

Groundwater use by native plants in response to changes in precipitation in an intermountain basin

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ABSTRACT

Many arid basins in western North America are likely to experience future changes in precipitation timing and amount. Where shallow water tables occur, plant acquisition of groundwater and soil water may be influenced by growing season precipitation. We conducted a rainfall manipulation experiment to investigate responses of four common native plant species to ambient, increased, and decreased summer monsoon rainfall. We measured plant xylem pressure potentials (Ψ) and stable oxygen isotope signatures ($\delta^{18}\text{O}$) to assess effects of altered precipitation on plant water relations and water acquisition patterns. Reduced rainfall decreased Ψ more in the grasses *Sporobolus airoides* and *Distichlis spicata* than the more deeply rooted shrubs *Sarcobatus vermiculatus* and *Ericameria nauseosa*. *E. nauseosa* had little response to natural or experimental differences in available soil water. Plant xylem water $\delta^{18}\text{O}$ indicated that *S. airoides* and *D. spicata* are almost entirely dependent on rain-recharged soil water, while *E. nauseosa* is almost entirely groundwater-dependent. *Sarcobatus vermiculatus* used groundwater during dry periods, but utilized precipitation from soil layers after large rainfall events. Persistent changes in precipitation patterns could cause shifts in plant community composition that may alter basin-scale groundwater consumption by native plants, affecting water availability for human and ecosystem uses.

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1. Introduction

Millions of hectares in arid and semiarid western North America are covered by plants that can acquire groundwater from shallow water tables. Precipitation and soil water availability in these regions are highly variable in timing and amount (Noy-Meir, 1973). Because water is the most limiting resource to plant growth, nutrient cycling, and net ecosystem productivity in arid environments (Noy-Meir, 1973; Smith et al., 1997), plants might be expected to respond rapidly to acquire growing season precipitation. However, plant species in arid regions vary considerably in their ability to utilize soil water recharged by pulses of summer rain (Ehleringer et al., 1991; Flanagan et al., 1992; Lin et al., 1996). This variation is largely a function of local climate and edaphic factors (Williams and Ehleringer, 2000), plant tissue hydraulic constraints (Hacke et al., 2000; Sperry and Hacke, 2002), and root distribution (Schenk and Jackson, 2002). Understanding this variation and how

it affects groundwater use by plants is critical for informing regional hydrologic models used to manage large, shallow aquifers.

Many perennial plants in arid and semiarid zones have a dimorphic root system composed of branched surface roots that can acquire water from shallow soil layers recharged by summer rains and deeper roots that can access perennially available groundwater (Williams and Ehleringer, 2000). Plants that can acquire groundwater from a shallow aquifer are commonly referred to as phreatophytes. Some phreatophytes appear to be largely dependent on groundwater while others are also able to acquire soil water recharged by summer rain (Chimner and Cooper, 2004; Sperry and Hacke, 2002). This variation in water acquisition patterns may represent local adaptation to different precipitation regimes. Williams and Ehleringer (2000) suggested that plants would be more likely to use growing season rain in arid regions with more consistent summer precipitation, such as the North American monsoon that occurs in late summer through much of the southwestern U.S. and parts of northern Mexico (Grantz et al., 2007). They found that the proportion of precipitation-recharged soil water taken up by the deep-rooted trees *Pinus edulis* and *Juniperus osteosperma* increased as the predictability of summer

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monsoon precipitation increased (Williams and Ehleringer, 2000). In Colorado's San Luis Valley, Chimner and Cooper (2004) found that the phreatophyte shrubs *Sarcobatus vermiculatus* and *Ericameria nauseosa* used groundwater in early summer, but acquired precipitation water during a typical late summer monsoon season. Much less is known about herbaceous phreatophyte species. However, the grass *Distichlis spicata* is reported to use rain-recharged soil water in greater proportions than co-occurring woody phreatophytes in an arid basin with shallow groundwater but lacking summer monsoon precipitation (Goedhart et al., 2010; Pataki et al., 2008).

A shift to either wetter or drier growing season conditions could affect plant growth and competition, triggering changes in community composition (Elmore et al., 2003; Knapp et al., 2002; Schlesinger et al., 1990; Weltzin et al., 2003) and subsequent changes in groundwater use. Several general circulation models project a transition toward a more arid climate in southwestern North America, accompanied by a decrease in summer rainfall (Cook et al., 2004; Seager et al., 2007). Other models predict an intensification of the North American monsoon system (Arritt et al., 2000; Grantz et al., 2007). The flow of monsoonal moisture produces some of the most intense rainfall events of the year, and delivers 50–70% of the total annual precipitation from July through mid-September in southwestern North America (Grantz et al., 2007). An increase in monsoon rainfall in southwestern North America could lead to increased phreatophyte use of growing season precipitation and reduced groundwater use. Or, if growing season precipitation decreases or becomes more variable from year to year, phreatophytes could become more reliant on groundwater.

The effects of altered precipitation regimes on plant production and community composition have been investigated in grasslands (Chimner and Welker, 2005; Knapp et al., 2002), and arid land plant communities (Bates et al., 2006; Lin et al., 1996; Miranda et al., 2009; Thomey et al., 2011; Yahdjian and Sala, 2006). However, few precipitation manipulation studies explain the mechanisms that may cause observed changes in production (but see Schwinning et al., 2005a,b). Plant water acquisition patterns may be one of the factors that explain these effects. Understanding how plant water acquisition could respond to precipitation changes is also an essential first step toward modeling future hydrologic impacts of vegetation change.

We investigated the water acquisition patterns of four common native plant species and how these patterns responded to changes in growing season precipitation using a rainfall manipulation experiment at a long-term study site in the San Luis Valley, Colorado. All four species are generally regarded as facultative phreatophytes (Robinson, 1958), able to acquire both groundwater and soil water recharged by precipitation. This work addressed the following questions: (1) how do plant water relations and water acquisition patterns (groundwater versus rain-recharged soil water) vary among these plant species under the current precipitation regime? and (2) how will plant water relations and water use respond to a change in growing season precipitation (e.g. intensified monsoon rainfall, or extended periods of drought)? During our experiment, we used xylem pressure potential to understand plant response to rainfall, and we used stable isotopes to understand the relative importance of groundwater versus rain-recharged soil water as the sources of water exploited by plants.

2. Site description

The San Luis Valley (SLV) is a high elevation intermountain basin in southern Colorado, USA (Fig. 1). The valley floor covers approximately 8400 km², is relatively flat, and averages 2350 m elevation. The southern portion of the SLV is drained by the Rio Grande, while

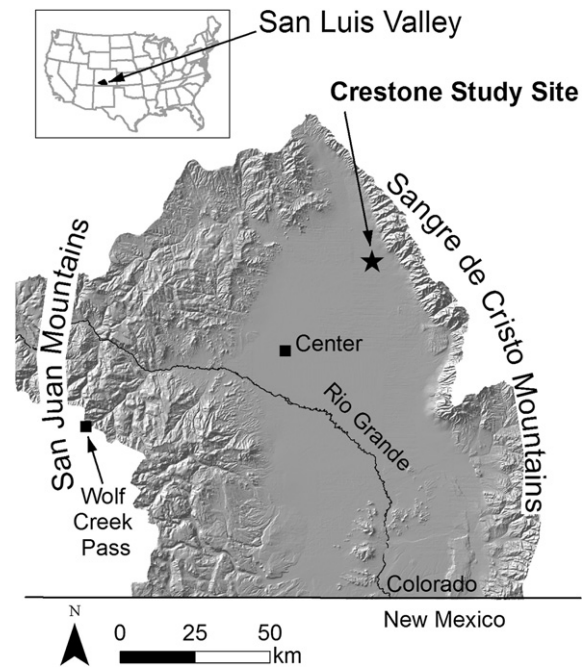


Fig. 1. Location of the Crestone study site and the San Luis Valley in Colorado, USA.

the northern 7600 km² is a hydrologically closed basin, with inflow from mountain streams but no natural surface water outlets.

