

THESIS

RESPONSE OF NATIVE PHREATOPHYTES TO CHANGES IN PRECIPITATION  
REGIME IN THE SAN LUIS VALLEY, COLORADO

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## ABSTRACT

### RESPONSE OF NATIVE PHREATOPHYTES TO CHANGES IN PRECIPITATION REGIME IN THE SAN LUIS VALLEY, COLORADO

Throughout western North America, semiarid and arid basins are likely to experience changes in the timing and amount of precipitation due to global climate change, which may alter regional water budgets. These hydrologic changes may exacerbate water limitations on agriculture, municipalities, and ecosystems in arid regions. Thus, accurate estimates of groundwater outflow from native plant evapotranspiration ( $ET_g$ ) are increasingly critical to managing water resources in basins with large, shallow aquifers. Phreatophytes can contribute significantly to total groundwater outflow on a watershed scale. Some phreatophytes can also acquire soil water recharged by precipitation, which may reduce or supplement their groundwater use. As a result, groundwater use by phreatophyte communities may vary both spatially and temporally in response to seasonal or long-term changes in growing season precipitation. I conducted a two-year rainfall manipulation experiment in the San Luis Valley, Colorado to investigate the responses of four common native phreatophyte species to ambient, increased, and decreased summer monsoon rainfall. Volumetric soil water content was measured in experimental plots to evaluate rainfall treatment effectiveness. I measured xylem pressure potentials ( $\Psi$ ) to assess the effects of altered precipitation on plant water relations, and compared stable oxygen isotope signatures ( $\delta^{18}O$ ) of plant

xylem water to surface (0-15 cm) and sub-surface (15-30 cm) soil layers and groundwater to identify plant water acquisition patterns.

The response of plant water relations and water acquisition patterns to changes in surface soil water availability differed by species. A decrease in rainfall had a larger influence on  $\Psi$  in the grasses *Sporobolus airoides* and *Distichlis spicata* than the more deeply rooted shrubs *Sarcobatus vermiculatus* and *Ericameria nauseosa*. *S. airoides*, *D. spicata* and *S. vermiculatus* had significantly lower  $\Psi$  when rainfall was naturally low or experimentally reduced, while  $\Psi$  of *E. nauseosa* did not respond 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 precipitation-recharged soil water, while *E. nauseosa* is almost entirely groundwater-dependent throughout the growing season. *S. vermiculatus* used groundwater during dry periods, but incorporated more precipitation from upper soil layers after heavy monsoon rainfall. These results suggest that changes in growing season precipitation are more likely to affect *S. airoides* and *D. spicata*, while *E. nauseosa* and to a lesser extent, *S. vermiculatus*, may be more affected by a decline in water table depth. Persistent changes in precipitation patterns may cause a shift in plant community composition that would alter basin-scale groundwater use by native plants. Results of this work could inform models for managing groundwater in the San Luis Valley, and may have implications for other water-limited regions.

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## 1. INTRODUCTION

Millions of hectares in arid and semiarid western North America are covered by phreatophytes, plants that can acquire groundwater from shallow water tables. In these environments, groundwater evapotranspiration ( $ET_g$ ) by phreatophyte communities may constitute a large proportion of the total water outflow on a basin scale (Nichols 1994, Cooper et al. 2006, Steinwand et al. 2006, Groeneveld et al. 2007, Sanderson & Cooper 2008). In many arid regions, groundwater is essential to support irrigated agriculture, provide reliable municipal water supplies, and maintain natural habitats. Therefore, accurate estimates of groundwater use by phreatophyte communities are critical for building regional hydrologic models that can be used to understand and manage large, shallow aquifers. In addition, climate conditions experienced over the past century are no longer a reliable guide to future hydrologic conditions (Milly et al. 2008). Water planners must anticipate how forecast changes in precipitation and temperature patterns will influence water table depth and soil water availability, and how these factors could affect vegetation composition and  $ET_g$  at large spatial scales.

Precipitation and soil water availability in arid and semiarid climates is 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, Schwinning et al. 2004), 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 & Ehleringer 1991, Flanagan et al. 1992, Donovan & Ehleringer 1994, Lin et al. 1996, Gebauer & Ehleringer 2000,

Schwinning et al. 2002). These variations are largely a function of local climate and edaphic factors, plant tissue hydraulic constraints (Gebauer et al. 2002, Sperry & Hacke 2002), and root distribution (Schenk & Jackson 2002).

