm (Figure 4), possibly a result of the petrocalcic layer at this site (Lowe 1999).

Extraction of soil water proceeded sequentially from shallower to deeper soil layers rather than simultaneously at all depths where roots were present (Figure 3). Soils above 30 cm were rapidly dried at the beginning of the season and drying progressed downward throughout the summer. In contrast, at a site about 3 km away, uptake by *Artemisia tridentata* occurred nearly simultaneously from most soil layers where roots were present (Ryel et al. 2002). Moorehead et al. (1989) used soil water loss models to show that simultaneous water removal from multiple soil layers occurs in a Chihuahuan desert community and results in greater soil water retention.

The soil was not dried to the same extent each year but appeared to become progressively drier over the 3-year study period. The soil was dried to a mean θ of 0.081, 0.073 and $0.059\text{ m}^3\text{ m}^{-3}$ in 1999, 2000 and 2001, respectively. Moreover, in 2001, water was extracted from the 120 cm soil depth suggesting that deeper water was not used until water in the upper layers was essentially depleted. Use of deep water is likely a result of new root growth and demonstrates that the petrocalcic layer does not necessarily preclude access to deep water or that it is deeper than 1 m in the vicinity of the psychrometers.

Redistribution of soil water (Richards and Caldwell 1987, Caldwell and Richards 1989, Caldwell et al. 1998) by the *J. osteosperma* root system following precipitation was evident (Figure 3). Hydraulic redistribution has been examined extensively in an associated study (Ryel et al. 2002). Therefore, we do not present an in-depth analysis of redistribution here, but cite three lines of evidence supporting the idea that water moved via *J. osteosperma* roots rather than bulk flow through macropores, capillary movement or vapor phase diffusion. (1) Rainwater was redistributed only to the layers from which water was extracted during the weeks before the rain event. We observed no water redistributed to 90 cm following the June 2000 rain event, but a small amount of water was redistributed to 90 cm in August 2000. Hence, water was only moved to soil layers from which water had been extracted previously (the active rooting depth). (2) Rainwater was received simultaneously at each depth rather than sequentially as would be expected from bulk flow. (3) Given the soils present at our study site, rain events of this size would not be expected to infiltrate to the depths that we observed (Ryel et al. 2002). Moreover, water moved deeper following the August 2000 rain

event than following the June 2000 rain event even though the June event was ~50% larger; deeper roots were active in August, but not in June. If the downward movement of water was by macropore flow it would be unlikely to vary in effectiveness in different months.

Hydraulic redistribution is an important component of soil water dynamics and plant water relations. It is thought that upward movement of water from deep soils can increase daily transpiration, promote nutrient uptake from upper, drier soils and maintain fine roots by keeping them hydrated (Caldwell et al. 1998). Redistribution downward, as we observed, can enhance transpiration by moving water away from the surface where it is subject to evaporation and plays a significant role in soil water dynamics related to spring recharge (Ryel et al. 2002).

Evapotranspiration (ET) was estimated from $\Delta\theta$ (modeled ET) and was calculated using all psychrometer data available from 1999 to 2001 (Table 2). Total annual estimates of ET are not possible because data were not collected in the winter. Monthly modeled ET was similar among years, with the exception of May and June (Figure 6), a result of variation in spring weather conditions. Although psychrometers provide long-term measurements of soil water potential, they do have drawbacks for calculations of ET. Psychrometer values must be converted to θ using the water release characteristics of the soil with corrections for the soil coarse fraction, integrate only a small soil volume and cannot be used to estimate ET when θ is high or increasing. Therefore, modeled ET (Equation 3) is likely to provide an underestimate of ET.

Eddy covariance data were available during 2001 and provided an additional estimate of ET (Figure 6). Total annual estimates of ET are not possible because the system did not function for the entire year. The highest ET was observed in March and April (~1.5 mm day⁻¹) and was below 1.0 mm day⁻¹ for the remainder of the year. In general, psychrometer data produced higher ET estimates than Equation 3, and the difference was most pronounced in the late spring and early summer. Psychrometer data also suggest that maximum ET is observed in May and June rather than March and April, likely a result of the inability to estimate ET with psychrometers when soil water content is increasing.

Daily transpiration (E_d), estimated from leaf-level gas exchange, was 0.59 mm day⁻¹ during the 2000 growing season. We also calculated an E of 0.50 mm day⁻¹ based on a limited amount of xylem sap flux data (see Granier 1985, 1987) from this site (A.J. Leffler, unpublished data). It is likely that E_d is an overestimate of E . Gas exchange measurements were made on the south side of trees on outer branches twice a day; shaded branches likely had lower E , and E was likely lower in the early morning and late afternoon. Although this method yields only a rough estimate of daily E , the values reported here are similar in magnitude to the diel E and ET estimates from the psychrometer and eddy flux data.

Estimates of total water use by juniper stands can be found in both the physiology and hydrology literature. Mean annual ET, estimated from the difference between precipitation and

runoff, was 414 mm (1.13 mm day⁻¹) in a Beaver Creek, AZ watershed from 1958 to 1980 (Lane and Barnes 1987). Annual E , calculated from a canopy diffusion model, in a piñon-juniper woodland of New Mexico ranged from 69 mm (0.19 mm day⁻¹) to 360 mm (0.99 mm day⁻¹), depending on elevation (Lane and Barnes 1987). Total water use (leaf area basis), calculated from leaf-level measurements, scaled to individual *J. occidentalis* trees, was 0.09 and 0.21 mm day⁻¹ in May and July 1984, respectively (Miller et al. 1987). These values can be compared with mean daily ET from two dramatically different western USA ecosystems including: 3.96 mm day⁻¹, measured with a Bowen ratio system, for a stand of the invasive riparian tree *Tamarix ramosissima* (Ledeb) in Nevada (Devitt et al. 1998) and 0.04 mm day⁻¹, measured with weighing lysimeters, in a *Larrea tridentata* (DC.) Cov. community in the Sonoran desert (Sammis and Gay 1979). Eddy covariance studies have become common around the globe. A water flux of about 2 mm day⁻¹ was reported from the boreal forests of Canada (Saugier et al. 1997) and researchers from the tropical savannas of northern Australia reported mean annual water fluxes of 2.6 mm day⁻¹ (Hutley et al. 2000) and 3.5 mm day⁻¹ (Eamus et al. 2001).

In 2000, our leaf-level A values, scaled to stand-level estimates of carbon acquisition, yielded a mean A_d between April 13 and October 17 of 0.13 mol m⁻² ground area day⁻¹. The eddy flux data that were available from March 26 to October 27, 2001 showed there was net CO₂ release (3.9 mol m⁻² ground area) from this *J. osteosperma* stand (Figure 6). This CO₂ release was not large but suggests that this ecosystem is a net source of CO₂, at least in some years. The CO₂ acquisition ended abruptly in late May; after May 22 net CO₂ uptake was only observed following rain events. We know of no other estimates of stand-level carbon acquisition in juniper.

We have identified physiological mechanisms that allow *J. osteosperma* to survive in harsh environments. We conclude that *J. osteosperma* vigorously utilizes water in the upper soil but remains capable of tolerating extremely dry soils, maintaining modest photosynthetic rates during drought and responding rapidly to summer rains when available. These characteristics likely contribute to the competitive success of *J. osteosperma* throughout western North America.

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