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Precipitation pulse use by an invasive woody legume: the role of soil texture and pulse size

Abstract Plant metabolic activity in arid and semi-arid environments is largely tied to episodic precipitation events or "pulses". The ability of plants to take up and utilize rain pulses during the growing season in these water-limited ecosystems is determined in part by pulse timing, intensity and amount, and by hydrological properties of the soil that translate precipitation into plant-available soil moisture. We assessed the sensitivity of an invasive woody plant, velvet mesquite (*Prosopis velutina* Woot.), to large (35 mm) and small (10 mm) isotopically labeled irrigation pulses on two contrasting soil textures (sandy-loam vs. loamy-clay) in semi-desert grassland in southeastern Arizona, USA. Predawn leaf water potential (Ψ_{pd}), the isotopic abundance of deuterium in stem water (δD), the abundance of ^{13}C in soluble leaf sugar ($\delta^{13}C$), and percent volumetric soil water content (θ_v) were measured prior to irrigation and repeatedly for 2 weeks following irrigation. Plant water potential and the percent of pulse water present in the stem xylem indicated that although mesquite trees on both coarse- and fine-textured soils quickly responded to the large irrigation pulse, the magnitude and duration of this response substantially differed between soil textures. After reaching a maximum 4 days after the irrigation, the fraction of pulse water in stem xylem decreased more rapidly on the loamy-clay soil than the sandy-loam soil. Similarly, on both soil textures mesquite significantly responded to the 10-mm pulse. However, the magnitude of this response was substantially greater for mesquite on the sandy-loam soil compared to loamy-clay soil. The relationship between Ψ_{pd} and $\delta^{13}C$ of leaf-soluble carbohydrates over the pulse period did not differ between plants at the two sites, indicating that differences in photosynthetic response of mesquite trees to the moisture pulses was a function of soil water availability within the rooting zone rather than differences in plant biochemical or physiological constraints. Patterns of resource acquisition by mesquite during the dynamic wetting–drying cycle following rainfall pulses is controlled by a complex interaction between pulse size and soil hydraulic properties. A better understanding of how this interaction affects plant water availability and photosynthetic response is needed to predict how grassland structure and function will respond to climate change.

Keywords *Prosopis velutina* · Mesquite · Soil texture · Pulse water uptake · Stable isotopes

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Introduction

In the arid southwestern United States, monsoon rainfall comprises up to 60% of total annual precipitation in some areas and is a key resource and driver of plant and ecosystem productivity and dynamics. Episodic or pulsed inputs of monsoon precipitation during the

summer growing season create a dynamic soil moisture regime that is favorable for plant growth only for brief time periods (Noy-Meir 1973; Huxman et al. 2004). Uptake of soil moisture from these pulsed inputs of summer precipitation varies markedly among the diverse plant functional types that occupy the arid and semi-arid landscapes of the region (Ehleringer et al. 1991; Schwinning et al. 2002). Although it is generally assumed that shallow-rooted herbaceous species are more dependent on summer precipitation than deep-rooted woody species (Dawson and Ehleringer 1991; Flanagan et al. 1992; Jackson et al. 1999), considerable variation in water source use has been observed within and among different plant lifeforms (Schulze et al. 1996; Lin et al. 1996; Reynolds et al 1999; Yoder and Nowak 1999; Williams and Ehleringer 2000).

Rainfall patterns (event size, timing and frequency) and soil hydraulic characteristics strongly mediate the dynamics of plant water uptake during the growing season in arid and semi-arid environments (Noy-Meir 1973; McAuliffe 1994; Hamerlynck et al. 2004; Huxman et al. 2004). Summer rainfall patterns in southeastern Arizona are characterized by the occurrence of frequent small rain events and infrequent large events (Fig. 1). The occurrence of just a few large rainfall events in such semi-arid systems is sufficient to generate a wet year (Golluscio et al 1998; Fravolini et al. 2003). The annual variability of large and small rainfall events in arid and semi-arid regions could have important implications for regulating plant productivity and vegetation dynamics (Weltzin et al. 2003). The occurrence of large rainfall events that percolate deep into the soil profile during wet summers may provide a water source that can be utilized by woody species which are typically not as sensitive to summer precipitation as shallow-rooted herbaceous species (Golluscio et al. 1988; Schwinning et al. 2003). However, to what extent these large summer pulses of water are utilized by deep-rooted plants will ultimately depend on the combined hydraulic characteristics of the rhizosphere and plant xylem.

Soil hydraulic properties play a major role in modifying the spatial and temporal availability of water to plants (Bristow et al. 1984; Smith et al. 1995; Schlesinger and Pilmanis 1998; Hacke et al. 2000; Sperry et al. 2002; Hamerlynck et al. 2004; Huxman et al. 2004). Soil texture can affect the timing of appearance and disappearance of soil moisture pulses and the length of time between periods of plant-available moisture. Unlike in mesic habitats, vegetation in arid habitats is substantially more vigorous and abundant on coarse, sandy soils than on fine-textured soils. This inverse texture effect is likely a result of differences in evaporation between soil types, rather than differences in drainage (Noy-Meir 1973). Less water is lost to evaporation in coarse-textured soils than in fine-textured soils. This is due to the large pore spaces in coarse soils that improve water percolation through the soil profile (Campbell 1985). The high infiltration rate and deep percolation of water in coarse soils is critical in regulating plant distribution and ecosystem productivity of desert regions where evaporative demand is extremely high.

In southeastern Arizona, spatial distribution of the invasive woody legume velvet mesquite (*Prosopis velutina* Woot.) varies across the landscape. Mesquite over the last 100 years has gradually expanded its range by encroaching into former grasslands (Archer 1995; McPherson 1997); however, this phenomenon is not spatially homogeneous. Mesquite trees have increased their abundance at a greater rate on sandy upland soils, developed on recently deposited Holocene alluvium, more than on clay-rich Pleistocene alluvial fans (Medina 1996).

The interaction between rainfall and soil texture may lead to differential acquisition and use of seasonal precipitation by mesquite trees across the landscape. Fine-textured soils restrict the wetting front to the upper soil layers, thereby inhibiting the uptake of summer rain by deep-rooted woody plants (Fravolini et al. 2003). Conversely, the coarse-textured Holocene soils allow summer rain to penetrate deeply into the soil profile after major precipitation pulses. Hydrologic differences observed across soil textures very likely lead to different exposure and use of summer precipitation pulses by deep-rooted plants such as mesquite.