The SLV experiences warm summers, cold winters, and high insolation year-round (Doesken and McKee, 1989). Mean monthly temperatures range from 17 °C in July to –9 °C in January (Western Regional Climate Center, 2011). Average annual precipitation on the valley floor is 178 ± 49 mm (mean ± 1SD, recorded at Center, CO from 1942–2009; Western Regional Climate Center, 2011). Approximately 2/3 of the annual precipitation occurs from July–September as monsoon rains (Cooper et al., 2006). Mean annual precipitation in the surrounding mountains ranges from 800 to 1500 mm a year, and occurs primarily as winter snow (Doesken and McKee, 1989). Snowmelt runoff from the mountains feeds numerous streams that flow over mountain-front alluvial fans composed of coarse-textured soil. Most of this runoff recharges an unconfined aquifer that underlies the closed basin, producing a shallow water table 1–5 m below the ground surface throughout much of the SLV (Cooper et al., 2006). The aquifer is drawn upon to supply over 2400 km² of irrigated agriculture, and supports more than 4850 km² of native plant communities composed entirely or partly of phreatophytes, which provide domestic livestock forage, wildlife habitat, and soil stabilization.

The Crestone study site (Fig. 1) is located within the closed basin portion of the SLV. During the study, the water table depth ranged from 105 to 150 cm below ground surface, and was generally highest in spring and lowest in late fall (Appendix A, Fig. A.1). Soils at the site are saline (electrical conductivity = 5–40 dS/m). Vegetation is representative of that occurring throughout the SLV, and is dominated by the shrubs greasewood (*Sarcobatus vermiculatus* (Hooker) Torrey) and rubber rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom and Baird ssp. *consimilis* (Greene) G.L. Nesom and Baird var. *oreophila* (A. Nelson) G.L. Nesom and Baird), and the grasses alkali sacaton (*Sporobolus airoides* (Torr.) Torr.) and saltgrass (*Distichlis spicata* (L.) Greene) (Appendix A, Fig. A.2). These species occur widely in arid regions of western North America, where *S. vermiculatus* alone occupies approximately 4.8 million hectares (Mozingo, 1987). Mean percent cover of the four study species in

the SLV is: 12.4% *S. vermiculatus*, 7.1% *E. nauseosa*, 8.2% *S. airoides*, 4.3% *D. spicata* (Cooper, unpublished data).

3. Materials and methods

3.1. Experimental design

The study was established as a split-plot design ($n = 5$ replicates), where rainfall treatment was the whole-plot factor, and species (*S. vermiculatus*, *E. nauseosa*, *S. airoides*, and *D. spicata*) were sub-plot factors. The experiment was conducted over two years (2008 and 2009). Plots were 3.7 m × 4.3 m in size and each included multiple individuals of the four study species. Plots within each block were randomly assigned to receive: (1) ambient rainfall (control), (2) reduced total rainfall under a rainout shelter (rain out), or (3) increased total rainfall by applying rain captured from rainout shelter roofs (rain addition).

Rainout shelter roofs were constructed from clear corrugated polycarbonate sheeting that transmitted 85–90% of photosynthetically active wavelengths of light and did not transmit UV wavelengths. Shelter roofs were 1.5 m above the ground, and open on all four sides to maximize air movement and minimize temperature and relative humidity artifacts. We measured surface soil temperature using copper-constantan thermocouples inserted at 2 cm depths on two dates (7 June and 29 July 2009) in each plot. We performed one-way ANOVA on measured soil temperatures and determined that no statistically significant differences in soil temperature occurred between sheltered and un-sheltered plots ($p > 0.475$, all comparisons).

Rainfall intercepted by shelter roofs was routed into storage tanks, and this stored rainwater was uniformly applied to rain addition plots using watering cans. Rain additions were typically applied within hours of natural rain events. Watering occurred in multiple shifts when necessary to minimize runoff and evaporation loss from ponded water. Control plots received 97 mm of growing season rainfall between 1 June and 15 September in 2008, and 67 mm in 2009. Rain addition treatments received 139 mm in 2008 and 97 mm in 2009, which represented a 43% and 30% increase over natural growing season rainfall. Rainout shelters excluded all direct precipitation from 4 July 2008 through 1 October 2009, and rain out plots received 5 mm of growing season rain in 2008 and 0 mm in 2009.

In both years, the rain addition treatments simulated strong late summer monsoonal conditions, bringing cumulative year-to-date precipitation to around 1 standard deviation above the 68-year mean (Fig. 2). However, intra-seasonal patterns differed substantially between 2008 and 2009. During 2008, there was little rainfall through early July, with cumulative totals near 1 standard deviation below average. This dry period was followed by strong monsoon-driven rains from late July through September, raising the cumulative precipitation total to near average (Fig. 2; see also Appendix A, Fig. A.1). In 2009, cumulative year-to-date precipitation was about 1 standard deviation above average at the beginning of the growing season. The monsoon was weak in 2009, so cumulative precipitation by the end of the growing season was near the long term average (Fig. 2). The rain out treatment resulted in growing season precipitation well below the long-term average in both years.

3.2. Field and laboratory methods

3.2.1. Soil and hydrologic data collection

Volumetric soil water content (VWC) was measured on 3–4 dates each year to assess treatment effects on VWC at 0–15 cm

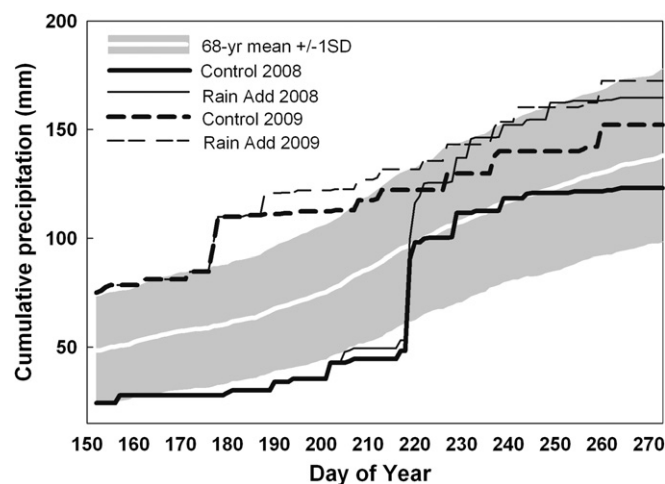


Fig. 2. Cumulative year-to-date precipitation during the growing season at Center, CO (mean \pm 1 SD, 1942–2009), and Crestone experimental treatments in 2008 (solid lines) and 2009 (dashed lines). Control (ambient) precipitation is represented by thick lines, and the rain addition treatment by thin lines. The rain out treatment received <5 mm of growing season precipitation in both years and therefore is not shown. We define the growing season as June 1 through September 30 (day of year 152–273).

and 15–30 cm depth. Samples consisted of one soil core extracted from each depth in each plot.

Precipitation was measured on-site using an unshielded Texas Instruments tipping-bucket rain gauge with a sensitivity of 0.254 mm. Measurements were stored on a Campbell CR10X data logger (Campbell Scientific, Inc., Logan, UT) every 15 min, and 15-min records were summed to yield daily precipitation totals. One groundwater monitoring well near the center of each treatment block was used to measure water table depth manually every 2–3 weeks during growing seasons. Water table depth was also recorded every 15 min at one monitoring well location central to all treatment plots using a GE Druck 1–5 psi water level sensor (GE Sensing, Billerica, MA).

3.2.2. Xylem pressure potential

We measured pre-dawn (Ψ_p) and mid-day (Ψ_m) xylem pressure potential of the study plant species in each plot using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR). Portions of foliated terminal branches (shrubs) or individual leaves (grasses) were cut and sealed into the chamber, which was pressurized gradually until xylem water appeared at the cut surface. Pre-dawn measurements occurred from 3:00 to 6:00 hours and mid-day measurements occurred during cloudless periods between 12:00 and 15:00 hours. Within each plot, we collected 3–5 samples from one marked shrub or grass patch on repeated occasions, and averaged these measurements on each date to obtain a plot-level value for each species.

3.2.3. Stable oxygen isotope analysis of plant water sources

We used naturally occurring differences in source water $\delta^{18}\text{O}$ signatures to determine the relative contributions of groundwater and rain-recharged soil water to plant water uptake for the four study species. We sampled plant xylem tissues, soil water from the active rooting zone (0–15 cm and 15–30 cm depths), and groundwater on 3 dates each year. We collected fully suberized stem sections from the shrub species, and non-photosynthetic belowground tissues from the grass species (rhizomes in *D. spicata*, and the crown regions of *S. airoides*). Soil samples were collected using a soil coring tool (Giddings, Inc., Windsor, CO). We collected groundwater samples from three monitoring wells by

bailing the well dry three times before collecting inflowing groundwater. Precipitation samples were obtained from covered rainwater storage containers at each rain out plot. All samples were placed in glass vials, sealed with screw caps and Parafilm, and immediately stored on ice until they were transferred to a $-10\text{ }^{\circ}\text{C}$ freezer, where they remained frozen until the time of extraction.

We extracted plant and soil waters using the cryogenic vacuum distillation method (Ehleringer and Osmond, 1989). The stable oxygen isotope ratio of all water samples was determined by CO_2 equilibration using a VG Microgas Injector coupled to a VG Optima Isotope Ratio Mass Spectrometer (VG Instruments, Manchester, UK). Oxygen isotope ratios of the samples are expressed in δ notation as follows:

$$\delta^{18}\text{O}(\text{‰}) = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \quad (1)$$

where R_{sample} and R_{standard} are the molar abundance ratios ($^{18}\text{O}/^{16}\text{O}$) of the sample and Vienna Standard Mean Ocean Water (VSMOW), respectively. More negative $\delta^{18}\text{O}$ values indicate depletion while more positive values indicate enrichment of heavier isotopes in sampled water, relative to the standard. At the study site, groundwater is typically more depleted in ^{18}O and thus has a more negative $\delta^{18}\text{O}$ value than water in upper soil layers that undergoes evaporation.

3.3. Statistical analysis

We used a repeated measures analysis of variance (ANOVA) (SAS version 9.2, SAS Institute, Cary, NC) to test for response differences between species, averaged over time (between-species effects), and change in response through time, averaged over species (within-species effects). The 2008 and 2009 growing seasons were analyzed separately. For each response variable, we considered ANOVA models with autoregressive, spatial power, and spatial exponential covariance structures, however the model with the lowest Akaike Information Criterion (AIC) value in all cases was a basic repeated measures ANOVA with a compound symmetry covariance structure.

Overall ANOVAs indicated highly significant species effects, and residual plots indicated large differences in variance between species. In addition, the species * date * treatment interaction was significant for most of the responses analyzed, indicating that the effect of the treatment * date interaction depended on species. For these reasons, we analyzed effects of date, treatment, and their interaction separately for each of the four species. We compared least-squares means using a Tukey multiple comparisons adjustment to identify significant differences between dates and treatments within a species.

We used analysis of covariance (ANCOVA) to examine the direct effect of soil water content on plant xylem pressure response by adding measured volumetric water content to our models as a covariate. For these analyses, 2008 and 2009 were grouped, but pre-dawn and mid-day Ψ responses were analyzed separately. We included random effects for plot and species * plot to adjust for repeated measurements on the same plants. We used these models to evaluate how the relationship between volumetric water content and xylem pressure potential differed among species.

4. Results

4.1. Treatment effects on soil volumetric water content

In 2008, volumetric water content (VWC) in the 0–15 cm soil layer was strongly affected by precipitation, but remained fairly constant at 15–30 cm depth (Fig. 3). Pre-treatment soil VWC in July was 7–8% at 0–15 cm and 13–15% at 15–30 cm, and as expected did not differ between plots in either layer ($p > 0.1$, all

comparisons). In control plots, mean soil VWC at 0–15 cm increased from 8% in July to 15% in August following monsoon rain events, and then declined to 7% by early September. Soil VWC at 15–30 cm remained between 15% and 17% on all sample dates.

In 2008, the rain out treatment resulted in lower VWC in the top 15 cm of soil compared to control and rain addition plots. Soil VWC in rain out plots was 8% lower than control plots on both August sample dates ($p \leq 0.0002$, Fig. 3). VWC declined in all plots during late summer but remained 5% higher in rain addition than rain out plots ($p = 0.02$). VWC did not differ between rain addition and control plots on any date ($p > 0.1$, all comparisons). In the 15–30 cm soil layer, VWC in all plots was higher and less variable than in the 0–15 cm layer (Fig. 3).

In 2009, soil VWC in control plots varied little and ranged from 7–8% at 0–15 cm, and 12–13% at 15–30 cm. Wet spring conditions and upward capillary movement of water from the shallow aquifer may have homogenized soil VWC across plots, and no significant treatment differences occurred in either soil layer in July ($p \geq 0.1$, all comparisons; Fig. 3). By late August, however, mean VWC in the 0–15 cm layer was 6% higher in rain addition than rain out plots ($p = 0.003$), although neither treatment differed significantly from control plots ($p > 0.1$).

4.2. Xylem pressure potential

In both years, highly significant differences in xylem pressure potential occurred between species (ANOVA; $253 \leq F \leq 2197$, $p < 0.001$) and dates ($52 \leq F \leq 289$, $p < 0.001$). Each species responded distinctly to natural and experimentally induced changes in soil water availability. *S. airoides* and *D. spicata* showed the largest increases in Ψ_p and Ψ_m following precipitation events. *S. vermiculatus* Ψ_p and Ψ_m also responded to changes in soil water content, but to a lesser degree than either grass species. *E. nauseosa* maintained a constant Ψ throughout 2008 and 2009, with little response to seasonal or treatment-induced changes in soil water availability.

In 2008, mean Ψ_p declined slightly for *S. vermiculatus* during the dry early summer, but there were no differences between control and treatment plants ($p > 0.1$, Fig. 4). After monsoon rains began in August, mean Ψ_p in control and rain addition plants were 0.5 MPa to 0.7 MPa higher than rain out plants ($p < 0.001$, all comparisons), with no significant difference between control and rain addition plants. The same pattern occurred for Ψ_m . In 2009, *S. vermiculatus* mean Ψ_p and Ψ_m declined across all plots by an average of 1.4 MPa as soil VWC decreased from July through September.

E. nauseosa xylem pressure potentials did not respond to rainfall treatments or seasonal trends in surface soil water availability (Fig. 4). In 2008, there were no differences in mean Ψ_p and Ψ_m between treatment and control plants, with one exception for each. In 2009, no significant differences occurred among treatments for Ψ_p or Ψ_m when averaged over dates ($p > 0.1$, both comparisons).