Several studies have evaluated the effect of rainfall size (Lauenroth et al 1987; Golluscio et al. 1998; Dougherty et al 1996; Schwinning et al 2003) or soil texture (Schlesinger and Pilmanis 1998; Hacke et al. 2000; Sperry et al. 2002; Hamerlynck et al. 2004) on plant water use. In this investigation, we assessed the effect that the interaction between rainfall pulse size and soil texture have on summer water use by velvet mesquite. Specifically, we used large (35 mm) and small (10 mm) irrigation inputs to evaluate the physiological responses of mesquite trees on two contrasting soil textures (sandy-loam vs. loamy-clay).
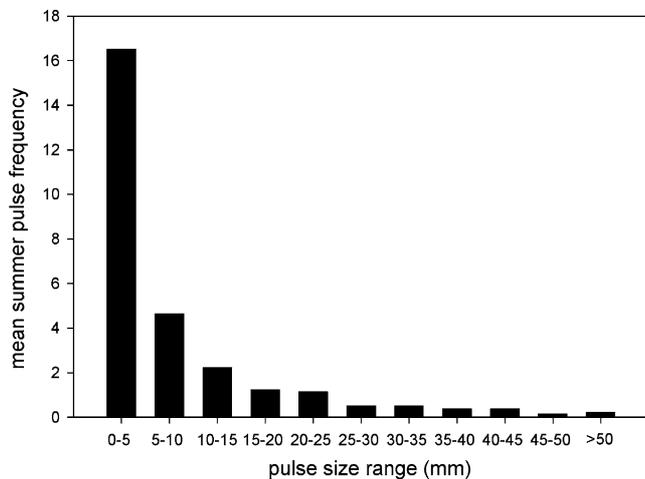

Fig. 1 Mean summer (July–September) rainfall pulse frequency according to event size. Data were compiled from the National Climate Data Center. Source NOAA (http://www.noaa.gov/)

We predicted that: (1) large pulses would have a greater impact on the physiology of mesquite trees on coarse sandy soils compared to fine-textured loamy-clay soils, and (2) that mesquite response to the small irrigation input would not be sufficient to activate a physiological response on either soil type.

Methods

Study site

The study was conducted at the Santa Rita experimental range (SRER), 35 km south of Tucson, AZ, USA. The mean annual air temperature, in this area, is 16°C. Daily maximum air temperatures in summer often exceed 35°C (McClaran et al. 2002). Mean annual rainfall (1972–2002) is 430 mm at the loamy-clay site and 394 mm at the sandy-loam site (rain gauges: 41 and rodent station; SRER database). More than 56% of the total annual precipitation at both sites occurs during the summer monsoon (July-September) with high inter-annual variation. During the winter and spring months preceding our study, both sites received an amount of precipitation close to the average for these two sites: from November 2001 to June 2002 the loamy-clay soil received 150 mm (average 160 mm) and the sandy-loam site received 133 mm (average is 146 mm; source SRER database).

Root morphology and water use of mesquite at the SRER

Velvet mesquite (*P. velutina*) on the SRER has been described as an intensive water exploiter with a dimorphic root system characterized by a deep taproot and a large number of primary and secondary lateral roots extending for several meters beyond the edge of the canopy (Clark 1947; Cable 1977). Although mesquite roots tend to extend vertically to great depths, it is likely that nearly all its active roots at the SRER are constrained to the upper soil layers since (1) the access to stable ground water is beyond reasonable rooting depth and (2) winter and summer precipitation rarely penetrates below 2 m of depth (Cable 1977; Cable 1980; Frasier and Cox 1994). The depth of mesquite taproots and the density and distribution of lateral roots at the SRER also vary depending on the vertical and horizontal distribution of available soil water across soil types (Clark 1947). In sandy-loam alluvial soils at the SRER, the mesquite root system is characterized by the dominance of a taproot that penetrates deep into the soil profile (Clark 1947). Numerous lateral roots depart from the taproot and form an extensive horizontal root system that can extend more than 15 m beyond the canopy. This well-developed lateral root system allows for intensive water exploitation in the inter-canopy area and is particularly important during periods of high transpiration demand or when the available water stored in the deep soil layers becomes scarce (Cable 1977). In clay-loam soils, the taproot does not dominate, probably due to the presence at this depth of a well-developed clay layer that limits deep percolation of water (Clark 1947). In this fine-textured soil, the lateral root system dominates and its root density approaches zero at a depth between 30.5 cm and 46 cm, extending in all directions for more than 15 m (Clark 1947).

Experimental design

Two sites were selected for irrigation experiments within the SRER based on their contrasting soil texture. One site was on a recently deposited Holocene alluvial fan surface (31° 47′N, 110° 50′W, 1,190 m elevation), while the other site was located on a much older Pleistocene surface (31° 47′N, 110° 54′W, 1,090 m elevation). The percentage of sand, silt and clay for each selected site is reported in Table 1 (Fravolini et al. 2003). The Holocene alluvial fan surface was composed of a sandy-loam soil with a bulk density of 2 g cm^{-3}, while the soil on the Pleistocene surface was loamy-clay and had a bulk density of 1.5 g cm^{-3}.

Twelve mature mesquite trees (1 to 3-m height) were randomly selected within one large (150 by 100 m) plot at each site, and four replicate trees were each randomly assigned to a large (35 mm)-, small (10 mm)-, and control-irrigation treatment. The probability frequency for each rainfall size on our site is reported in Fig. 1. On average, from summer 1989 to summer 2003, precipitation events between 5 and 15 mm accounted for 30% of total rainfall while events between 30 and 35 mm comprised 21% of summer precipitation. Irrigation water was applied on the evening of 21 June 2002. In order to distinguish irrigation water from naturally occurring soil water, the irrigation water was labeled with D_2O to obtain a δD value of 160‰; the δD value of soil water prior to irrigation in June was −50‰. Irrigation water was applied at a rate of 2 mm/min over a 2.5-m radius around the base of each experimental tree. The perim-

Table 1 The percentage of sand, silt, and clay measured from soil pits taken in each of the two experimental sites (Fravolini et al. 2003)

Soil depth (cm)	Sand fraction (%)	Silt fraction (%)	Clay fraction (%)
Sandy loam (Holocene)			
−5	85.1	8.9	6.1
−10	85.1	7.9	7
−30	80	10.2	9.8
−60	78.7	12.4	8.9
Loamy clay (Pleistocene)			
−5	74.8	12.1	13.1
−10	76.1	11.2	12.7
−30	62	12.7	25.3
−60	45.6	15.6	38.8

eter of each irrigation plot was trenched to a depth of 10 cm to prevent runoff.

Three 60 by 120-cm trenches were dug to a depth of 70 cm in the inter-canopy spaces at each site. Custom built time-domain reflectometry probes (TDR; Ledieu et al. 1986; Risler et al. 1996) were installed horizontally in the trench faces to measure volumetric soil water content (θ_v) within the soil profile at 10–15, 20, 30, 40, and 50 to 55-cm depths. A single TDR probe was installed at each depth. The trenches were backfilled and tamped after rod installation and each TDR plot was randomly assigned to control-, small-, or large-irrigation treatments. Irrigation was applied to the non-control TDR plots using the same protocol described above for irrigating the trees. Care was taken to avoid applying water directly to the backfilled trenches. Each TDR probe was calibrated in the laboratory using soils (<2 mm) from the sandy-loam and loamy-clay sites with known volumetric water contents from 0 to 20%. TDR probes were monitored using a portable computer connected to a Campbell TDR-100 cable tester (Campbell Scientific, Logan, UT, USA).

Plant and soil measurements and isotope sampling were carried out on the day before irrigation and on days 1, 2, 4, 6, 8, 11, and 14 following irrigation. No natural rainfall events occurred on our sites during the above observational period. Between three to four suberized twig samples were collected for deuterium isotope analysis from various canopy locations and cardinal directions at midday of each sample day. Twig samples were placed in borosilicate glass vials, closed with screw caps, wrapped with parafilm, placed in an ice cooler, and immediately transported to the laboratory where they were kept frozen until extraction. Water was subsequently extracted from the stems by cryogenic vacuum distillation (Ehleringer and Osmond 1989) and its deuterium isotope composition (δD) was measured on a dual-inlet, isotope ratio mass spectrometer with a measurement precision of 0.5‰ (Delta-S, Finnigan MAT, San Jose, CA, USA) at the Laboratory of Isotope Geochemistry, Department of Geosciences, University of Arizona. The proportion (%) of irrigation pulse water present in the stem xylem (PWU) was calculated using the equation:

$$\%PWU = \left(1 - \frac{\delta D_{irr} - \delta D_{xi}}{\delta D_{irr} - \delta D_{xcon}}\right) \times 100 \qquad (1)$$

where δD_{irr} is the notation for the stable isotope ratio of hydrogen in irrigation water and is expressed in parts per thousand (‰), δD_{xi} that of twig xylem water of irrigated plants and δD_{con} that of control plants for samples collected on the same day.

Predawn leaf water potential (Ψ_{pd}) was measured between 02:00 h and 04:00 h using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA). Mesquite twigs were cut with a sharp razor blade, and immediately placed in a sealed plastic bag containing a moist paper towel before measurement with the pressure chamber.

Short-term ^{13}C fixation into soluble leaf carbohydrates was used to evaluate the photosynthetic response of mesquite trees to the irrigation pulse treatments. The $\delta^{13}C$ in soluble carbohydrates may be used to infer gas exchange (photosynthesis, A and/or stomatal conductance, g) variations over short time periods (1–3 days; Brugnoli et al. 1988). The composition of $\delta^{13}C$ in leaf-soluble carbohydrates reflects the carboxylation and diffusion discrimination against the heavier carbon isotope (^{13}C) compared to the lighter isotope (^{12}C) occurring during photosynthetic CO_2 uptake (Brugnoli et al. 1988; Brugnoli and Farquhar 1998). Ten to fifteen leaves were collected for carbohydrate extraction at midday on all but the last (14 days post-irrigation) sampling date. Leaf tissue was immediately immersed in liquid nitrogen after collection to prevent further metabolic activity, and then temporarily stored in a cooler containing dry ice. The samples were transported to the lab where they were freeze-dried and then ground to a fine powder. The leaf-soluble carbohydrates were extracted in distilled water followed by a purification procedure according to Brugnoli et al. (1988). This extraction was performed at the laboratory facilities of the National Research Center (CNR) in Porano (Umbria), Italy. The $\delta^{13}C$ values of carbohydrate samples were determined using a continuous-flow isotope ratio mass spectrometer (IsoPrime, Micromass UK Ltd., Manchester, UK) at the University of Wyoming Stable Isotope Facility, Department of Renewable Resources, University of Wyoming, Laramie, WY, USA.

Data analysis

The experiment was a longitudinal study with a randomized 2×3 factorial treatment design with: two soil textures (sandy-loam and loamy-clay); three irrigation treatments of a large (35 mm of precipitation applied to each tree), small (10 mm of precipitation applied) and control (no precipitation applied), size; and four replicates for each soil-texture-by-irrigation-treatment combination.

Multivariate analysis for repeated measures (MANOVA) was performed on untransformed data to test the effect of soil textures, water treatments, time, and their interaction using VWC, predawn leaf water potential, percentage of irrigation water in the stem xylem, and the $\delta^{13}C$ value of soluble leaf carbohydrates as response variables. To identify the differences in treatment effect across soil textures that were statistically meaningful, a least-significant difference (LSD) contrast analysis was performed within the MANOVA framework.

Since the response of all dependent variables followed a quadratic rather than a linear trend through time, a quadratic matrix for each dependent variable was used within the MANOVA framework to test whether there were significant differences in the trend between treatments through time. Result from the quadratic trans-

formation analysis are discussed only at the highest level of significance ($P \leq 0.05$). The JMP 4 software for PC (SAS Institute, Inc., Cary, NC, USA) was used to perform the statistical analysis.