Sporobolus airoides and *Distichlis spicata* xylem pressure potentials responded similarly to rainfall treatments in 2008. While soil VWC was low in July, mean Ψ_p and Ψ_m for both grass species increased slightly, but did not differ between treatment and control plants ($p > 0.1$, all comparisons, Fig. 4). After the start of the monsoon rains in August, *S. airoides* mean Ψ_p were 1.5 MPa to 2.0 MPa higher for control and rain addition plants than rain out plants ($p < 0.0001$, all comparisons), and *D. spicata* Ψ_p were 0.8 MPa to 1.4 MPa higher for control and rain addition plants than rain out plants ($p < 0.02$, all comparisons). By early September, mean Ψ_p were still 1.1 MPa higher for *S. airoides* control and rain addition plants and *D. spicata* rain addition plants, compared with rain out plants ($p < 0.002$, all comparisons). Treatments had a similar but smaller effect on mean Ψ_m for both grass species in August and September 2008.

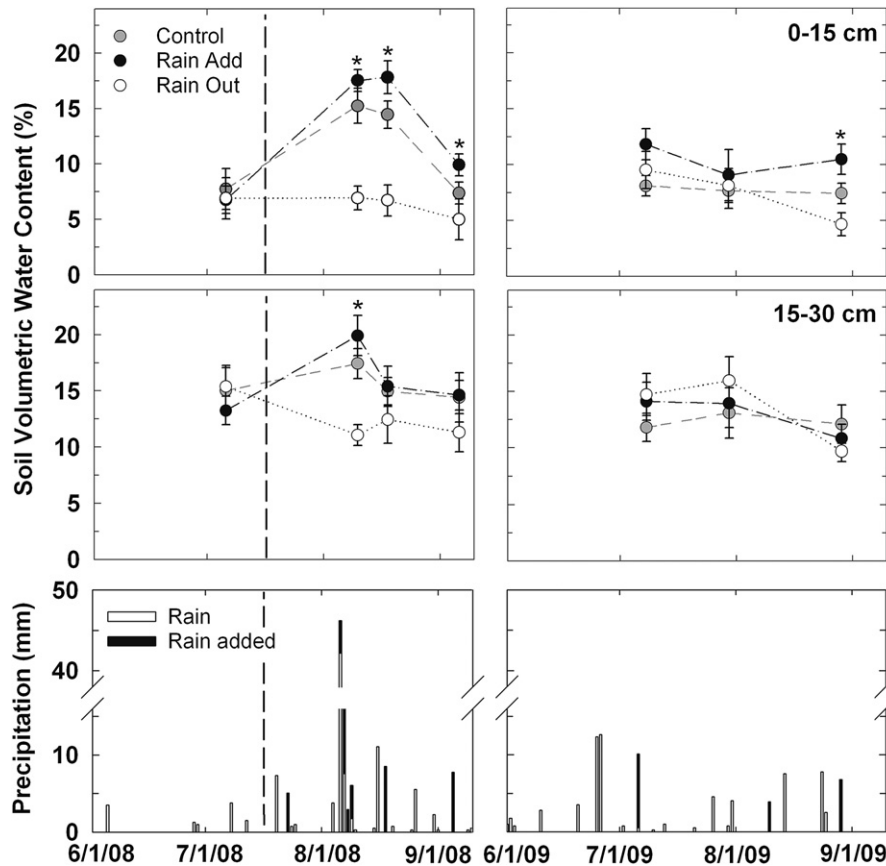


Fig. 3. Mean (± 1 SE) volumetric soil water content for control and treatment plots in 2008 (left column) and 2009 (right column) for the 0–15 cm (upper panels) and 15–30 cm (middle panels) soil layers. Daily precipitation for June–September (white bars) and rain additions (black bars) are shown as stacked bars in the lowest panel. The dashed vertical line separates pre- and post-treatment periods. Asterisks indicate significant differences between control and treatment means at the $\alpha = 0.05$ level.

Following the wet spring of 2009, *S. airoides* and *D. spicata* Ψ_p were higher for control and rain addition plants than rain out plants in June ($p \leq 0.001$, all comparisons). Mean Ψ_p in *S. airoides* control and rain addition plants remained higher than rain out plants for most of the summer, while mean Ψ_m did not differ between control and treatment plants on most dates. Mean Ψ_p and Ψ_m for *D. spicata* also did not differ between control and treatment plants on most dates after June. On average, Ψ for both grass species declined through the 2009 growing season as soil VWC decreased across all plots. *D. spicata* Ψ_m dropped from -2.7 MPa to -5.2 MPa, and *S. airoides* Ψ_m from -3.0 MPa to -3.7 MPa.

Changes in soil VWC at the 0–15 cm depth directly affected xylem pressure potential in all four species (ANCOVA; VWC effect $p < 0.001$; Fig. 5). The relationship between soil water and xylem pressure potential responses in both years differed between shrubs and grasses ($p < 0.0001$). All species Ψ_p and Ψ_m responded similarly at higher soil VWC, but grass Ψ_p and Ψ_m declined more rapidly than shrubs at low soil VWC ($p < 0.0001$ at VWC $< 15\%$). The response of Ψ_p and Ψ_m to changes in soil VWC did not differ significantly between *S. airoides* and *D. spicata*, but did differ between *E. nauseosa* and *S. vermiculatus* ($p < 0.0001$).

4.3. Stable oxygen isotope analysis

4.3.1. $\delta^{18}\text{O}$ of plant water sources

The isotopic signature of groundwater varied little during the 2008 and 2009 growing seasons, with $\delta^{18}\text{O}$ values between -13.8 and -14.2‰ (Fig. 6). However, soil water $\delta^{18}\text{O}$ at 0–15 cm was variable and reflected the signature of summer rain and/or

evaporative enrichment, while soil water at 15–30 cm was more depleted in ^{18}O than the surface layer but more enriched than groundwater on most dates (Fig. 6).

In July 2008 pre-treatment mean soil water $\delta^{18}\text{O}$ ranged from -2.8 to -4.3‰ at 0–15 cm and -8.4 to -9.9‰ at 15–30 cm, but did not differ between control and treatment plots within either soil layer ($p \geq 0.1$, all comparisons). After August monsoon rainfall events, soil water in control and rain addition plots reflected the isotopic signature of rainwater, but was unchanged in rain out plots. In September 2008, soil water in control and rain addition plots remained 2.2 – 2.4‰ more depleted than rain out plots at 0–15 cm, but was similar in all plots at 15–30 cm depth.

Soil water was more depleted in early July 2009 than early July 2008 (Fig. 6), likely reflecting the input of cold spring rain as well as a higher water table in 2009. By mid-summer, soil drying resulted in significant enrichment of surface soils ($p = 0.05$), but not deeper soils. However, by late August, soil water was more enriched at both soil depths ($p \leq 0.03$, both comparisons), although much greater enrichment occurred at 0–15 cm (late August 2009 mean soil water $\delta^{18}\text{O} = -2.0\text{‰}$ at 0–15 cm, and -9.1‰ at 15–30 cm).

4.3.2. $\delta^{18}\text{O}$ of plant xylem water

Xylem water $\delta^{18}\text{O}$ was significantly different between the four study species in both years (ANOVA; $134 < F < 207$, $p < 0.001$; Fig. 7). *S. airoides* and *D. spicata* had similar xylem water isotopic signatures on most dates, and their xylem water was enriched in $\delta^{18}\text{O}$ compared to *S. vermiculatus* and *E. nauseosa* throughout both growing seasons ($p < 0.01$, all comparisons). Mean xylem water signatures of *S. vermiculatus* and *E. nauseosa* differed during 2008 but not during 2009.