Results

Dynamics of soil water content

The sandy-loam soil (Holocene surface) showed larger relative changes in volumetric water content (θ_v) at depths between 10 cm and 50 cm than the loamy-clay soil (Pleistocene surface) following the small (10 mm) and large (35 mm) irrigation pulses (Fig. 2). Moreover, the wetting front advanced to deeper layers on the sandy-loam soil than in the loamy-clay soil. Changes in θ_v were small in the sandy-loam soil in response to the 10 mm pulse. Within the first 24 h, θ_v in sandy-loam soils increased dramatically in the upper 30 cm in response to the large pulse. Increases in θ_v were less significant, but present, at 50 cm (Fig. 2b). Patterns of infiltration were substantially different in loamy-clay soils following irrigation. We detected a negligible increase in soil moisture at 10 cm in response to the small pulse (Fig. 2c). Small increases in θ_v were detected following the large pulse; at 10 cm, θ_v increased from 1.6 to 3.3% 8 days after the pulse. The wetting front advanced to 30 cm by day 14, as θ_v increased slightly from an initial value of 7.6% to 8.1% (Fig. 2d).

Changes in plant water status

Predawn leaf water potential (Ψ_{pd}) substantially mirrored changes in θ_v over the 14-day observation period. Mesquite on the loamy-clay soil had higher Ψ_{pd} than mesquite on the sandy-loam soil prior to the irrigation (Fig. 3a–b). Following irrigation, mesquite trees that received the 35-mm pulse achieved higher predawn leaf water potential than mesquite treated with the 10-mm pulse on both the sandy-loam and the loamy-clay soil. The treatment-by-time interaction was statistically significant on each soil type (Table 2). The significance of this interaction is confirmed by the difference in the quadratic term between treatments over time ($F_{2,18} = 23.77$, $P < 0.001$). On both soil textures, irrigation enhanced Ψ_{pd} regardless of pulse size, until day 4 when Ψ_{pd} declined toward the pre-pulse level (Fig. 3).

Values of Ψ_{pd} showed a greater increase on the sandy-loam soil than on the loamy-clay soil following the small irrigation ($F_{1,18} = 7.37$, $P < 0.01$). Conversely, leaf water potential at both sites showed a similar pattern through time in response to the large pulse ($F_{1,18} = 0.21$, $P = 0.64$ from linear contrast). Although Ψ_{pd} in plants that received the large irrigation pulse had the same
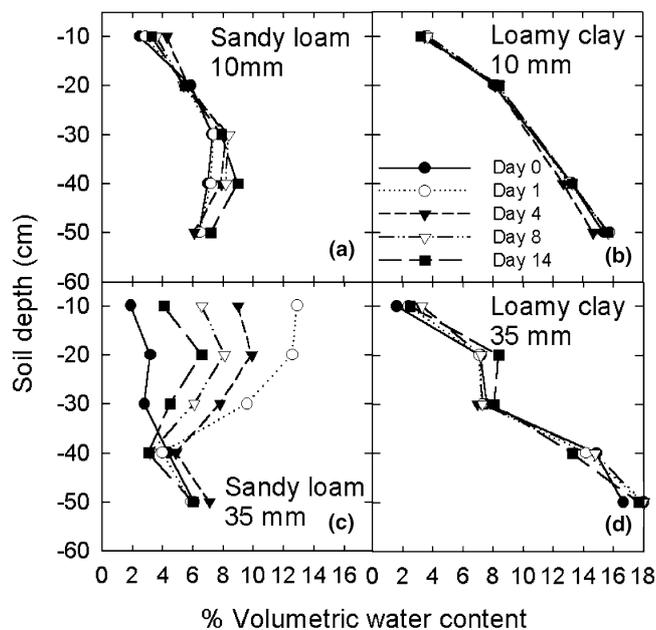
Fig. 2 Volumetric soil water content (θ_v) of sandy-loam and loamy-clay soils measured with time domain reflectometry probes in late June and early July 2002. Measurements were taken at 10, 20, 30, 40, and 50-cm depths the day prior to the application of either a large (35 mm) or a small (10 mm) irrigation pulse (day 0), and on days 1, 4, 8, and 14 after the release of the pulse
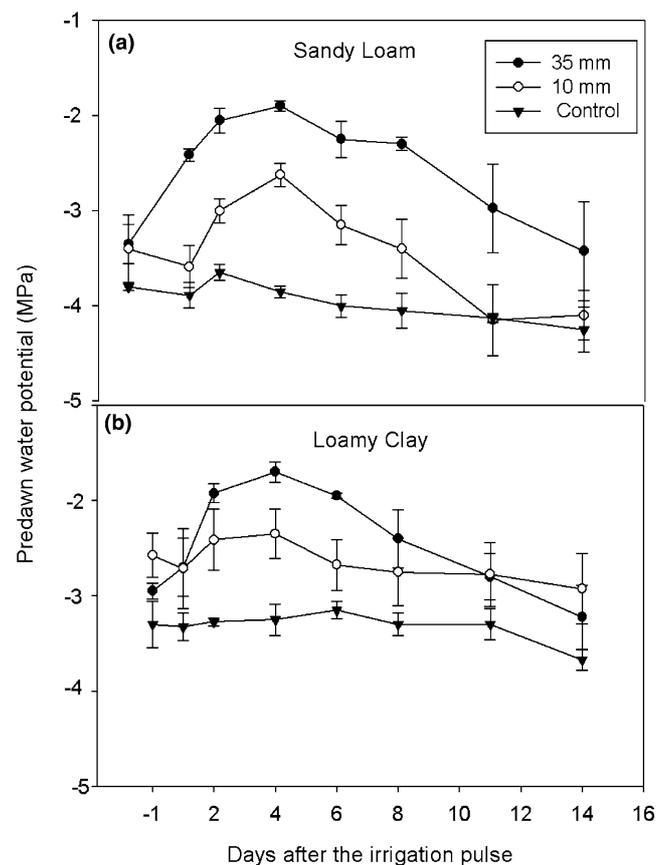
Fig. 3 Predawn leaf water potential (Ψ_{pd}) of mesquite trees across two contrasting soil textures following either a large (35 mm), small (10 mm), or no irrigation treatment. Day 0 is 21 June 2002. *Error bars* indicate ± 1 SE

proportional increase across soil textures, plants on the sandy-loam surface overall maintained more negative Ψ_{pd} values after irrigation (Fig. 3).

Pulse water uptake

There was an effect of the soil texture-by-treatment-by-time interaction on the percent pulse water uptake, indicating that trees on different soil textures responded differently to small and large irrigation pulses over time (Table 2).

Mesquite tree at the two sites differed significantly in their uptake of irrigation water over time ($F_{1,12} = 51.4$, $P < 0.0001$; Fig. 4). The percent of pulse water use increased dramatically following the 35-mm irrigation on both soil types (Fig. 4a–b). However, after reaching a maximum at day 4, the pulse water uptake by mesquite trees declined more rapidly on the loamy-clay than on the sandy-loam soil. The percent pulse water uptake in mesquite stem water following the small pulse was higher on the sandy-loam soil than on the loamy-clay soil (pulse-by-soil texture-by-time interaction, ($F_{6,7} = 12.20$, $P = 0.002$; Table 2).

For the sandy-loam site, mesquite trees that received the large irrigation reached the maximum percent pulse use more rapidly than mesquite that received the small pulse (Fig. 4a). Mesquite trees on the loamy-clay soil had a significant response to the large pulse, while mesquite response to the small pulse on this soil was substantially lower in magnitude, although still signifi-

cant ($F_{1,3} = 68.84$ $P = 0.0037$; Fig. 4b). Percent pulse water uptake and Ψ_{pd} were positively correlated during the experiment and the dynamic of this relationship was similar in both soil textures (Fig. 5).

Differences in carbon isotope ratios

A significant amount of variation in carbon isotope ratios ($\delta^{13}C$) of soluble carbohydrates extracted from mesquite leaves was explained by the treatment-by-time interaction, but differences in $\delta^{13}C$ between soil textures over time were not significant (Table 2). Prior to the irrigation pulse, $\delta^{13}C$ of soluble carbohydrates was more negative for mesquite trees on the loamy-clay surface than for those on the sandy-loam surface (Fig. 6a–b). On both surfaces, mesquite trees that received irrigation had lower $\delta^{13}C$ values than those that did not receive irrigation ($F_{1,18} = 6.68$, $P = 0.01$). Mesquite trees that received the 35-mm irrigation treatment on the sandy-loam surface had lower $\delta^{13}C$ values than did those that received the small irrigation pulse ($F_{1,18} = 3.32$, $P = 0.08$; Fig. 6a). Carbon isotope ratios differed significantly between water treatments in their response over time ($F_{5,6} = 4.27$, $P = 0.05$). Mesquite trees on the sandy-loam soil responded immediately to the irrigation pulse, shifting the $\delta^{13}C$ value of soluble carbohydrate by $-2\permil$ 1 day after the pulse (Fig. 6). Conversely, $\delta^{13}C$ of carbohydrates on the loamy-clay soil shifted less than $-0.5\permil$ the day following the irrigation and reached its maximum value 6 days after the pulse.

Table 2 Mean squares (MS), degrees of freedom (df), F-statistic (F) corresponding P values from the MANOVA repeated measures statistical analysis of predawn leaf water potential (Ψ_{pd}), percent pulse water uptake (PWU) in stem water and $\delta^{13}C$ of leaf-soluble carbohydrates of mesquite trees following an irrigation pulse

Factors	Mean square	df	F	P value
ψ_{pd}				
Soil texture	12.52	1,18	81.41	***
Water treatment	20.05	2,18	130.37	***
Soil texture × water treatment	0.05	2,18	3.63	**
Soil texture × time	0.14	7,12	0.94	NS
Water treatment × time	0.52	14,24	3.36	***
Soil texture × water treatment × time	0.13	14,24	0.87	NS
Time	2.62	7,12	17.06	***
Error	0.15	126		
PWU				
Soil texture	0.59	1,12	87.46	***
Water treatment	3.2	1,12	474.44	***
Soil texture × water treatment	0.13	1,12	19.17	**
Soil texture × time	0.04	6,7	6.68	**
Water treatment × time	0.04	6,7	6.49	**
Soil Texture × water treatment × time	0.06	6,7	9.29	**
Time	0.31	6,7	46.75	***
Error	0.007	84		
$\delta^{13}C$				
Water treatment	3.14	2,18	4.55	**
Soil texture × water treatment	0.09	2,18	0.14	NS
Soil texture × time	0.57	6,13	0.83	NS
Water treatment × time	1.33	12,26	1.94	*
Soil texture × water treatment × time	0.67	12,26	0.97	NS
Time	3.02	6,13	4.38	**
Error	0.69	84		

The actual P values are reported when $P > 0.1$ and $P < 0.2$ NS not significant
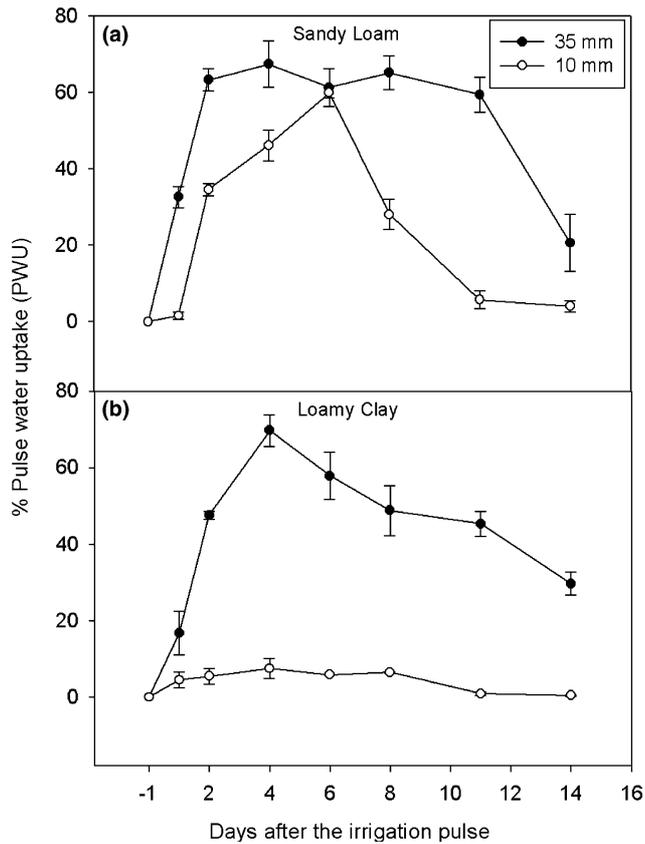*$P \leq 0.1$; **$P \leq 0.05$; ***$P \leq 0.001$