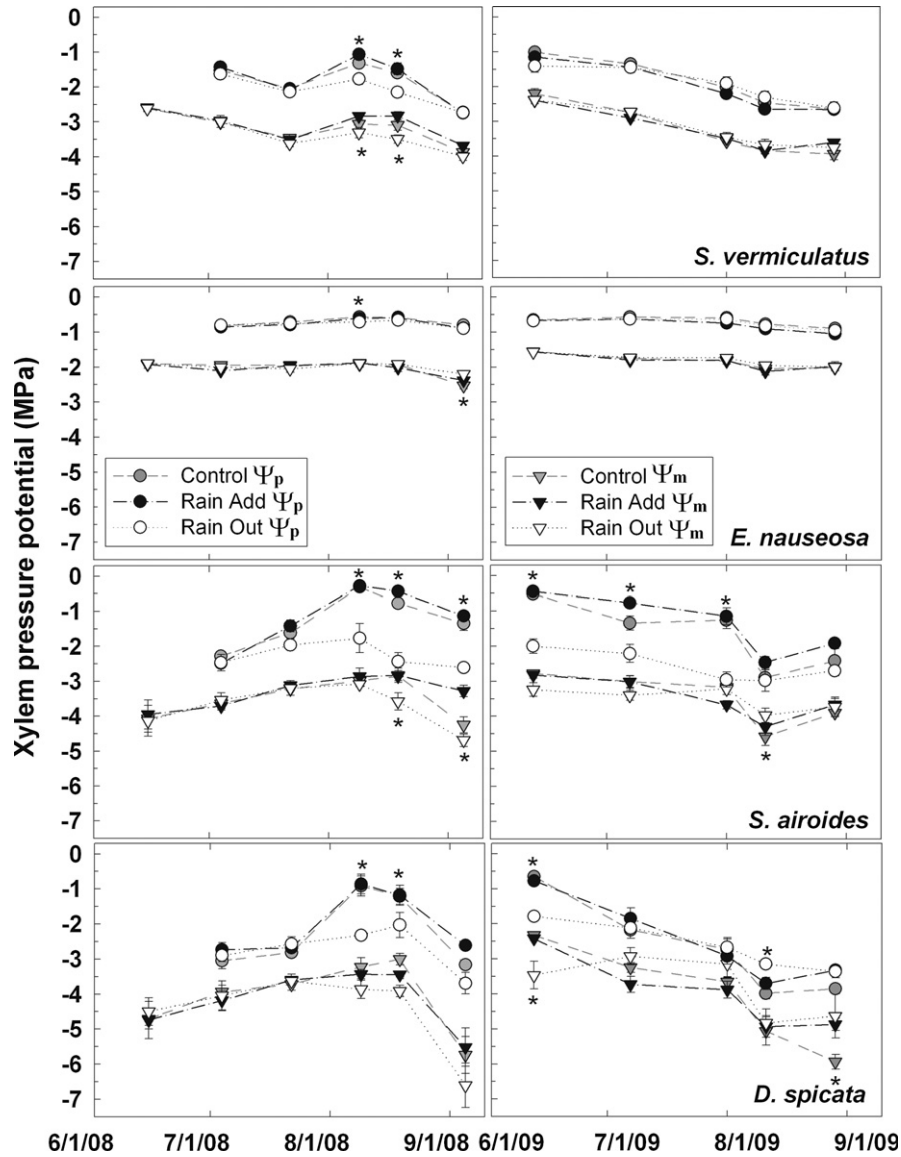


Fig. 4. Mean (± 1 SE) pre-dawn (Ψ_p , circles) and mid-day (Ψ_m , triangles) xylem pressure potentials for plants in control and treatment plots in 2008 (left column) and 2009 (right column). Asterisks located above Ψ_p or below Ψ_m comparisons on each date indicate significant differences between control and treatment means at the $\alpha = 0.05$ level.

As expected, pre-treatment xylem water $\delta^{18}\text{O}$ for each species was similar in all plots in 2008 ($p \geq 0.1$, all comparisons). During July 2008 there were no differences in mean xylem $\delta^{18}\text{O}$ between *S. vermiculatus* and *E. nauseosa* ($p = 0.5$), and xylem water in both shrubs was similar to groundwater (Fig. 7). *S. airoides* and *D. spicata* xylem water was significantly enriched relative to both shrubs ($p < 0.001$, all comparisons; Fig. 7), and similar to soil water. After August rains occurred, mean xylem water $\delta^{18}\text{O}$ for both *S. airoides* and *D. spicata* was nearly identical to the $\delta^{18}\text{O}$ of rain-derived soil water in both upper layers. Xylem water $\delta^{18}\text{O}$ for the two grass species remained similar to surface soil water $\delta^{18}\text{O}$ in September. *S. vermiculatus* xylem water $\delta^{18}\text{O}$ was more enriched than *E. nauseosa* by 2.4‰ in August ($p = 0.001$) and 4.5‰ in September ($p < 0.001$). *S. vermiculatus* xylem water was more similar to soil water during the monsoon period, while *E. nauseosa* was similar to groundwater during the entire 2008 growing season.

In early July 2009, xylem $\delta^{18}\text{O}$ did not differ between shrub species ($p > 0.9$) or between grass species ($p > 0.9$), but grass species xylem water was 4.6–5.2‰ more enriched than either shrub ($p < 0.0001$, all

comparisons). Xylem water $\delta^{18}\text{O}$ in both grasses was similar to soil water at 0–15 cm, while shrub xylem water was most like deeper soil water and groundwater. Grass xylem water remained significantly enriched relative to both shrubs through July ($p < 0.0001$, all comparisons). Xylem $\delta^{18}\text{O}$ did not differ between grass species in any treatment in late August, but rain out *S. airoides* plants were up to 4.8‰ more depleted than control and rain addition plants ($p < 0.0001$), suggesting soil water acquisition from 15–30 cm. Xylem water in both shrub species was similar to groundwater by late August. *S. vermiculatus* mean xylem water $\delta^{18}\text{O}$ varied little between dates in 2009 ($p > 0.1$) while *E. nauseosa* xylem water became slightly more depleted late in the growing season ($p < 0.001$).

5. Discussion

The four native plant species studied in the SLV have been described as phreatophytes (Nichols, 1994; Robinson, 1958; Sorenson et al., 1991), yet their water relations and water acquisition patterns varied considerably. Natural seasonal and

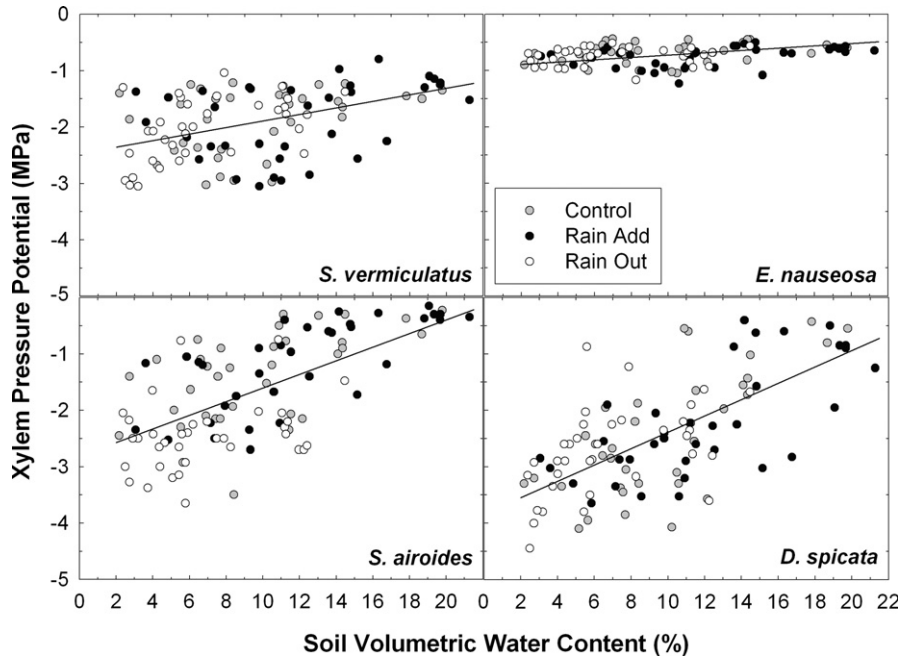


Fig. 5. Relationships between soil volumetric water content at 0–15 cm and pre-dawn plant xylem pressure potential (Ψ_p) during the 2008–2009 growing seasons. Points represent plot-level soil VWC and plant responses recorded on seven dates. Relationships between soil VWC and mid-day xylem pressure potential (Ψ_m) followed the same patterns as Ψ_p (data not shown).

experimentally driven changes in near surface soil water availability had a larger influence on the Ψ of *S. airoides* and *D. spicata* than the more deeply rooted shrubs *S. vermiculatus* and *E. nauseosa*. Both shrub species used groundwater in larger proportions than either grass species, and groundwater use differed between shrub species in the strong monsoon year of 2008.