Fig. 4 Percent pulse water in the stem xylem of mesquite trees across two contrasting soil textures following either a large (35 mm), small (10 mm), or no irrigation treatment. Day 0 is 21 June 2002. *Error bars* indicate ±1 SE
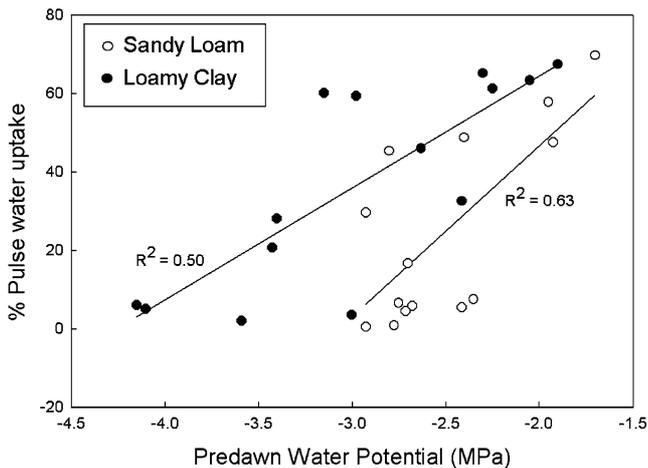

Fig. 5 Relationship between mean daily Ψ_{pd} and percent pulse water uptake in mesquite trees following the release of large and small irrigation treatments across two contrasting soil textures

Values of $\delta^{13}C$ and Ψ_{pd} were positively correlated during the experiment and the dynamic of this relationship was similar across both soil textures (sandy-loam $R^2 = 0.37$; loamy-clay $R^2 = 0.45$).
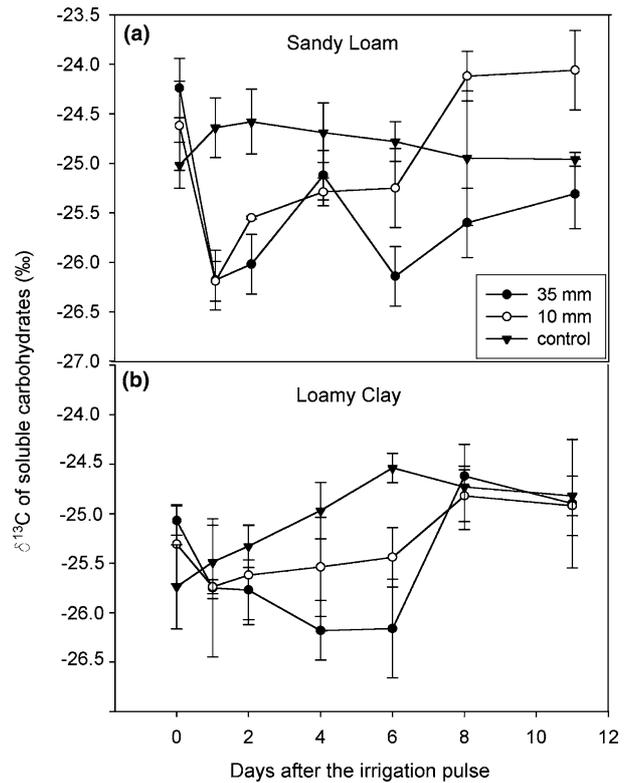

Fig. 6 ^{13}C isotope composition ($\delta^{13}C$) of soluble leaf carbohydrates of mesquite trees across two contrasting soil textures following either a large (35 mm), small (10 mm), or no irrigation treatment. Day 0 is 21 June 2002. *Error bars* indicate ±1 SE

Discussion

In this study, mesquite response to both large and small summer pulses of moisture was strongly affected by soil texture. Although mesquite trees on both coarse- and fine-textured soils quickly took up water from a large irrigation pulse, the duration of this response substantially differed between soil textures. After reaching a maximum 4 days after the irrigation, the fraction of pulse water in stem xylem decreased more rapidly on the loamy-clay soil than the sandy-loam soil. Not surprisingly, the presence of a well-developed clay layer in the subsurface of the loamy-clay soil limits infiltration of moisture inputs during summer, thus reducing the effectiveness of both large and small rainfall events for mesquite. Differential mesquite water acquisition across the two soil textures also was observed following the 10-mm pulse, with mesquite extracting substantially higher amounts of irrigation water on the coarse-textured soil than on the fine-textured soil.

Woody plants of arid and semi-arid regions can respond to pulses of summer rain especially after prolonged periods of drought (Golluscio et al. 1998; Williams and Ehleringer 2000; Snyder et al. 2004). Soil moisture availability during the hot summer months is critical for the establishment and growth of mesquite

trees in this arid ecosystem (Weltzin and McPherson 1997). The ability of mesquite trees on the sandy-loam soil to fully utilize large rain events during their growing season combined with their high responsiveness to small rain events may facilitate the encroachment of this woody legume on coarse-textured soils.

Shallow argillic horizons on Pleistocene surfaces, common on the bajada slopes of the Basin and Range physiographic province, likely reduce infiltration following precipitation pulses and thereby limit the uptake of pulse water by woody desert plants (McAuliffe 1994, McDonald et al. 1996; Hamerlynck et al. 2004). The effect of clay-rich layers on the depth of the soil wetting front and response of woody plants should be especially manifested during small precipitation events. The limited uptake of the 10-mm irrigation pulse by mesquite on the loamy-clay surface was in sharp contrast to the very significant response of mesquite to the same pulse size on the sandy-loam soil. The fraction of xylem water derived from the 10-mm pulse never rose above 10% on the loamy-clay soil, but rose to 60% on the sandy-loam soil. In the loamy-clay soil, there was no measurable infiltration in the inter-canopy spaces following the 10-mm irrigation pulse. The presence of high clay contents in Pleistocene soils likely prevented significant percolation of the small pulse to the rooting zone, given that mesquite roots at the Santa Rita Range are rarely found in the top 10 cm of the soil profile (Parker and Martin 1952, Cable 1977).