5.1. Response of plant water relations to precipitation

Natural seasonal and experimentally altered changes in soil water content affected water relations in *S. vermiculatus*, indicating that this species responded to growing season precipitation. *S. vermiculatus* Ψ_p and Ψ_m increased in 2008 after monsoon rainfall events recharged surface soil layers, yet when little rain fell during the monsoon period in 2009, Ψ declined steadily through the summer. Thus, although *S. vermiculatus* can acquire groundwater, its water status improved in response to rain-recharged soil water. Romo and Haferkamp (1989) observed a similar Ψ response to a rain-driven increase in surface soil moisture for *S. vermiculatus* in southeastern Oregon, where summer precipitation is uncommon. Seasonal xylem pressure trends for *S. vermiculatus* in the SLV during two years with different precipitation patterns were similar to

those reported for other western U.S. populations of this species, suggesting that it functions similarly in regions with and without monsoon rains (Donovan et al., 1996; Sorenson et al., 1991; Sperry and Hacke, 2002; Trent et al., 1997).

E. nauseosa, in contrast to *S. vermiculatus*, maintained relatively constant Ψ_p and Ψ_m throughout the study period, despite large differences in soil water availability. This pattern is consistent with research from regions where winter precipitation dominates (Donovan and Ehleringer, 1994; Ehleringer et al., 1991; Flanagan et al., 1992; Goedhart et al., 2010), indicating that this species also appears to function similarly under a wide range of precipitation regimes across the western U.S.

Unlike the shrubs, *D. spicata* and *S. airoides* had highly significant Ψ responses to natural seasonal and experimentally controlled soil water availability, suggesting that both species acquire water with roots that are concentrated in upper soil layers. In control and rain addition plots, monsoon rain in 2008 resulted in large Ψ_p increases for both species, suggesting that both species recovered overnight from very low daytime xylem potentials. Plants in the rain out plots experienced continuous water stress. During 2009, when little summer rain fell, both grass species experienced a decline in Ψ as soil VWC decreased in all treatments. In the Owens Valley,

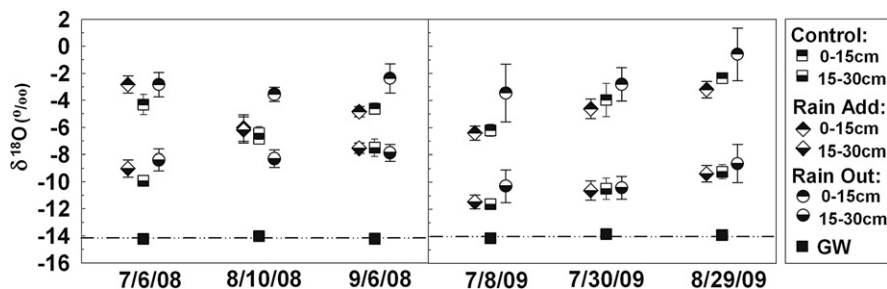


Fig. 6. Mean oxygen isotope composition ($\delta^{18}\text{O}$, $\pm 1\text{SE}$) of soil water from 0–15 cm and 15–30 cm soil layers, and groundwater (GW) in 2008 (left column) and 2009 (right column). Control plots are represented by squares, rain addition plots by diamonds, and rain out plots by circles.

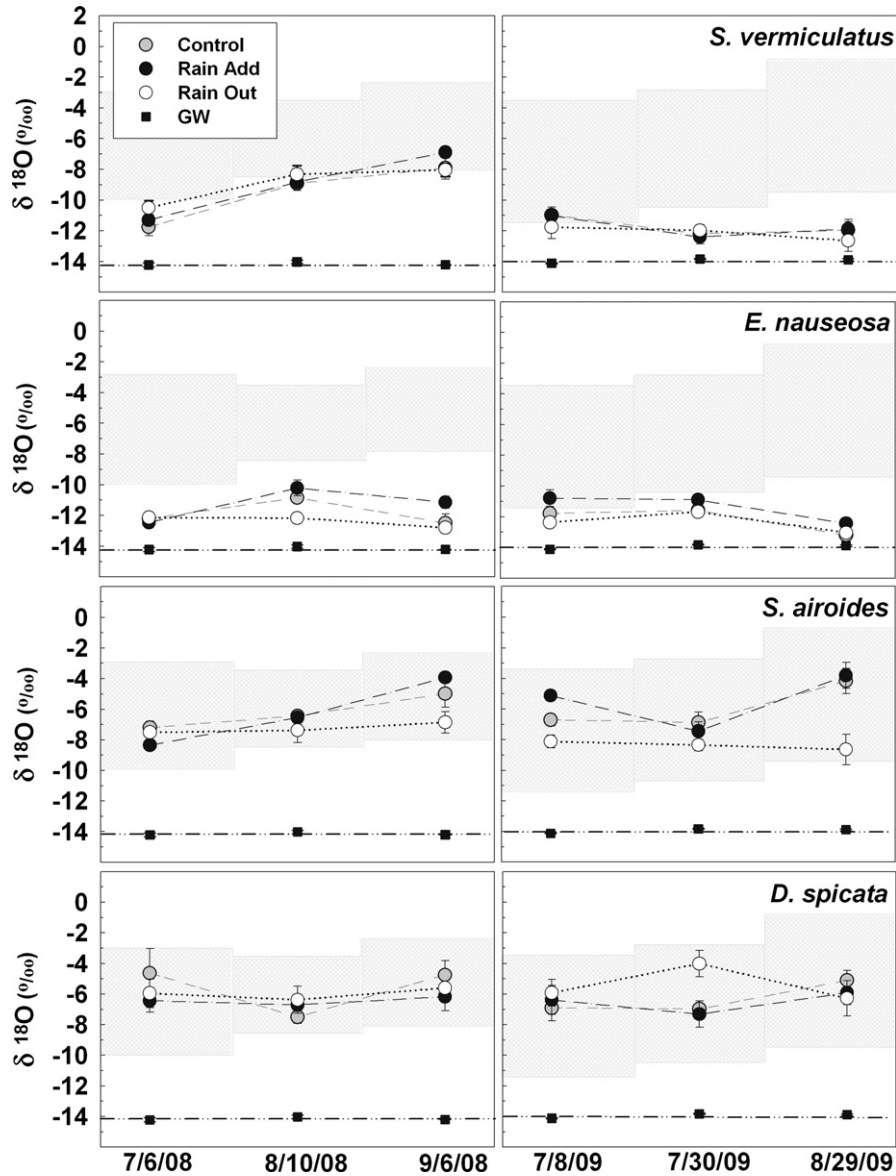


Fig. 7. Mean plant xylem oxygen isotope composition ($\delta^{18}\text{O}$, $\pm 1\text{SE}$) in control and treatment plots for *S. vermiculatus*, *E. nauseosa*, *S. airoides* and *D. spicata* in 2008 (left column) and 2009 (right column). Groundwater (GW) $\delta^{18}\text{O}$ values are indicated by black squares, and the range of mean soil water $\delta^{18}\text{O}$ values in the top 30 cm for all treatments is shown by the shaded regions behind plant xylem $\delta^{18}\text{O}$ values.

California, *D. spicata* Ψ_p was also responsive to near surface soil water availability, despite the presence of a shallow water table (Goedhart et al., 2010).

During the strong monsoon season in 2008, the Ψ patterns for *S. vermiculatus*, *S. airoides* and *D. spicata* were clearly driven by August monsoon rains, and the rain out treatment led to significantly lower Ψ in these species. However, the rain addition treatment did not significantly increase Ψ over control plots for any species, suggesting that a modest short term increase in rainfall (30–50% addition to the growing season total) may not dramatically affect plant water relations for these species.

5.2. $\delta^{18}\text{O}$ of plants and water sources

The distinct $\delta^{18}\text{O}$ signatures of SLV groundwater and soil water allowed us to identify the primary water source(s) used by each plant species. The $\delta^{18}\text{O}$ value of groundwater reflected the depleted isotopic signature of mountain snowmelt water that recharged

regional aquifers. In contrast, soil water $\delta^{18}\text{O}$ at 0–15 cm varied widely in response to inputs of rain, while soil water at 15–30 cm was less variable, and influenced by both rain events and the periodic rise of capillary groundwater (Chimner and Cooper, 2004).

The water acquisition patterns of *S. vermiculatus* differed by year. During the dry early summer of 2008, it used primarily groundwater; however its uptake of rain-recharged soil water increased during the monsoon season. Thus, although *S. vermiculatus* can rely largely on groundwater, as it did during 2009, it also utilizes rain-recharged soil water, as it did in 2008.

E. nauseosa utilized primarily groundwater during both 2008 and 2009 even when rain-recharged soil water was abundant. In the Owens Valley and Great Basin *E. nauseosa* did not utilize summer rain (Donovan and Ehleringer, 1994; Ehleringer et al., 1991; Flanagan et al., 1992). However, we expected this species to use rain water in the SLV due to the annually consistent and generally strong summer monsoon. In addition, Chimner and Cooper (2004) found that *E. nauseosa* utilized groundwater in early summer and soil

water recharged by monsoon rain in late summer in the SLV, but their study occurred in areas with deeper water tables, indicating that *E. nauseosa* may vary in water acquisition patterns across hydrologic settings rather than across climatic regions.

In contrast to the shrub species, both *S. airoides* and *D. spicata* acquired water almost entirely from the upper 30 cm of the soil profile throughout the study and used little or no groundwater. In the Owens Valley, *D. spicata* also accessed shallow soil water (Goedhart et al., 2010; Pataki et al., 2008). However, Elmore et al. (2006) used Owens Valley satellite imagery to determine that areal cover of both *S. airoides* and *D. spicata* was more sensitive to changing groundwater depth than to variations in summer precipitation at sites with water tables less than 2.5 m below the surface. Although the phreatophytic nature of these species in the Owens Valley is unclear, they do not appear to function as phreatophytes at the San Luis Valley study site.

Differences in physiological traits among the four study species may explain the difference in their use of summer rain. These species vary in drought and salt tolerance in addition to assumed differences in functional rooting depth (Pataki et al., 2008; Sperry and Hacke, 2002). *E. nauseosa* is more susceptible to xylem cavitation (Hacke et al., 2000; Sperry and Hacke, 2002) and leaf cell dehydration (Dileanis and Groeneveld, 1989) than the co-occurring shrub species in its range including *S. vermiculatus*, which may explain its strong groundwater dependence and consistently high Ψ . By contrast, *S. vermiculatus*, *S. airoides*, and *D. spicata* all use osmotic adjustment to maintain xylem conductivity and leaf cell turgor, enabling these species to transpire and extract water from increasingly dry and saline soil (Dileanis and Groeneveld, 1989; Donovan et al., 1996; Marcum, 1999). The dramatically lower Ψ measured in plants within the rain out plots in 2008 and plants in all plots during the dry late summer of 2009 likely reflect osmotic adjustments in these three species, all of which acquired surface soil water at least periodically.

5.3. Implications for plant community composition and groundwater use

Our results demonstrate that a broad range of water acquisition strategies exist for the four co-occurring species that dominate the native vegetation of the SLV. Water relations of the grass species are clearly more sensitive to summer rainfall than the shrub species, which utilize primarily groundwater (Figs. 4, 5 and 7). The grass and shrub species are likely to respond differently to changes in growing season precipitation, which could affect plant community composition over time. Climate-driven changes in vegetation composition could also lead to changes in site level rates of groundwater evapotranspiration (ET_g).

A moderate, short duration increase in summer rainfall may not change current plant community composition or groundwater acquisition rates in the SLV. Rainfall manipulation experiments in similar ecosystems have suggested that productivity in semiarid plant communities may be largely unaffected by short-term rainfall changes for up to four years (Bates et al., 2006; Miranda et al., 2009, 2011). However, a long-term increase in growing season rainfall in the SLV could improve the water status of both grass species and, to a lesser extent, *S. vermiculatus*. Reduced water stress may increase productivity and canopy cover of these species. An increase in productivity of *S. airoides* and *D. spicata* is unlikely to affect ET_g rates because these species use little groundwater. Likewise, because both shrub species use largely groundwater, they may be less affected by changes in total summer rainfall and continue to utilize groundwater at current rates in the SLV.

Conversely, a decrease in summer rainfall would likely increase water stress in the grass species. An extended multi-year drought

could force these grass species beyond critical water stress thresholds, leading to reduced productivity (Miranda et al., 2011; Yahdjian and Sala, 2006), or plant mortality (Schwinning et al., 2005b). Reduced grass cover could allow shrub expansion (Elmore et al., 2003; Schlesinger et al., 1990), and result in vegetation that is increasingly dominated by shrubs. A significant expansion of shrub cover could increase groundwater consumption on local or regional scales.

6. Conclusion

Native vegetation can have a substantial influence on regional water budgets of arid basins with shallow aquifers through groundwater evapotranspiration (Cooper et al., 2006; Nichols, 1994; Steinwand et al., 2006). ET_g from native vegetation accounts for nearly 1/3 of the total annual groundwater outflow in the SLV (Rio Grande Decision Support System, 2006). As human demand for dependable water supplies grows, accurate estimates of groundwater use by vegetation are increasingly critical for sustainable groundwater management. Rates of ET_g will likely change as plants and plant communities adjust to changing temperature and precipitation regimes, yet few studies to date have examined how climate-driven changes in plant water acquisition patterns and vegetation composition could affect the patterns of groundwater consumption at any spatial scale. This study demonstrated that water relations and water acquisition patterns varied markedly for the study plant species in response to seasonal and experimentally controlled changes in precipitation, suggesting that these species will differ in their sensitivity to changes in climate.

Water relations of the grass species *S. airoides* and *D. spicata* were tightly coupled to rain-recharged soil water, and isotopic evidence indicated that both grass species depend almost entirely on growing season rainfall, despite the presence of shallow groundwater. Contrary to previous research, *S. airoides* and *D. spicata* do not function as phreatophytes in this portion of the SLV. In contrast, *E. nauseosa* acquired little or no precipitation-recharged soil water, and its water status was unaffected by changes in soil water availability, indicating strong groundwater dependence. *S. vermiculatus* was flexible in water acquisition, relying on groundwater during dry periods, but increasing its uptake of soil water after periods of high monsoon rainfall. Therefore, changes in growing season precipitation are most likely to affect *S. airoides* and *D. spicata*, while *E. nauseosa* and to a lesser extent *S. vermiculatus* may be more affected by a water table decline. Persistent changes in precipitation patterns may cause a shift in plant community composition and may affect basin-scale groundwater use under future climate conditions. The effects of plant-climate feedbacks on basin-scale ET_g must be incorporated into hydrologic models used to manage groundwater in the SLV, and similar arid regions across western North America.