Alternatively, fine-textured soils may retain water longer from previous precipitation, limiting percolation and mesquite utilization of new pulses of rain. Long-term leaf water potential measured in mature mesquite trees along a soil texture gradient on the SRER showed that trees on coarse-textured soils experience greater levels of water deficit compared to trees on fine-textured soils before the onset of the monsoon (Fravolini et al. 2003). The ability of fine-textured soils to retain water for extended periods may be beneficial for desert plants exposed to prolonged drought, as long as water is held at water potentials high enough for plant extraction to occur. However, during summer rainfall the presence of winter water held in soil micropores may limit percolation of new pulses, thereby facilitating runoff or ponding and subsequent evaporation at the soil surface.

The observed relationship between percent pulse water uptake and Ψ_{pd} was similar across soil textures and was positively correlated (Fig. 5). Different degrees of hydraulic constraints have been observed within species occurring on different soil textures (Jackson et al. 1996; Sperry et al. 2002). Coarse-textured soils have greater loss of rhizosphere hydraulic conductivity per unit drop of soil water potential than fine-textured soils (Campbell 1985). As a result, plants in coarse soils can be more exposed to hydraulic failure in the rhizosphere than plants in fine soils without significant adjustment of the root-to-leaf surface area ratio (Sperry et al. 1998, Hacke et al. 2000). Although trees on the coarse-tex-

tured soil experienced the greatest level of water deficit prior to irrigation in our study, there was no difference in the dynamics of water uptake between soil textures. The relationship between predawn water potential (an index of rhizosphere water availability) and uptake of pulse water was similar on both soil textures. Therefore, mesquite acquisition of irrigation pulses was likely a function of pulse water availability, which differed between the two soils, rather than to different plant uptake capacities across soil textures.

The differences in pulse utilization observed in mesquite on the two soils were reflected in changes in $\delta^{13}C$ of soluble carbohydrates extracted from leaves. Carbon isotope values of soluble carbohydrates in C_3 leaves may be used to infer c_i/c_a variations over short and medium time scales (Brugnoli et al. 1998). In this study, shifts in $\delta^{13}C$ of soluble carbohydrates were correlated with changes in predawn leaf water potential in a similar fashion across soil textures. Conversely, summer moisture inputs did not alter rates of leaf gas exchange in deep-rooted shrubs in comparatively summer-dry environments (Snyder et al. 2004, Schwinning et al. 2003). Maintenance of low leaf photosynthetic activity in perennial woody species during long periods of drought in these summer dry habitats can be energetically efficient, allowing them to survive over extended periods with little or no available water (Schwinning et al. 2003). However, the maintenance of low photosynthetic activity during rainless periods could prevent rapid photosynthetic responses of desert shrubs to sudden pulses of water since it could be difficult and energetically expensive for leaves to quickly restore their photosynthetic apparatus. In our study, mesquite trees were exposed to an extended period of drought (the last rainfall prior to the irrigation on both study sites was a 5-mm rainfall event on 19 February, 119 days prior to our experiment) and mesquite on the sandy-loam soil had lower predawn water potential than mesquite on the clay-loam soil. However, despite the prolonged drought and the difference in water deficit measured across soil textures, $\delta^{13}C$ of soluble carbohydrates very quickly responded to the irrigation pulses regardless of the soil texture. Moreover, on both sites Ψ_{pd} and $\delta^{13}C$ were positively correlated, suggesting that the response of carbon assimilation to irrigation pulses was a function of soil water availability rather than to differences in physiological or photosynthetic limitations. Soil water availability was the major factor controlling the uptake of pulse water by mesquite. In a water-limited ecosystem characterized by predictable summer rainfall, the ability to quickly utilize rain inputs whenever available may be critical to enhance growth and reproduction.

The sensitivity of dominant woody plants to pulses of summer moisture can have important implications for vegetation response to climate change and ecosystem water balance (Schlesinger et al. 1990; Jackson et al. 1996; Schulze et al. 1996; Ehleringer et al. 1998). An understanding of the complex interaction between soil texture and plant water availability is critical to predict

how future changes in precipitation patterns will affect plant community and ecosystem dynamics (Schlesinger et al. 1990, Huxman et al. 2004). Mesquite on fine-textured soils are highly sensitive to large rain events, which occur at low frequency during the summer North American monsoon, and are less sensitive to frequent small pulses. Conversely, mesquite trees on coarse-textured sandy soils respond to both large and small summer rainfall pulses. Intra-annual variation in summer precipitation patterns may strongly govern shifts in mesquite function, and possibly its distribution across the heterogeneous desert landscape. One consistent prediction from global and regional circulation models is that summer rainfall in the southwestern United States will become more variable from year to year and extremely large rainfall events will be more common during wet years (Giorgi et al. 1998; USGC committee research report 2000). A decrease in the number of small rain events accompanied by a shift toward large summer rainfall events could diversely affect plant community structure and function of arid and semi-arid grasslands. Large rain events during wet summers apparently can enhance water uptake and photosynthetic metabolism of mesquite on coarse-textured soils more so than on fine-textured soils. Similarly, during summers with average precipitation, the prevalence of small rain events over large rain events may selectively favor mesquite production on coarse-textured soils, potentially exacerbating the actual differences in tree distribution across the landscape.

References

Archer SA (1995) Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83–99

Bristow KL, Campbell GS, Calissendorf C (1984) The effects of texture on the resistance to water movement within the rhizosphere. Journal of the Soil Science Society of America 42:657–659

Brugnoli E, Farquhar GD (1998) Photosynthetic fractionation of carbon isotopes. In Photosynthesis: physiology and metabolism, advances in Photosynthesis. In: Leegood RC, Sharkey TD, von Caemmerer (eds) Kluwer Academic Publishers, Dordrecht

Brugnoli E, Hubick KT, von Caemmerer S, Wong SC, Farquhar GD (1988) Correlation between carbon isotope discrimination in leaf starch and carbohydrates of C_3 plants and the ratio of intercellular and atmospheric partial pressures of carbon dioxide. Plant Physiology 88:418–1424

Cable DR (1977) Seasonal use of soil water by mature velvet mesquite. Journal of Range Management 30:4–11

Cable DR (1980) Seasonal patterns of soil water recharge and extraction on semidesert ranges. Journal of Range Management 33:9–15

Campbell GS (1985) Soil physics with basic, transport models for soil-plant systems. Elsevier, Amsterdam, Netherlands

Clark MS (1947) The effect of mesquite control on the soil moisture content of mesquite – infested range land in southern Arizona. Tucson AZ, University of Arizona. 36 p. Thesis (This thesis is available on special collection at the UofA library: call number is E 9791 1947 29)

Dawson TE, Ehleringer JR (1991) Streamside trees that do not use stream water. Nature 350:335–337

Dougherty RL, Lauenroth WK, Singh JS (1996) Response of a grassland cactus to frequency and size of rainfall events in a North American shortgrass steppe. Journal of Ecology 84:177–183

Ehleringer JR, Osmond CB (1989) Stable isotopes. In: RW Pearcy, JR Ehleringer, HA Mooney, PW Rundel (eds) Plant physiological ecology: field methods and instrumentation. Chapman & Hall, London, pp 281–300

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 D (1998) Assessing sensitivity to change in desert ecosystems –a stable isotope approach. In: Griffiths H (ed) Stable isotope integration of biological, ecological, and geochemical processes. BIOS Scientific Publisher, Oxford, pp 233–237

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 15:15–28

Frasier GW, Cox JR (1994) Water balance in pure stand of Lehmann lovegrass. J Range Manage 47:373–378

Fravolini A, Hultine KR, Koepke DF, Williams DG (2003) The role of soil texture on mesquite water relations and response to summer precipitation. In: Santa Rita experimental range: 100 years of accomplishment and contributions, conference proceedings, 30 October–1 November 2003. Tucson, pp 125–129

Giorgi F, Mearns LO, Shields C, McDaniel L (1998) Regional nested model simulations of present day and $2 \times CO_2$ climate over the central plains of the United States. Climate Change 40:457–493

Golluscio RA, Sala OE, Lauenroth WK (1998) Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. Oecologia 115:17–25

Hacke UE, Sperry JS, Ewers BE, Ellsworth DS, Schafer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus taeda*. Oecologia 124:495–505

Hamerlynck EP, Huxman TE, McAuliffe JR, Smith SD (2004). Carbon isotope discrimination and foliar nutrient status of *Larrea tridentata* (creosote bush) in contrasting Mojave Desert soils. Oecologia 138:210–215

Huxman TE, Cable JM, Ignace DD, Eilts AJ, English NB, Weltzin J, Williams DG (2004) Response of net ecosystem gas exchange to a simulated precipitation pulse in a semi-arid grassland: the role of native versus non-native grasses and soil texture. Oecologia (in press)

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global review of rooting patterns. I. Root distribution by depth for terrestrial biomes. Oecologia 108:389–411

Jackson PC, Meinzer FC, Bustamante M, Goldstein G, Franco A, Rundel PW, Caldas L, Igler E, Causin F (1999) Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. Tree Physiol 19:717–724

Lauenroth WK, Sala OE, Milchunas DG, Lathrop RW (1987) Root dynamics of *Bouteloua gracilis* during short term recovery from drought. Funct Ecol 1:117–124

Ledieu, J, Deridder P, DeClerck P, Dautrebande S (1986) A method of measuring soil moisture by time-domain reflectometry. J Hydrol 88:319–328

Lin G, Phillips SL, Ehleringer JR (1996) Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. Oecologia 106:8–17

McAuliffe JR (1994) Landscape, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. Ecol Monogr 64:111–148

McClaran MP, Angell DL, Wissler C (2002) Santa Rita experimental range digital database: user's guide. USFS Forest Service General Technical Report RMRS-GTR-100. Rocky Mountain Research Station, Ogden

McDonald EV, Pierson FB, Flerchinger GN, McFadden LD (1996) Application of a process based soil water balance model to evaluate the influence of Late Quaternary climate change on soil-water movement in calcic soils. Geoderma 74:167–192

McPherson GR (1997) Ecology and management of North American savannas. University of Arizona Press, Tucson

Medina AL (1996) The Santa Rita Experimental Range: history and annotated bibliography (1903–1988). General Technical Report RM-GTR-276. Rocky Mountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture, Tucson

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4:23–51

Parker KW, Martin SC (1952) The mesquite problem on southern Arizona ranges. US Department of Agriculture Circular 908 70p. Washington DC

Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol Monogr 69:21–24

Risler PD, Wraith JM, Gaber HM (1996) Solute transport under transient flow conditions estimated using time domain reflectometry. Soil Sci Soc Am J 60:1297–1305

Schlesinger WH, Pilmanis AM (1998) Plant-soil interactions in deserts. Biogeochemistry 42:169–187

Schlesinger WH, Reynolds JF, Cunningham GL, Heunneke LF, Jarrell WM, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. Science 247:1043–1048

Schulze E-D, Mooney HA, Sala OE, Jobaggy E, Buchmann N, Bauer G, Canadell J, Jackson RB, Loreti J, Osterheld M, Ehleringer JR (1996) Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia 108:389–411

Schwinning S, Davis K, Richardson L, Ehleringer JR (2002) Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. Oecologia 130:245–255

Schwinning S, Starr BI, Ehleringer JR (2003) Dominant cold desert plants do not partition warm season rainfall by event size. Oecologia 136:252–260

Smith SD, Herr CA, Leary KL, Piorkowski JM (1995) Soil plant water relations in a Mojave Desert mixed shrub community: a comparison of three geomorphic surfaces. J Arid Environ 29:339–351

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 (in press)

Sperry JS, Adler FR, Campbell GS, Comstock JP (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. Plant, Cell Environ 21:347–359

Sperry JS, Hacke UG, Oren R, Comstock JP (2002) Water deficits and hydraulic limits to leaf water supply. Plant, Cell Environ 25:251–263

USGC (United State Global Change) (2000) Research report: preparing for a change in climate: the potential consequences of climate variability and change. A report of the Southwest Regional Assessment Group; source: http://www.usgcrp.gov/usgcrp/nacc/sw.htm

Weltzin JF, McPherson GR (1997) Spatial and temporal soil moisture resource partitioning by trees and savannas in a temperate savanna, Arizona. Oecologia 112:156–164

Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Lin G, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53:941–952

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

Yoder CK, Nowak RS (1999) Soil moisture extraction by evergreen and drought-deciduous shrubs in the Mojave Desert during wet and dry years. J Arid Environ 42:81–96