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Appendix A. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.jaridenv.2012.03.009.

References

- Arritt, R.W., Goering, D.C., Anderson, C.J., 2000. The North American monsoon system in the Hadley Centre coupled ocean-atmosphere GCM. *Geophysical Research Letters* 27, 565–568.
- Bates, J.D., Svecar, T., Miller, R.F., Angell, R.A., 2006. The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments* 64, 670–697.
- Chimner, R.A., Cooper, D.J., 2004. Using stable oxygen isotopes to quantify the water source used for transpiration by native shrubs in the San Luis Valley, Colorado USA. *Plant and Soil* 260, 225–236.
- Chimner, R.A., Welker, J.M., 2005. Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a mixedgrass prairie, WY, USA. *Biogeochemistry* 73, 257–270.
- Cook, E.R., Woodhouse, C.A., Eakin, C.M., Meko, D.M., Stahle, D.W., 2004. Long-term aridity changes in the western United States. *Science* 306, 1015–1018.
- Cooper, D.J., Sanderson, J.S., Stannard, D.I., Groeneveld, D.P., 2006. Effects of long-term water table drawdown on evapotranspiration and vegetation in an arid region phreatophyte community. *Journal of Hydrology* 325, 21–34.
- Dileanis, P.D., Groeneveld, D.P., 1989. Osmotic potential and projected drought tolerance of four phreatophytic shrub species in Owens Valley, California. *US Geological Survey Water-Supply Paper* 2370-D.
- Doesken, N.J., McKee, T.B., 1989. The incredible climate of the San Luis Valley. In: Harmon, E.J. (Ed.), *Water in the Valley: A 1989 Perspective on Water Supplies, Issues, and Solutions in the San Luis Valley*. Colorado Groundwater Association, Colorado, pp. 79–98.
- Donovan, L.A., Ehleringer, J.R., 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology* 8, 289–297.
- Donovan, L.A., Richards, J.H., Muller, M.W., 1996. Water relations and leaf chemistry of *Chrysothamnus nauseosus* ssp. *consimilis* (Asteraceae) and *Sarcobatus vermiculatus* (Chenopodiaceae). *American Journal of Botany* 83, 1637–1646.
- Ehleringer, J.R., Osmond, C.B., 1989. Stable isotopes. In: Pearcy, R.W., Ehleringer, J.R., Mooney, H.A., Rundel, P.W. (Eds.), *Plant Physiological Ecology: Field Methods and Instrumentation*. Chapman and Hall, New York, pp. 281–290.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. *Oecologia* 88, 430–434.
- Elmore, A.J., Mustard, J.F., Manning, S.J., 2003. Regional patterns of plant community response to changes in water: Owens Valley, California. *Ecological Applications* 13, 443–460.
- Elmore, A.J., Manning, S.J., Mustard, J.F., Craine, J.M., 2006. Decline in alkali meadow vegetation cover in California: the effects of groundwater extraction and drought. *Journal of Applied Ecology* 43, 770–779.
- Flanagan, L.B., Ehleringer, J.R., Marshall, J.D., 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant, Cell and Environment* 15, 831–836.
- Goedhart, C.M., Pataki, D.E., Billings, S.A., 2010. Seasonal variations in plant nitrogen relations and photosynthesis along a grassland to shrubland gradient in Owens Valley, California. *Plant and Soil* 327, 213–223.
- Grantz, K., Rajagopalan, B., Clark, M., Zagona, E., 2007. Seasonal shifts in the North American Monsoon. *Journal of Climate* 20, 1923–1935.
- Hacke, U.G., Sperry, J.S., Pitterman, J., 2000. Drought experience and cavitation resistance in six desert shrubs of the Great Basin, Utah. *Basic and Applied Ecology* 1, 31–41.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S., McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298, 2202–2205.
- Lin, G., Phillips, S.L., Ehleringer, J.R., 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* 106, 8–17.
- Marcum, K.B., 1999. Salinity tolerance mechanisms of grasses in the subfamily Chloridoideae. *Crop Science* 39, 1153–1160.
- Miranda, J.D., Padilla, F.M., Lazaro, R., Pugnaire, F.I., 2009. Do changes in rainfall patterns affect semiarid annual plant communities? *Journal of Vegetation Science* 20, 269–276.
- Miranda, J.D., Armas, C., Padilla, F.M., Pugnaire, F.I., 2011. Climatic change and rainfall patterns: effects on semi-arid plant communities of the Iberian Southeast. *Journal of Arid Environments* 75, 1302–1309.
- Mozingo, H.N., 1987. *Shrubs of the Great Basin*. University of Nevada Press, Reno.
- Nichols, W.D., 1994. Groundwater discharge by phreatophyte shrubs in the Great Basin as related to depth to groundwater. *Water Resources Research* 30, 3265–3274.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25–51.
- Pataki, D.E., Billings, S.A., Naumburg, E., Goedhart, C.M., 2008. Water sources and nitrogen relations of grasses and shrubs in phreatophytic communities of the Great Basin Desert. *Journal of Arid Environments* 72, 1581–1593.
- Rio Grande Decision Support System (RGDSS), 2006. *Groundwater Model Water Budget, San Luis Valley*. Exhibit RG-25. In: *Confined Aquifer New Use Rules for Division 3 Case No. 2004 CW 24*. District Court, Water Division No. 3, Alamosa, Colorado. 24 March 2006.
- Robinson, T.W., 1958. *Phreatophytes*. U.S. Geological Survey Water-Supply Paper 1423.
- Romo, J.T., Haferkamp, M.R., 1989. Water relations of *Artemisia tridentata* ssp. *wyomingensis* and *Sarcobatus vermiculatus* in the steppe of southeastern Oregon. *American Midland Naturalist* 121, 155–164.
- Schenk, H.J., Jackson, R.B., 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90, 480–494.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. *Science* 247, 1043–1048.
- Schwinning, S., Starr, B.L., Ehleringer, J.R., 2005a. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water uptake. *Journal of Arid Environments* 60, 547–566.
- Schwinning, S., Starr, B.L., Ehleringer, J.R., 2005b. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part II: effects on plant carbon assimilation and growth. *Journal of Arid Environments* 61, 61–78.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H., Harnik, N., Leetmaa, A., Lau, N., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181–1184.
- Smith, S.D., Monson, R.K., Anderson, J.E., 1997. *Physiological Ecology of North American Desert Plants*. Springer, New York.
- Sorenson, S.K., Dileanis, P.D., Branson, F.A., 1991. Soil water and vegetation responses to precipitation and changes in depth to ground water in Owens Valley, California. *US Geological Survey Water-Supply Paper* 2370-G.
- Sperry, J.S., Hacke, U.G., 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* 16, 367–378.
- Steinwand, A.L., Harrington, R.F., Or, D., 2006. Water balance for Great Basin phreatophytes derived from eddy covariance, soil water, and water table measurements. *Journal of Hydrology* 329, 595–605.
- Thomey, M.L., Collins, S.L., Vargas, R., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens, M.T., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Global Change Biology* 17, 1505–1515.
- Trent, J.D., Blank, R.R., Young, J.A., 1997. Ecophysiology of the temperate desert halophytes *Allenrolfea occidentalis* and *Sarcobatus vermiculatus*. *Great Basin Naturalist* 57, 57–65.
- Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C., 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53, 941–952.
- Western Regional Climate Center, 2011. Available at: <<http://www.wrcc.dri.edu/index.html>> (accessed 10.01.11).
- Williams, D.G., Ehleringer, J.R., 2000. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. *Ecological Monographs* 70, 517–537.
- Yahdjian, L., Sala, O.E., 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology* 87, 952–962.