Phreatophytes develop deep roots that can tap groundwater to avoid periodic limitations in available soil water, yet there is also variation among phreatophyte species in their use of summer precipitation (Sperry & Hacke 2002; Chimner & Cooper 2004). Some phreatophytes are able to acquire soil water recharged by precipitation, which may reduce or supplement their groundwater use, while others appear to rely entirely on groundwater. Some of this variation may represent local adaptation to different precipitation regimes, and in particular the frequency of growing season rainfall inputs. Williams and Ehleringer (2000) proposed that plants would be more likely to use summer rain in arid regions with a reliable summer precipitation pattern, such as the North American monsoon system. They found that the proportion of surface soil water taken up by the deep-rooted trees *Pinus edulis* and *Juniperus osteosperma* increased as the predictability of summer monsoon precipitation increased (Williams & Ehleringer 2000). In Colorado's San Luis Valley, which typically receives summer monsoon rainfall, the phreatophytes *Sarcobatus vermiculatus* and *Ericameria nauseosa* used groundwater in early summer, but acquired precipitation-recharged soil water during the late summer monsoon season (Chimner & Cooper 2004). Herbaceous phreatophyte species are less studied, but *Distichlis spicata* was recently reported to use rain-recharged soil water in greater proportions than co-occurring woody phreatophytes in a shallow groundwater environment without a summer monsoon (Goedhart et al. 2010, Goedhart & Pataki 2010). Thus, for phreatophyte species with differential capacities to use rain, groundwater

use may vary in response to seasonal or long-term changes in growing season precipitation.

Water-limited ecosystems will be particularly sensitive to changes in the timing and amount of precipitation affected by global climate change (Schlesinger et al. 1990, Weltzin et al. 2003, IPCC 2007). Several general circulation models (GCMs) 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). Alternatively, other climate models predict an intensification of the North American monsoon system (Arritt et al. 2000, Grantz et al. 2007), a major climate driver in southwestern North America. The flow of monsoonal moisture produces some of the most intense rainfall events of the summer, and may deliver 50-70% of the total annual precipitation from July through mid-September (Grantz et al. 2007). Increased summer monsoon rainfall would produce more plant-available soil water at times of peak transpiration demand. A shift to either wetter or drier summer conditions could affect plant growth and competition (Fowler 1986), triggering changes in community composition (Schlesinger et al. 1990, Knapp et al. 2002). Vegetation shifts and associated changes in regional evapotranspiration may feedback on local climate, further altering precipitation patterns (Narisma & Pitman 2003) and groundwater recharge.

Changes in precipitation regimes are uncertain for many water-limited regions; thus, it is critical to understand how changes in the timing and amount of precipitation could influence plant functioning and regional water budgets for both wetter and drier futures. Will increased monsoon rainfall in southwestern North America lead to increased plant use of soil water and reduced groundwater use during the growing season? Or if

growing season precipitation decreases or becomes more variable from year to year, will plants become more reliant on groundwater? The effects of altered precipitation regimes on plant productivity and community composition have been investigated in grasslands (Knapp et al. 2002, Fay et al. 2003, Harper et al. 2005, Chimner & Welker 2005), and arid land plant communities (Lin et al. 1996, Bates et al. 2006, West et al. 2007).

However, few studies have explored the effects of precipitation changes on plant water acquisition patterns (Schwinning et al. 2005a-b), and none have considered how changes in plant water acquisition may influence basin-scale groundwater consumption by plant communities. This question is highly relevant to water planning in groundwater-dependent regions, as the human demand for water in arid environments increases.

I investigated the response of four common native phreatophyte species to changes in growing season precipitation using a rainfall manipulation experiment at a long-term study site in the San Luis Valley, Colorado. I addressed the following questions: **(1)** how do plant water relations and water acquisition patterns (groundwater versus rain-recharged soil water) vary among native phreatophyte 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)? The overall goal of my research was to understand how plant community adjustment to climate change in the San Luis Valley could affect regional groundwater resources.

## 2. SITE DESCRIPTION

The San Luis Valley (SLV) is a high elevation intermountain basin located in southern Colorado (Figure 1). The valley floor covers approximately 8400 km<sup>2</sup>, is relatively flat, and averages 2350 m elevation. The SLV is bordered by the San Juan Mountains to the west and the Sangre de Cristo Mountains to the east, where elevations in both ranges exceed 4270 m. The southern edge of the valley is drained by the Rio Grande River, which originates in the San Juan Mountains. The northern 7600 km<sup>2</sup> of the SLV 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 & McKee 1989). Mean temperatures range from 17°C in July to -9°C in January (Western Regional Climate Center 2008). The SLV is the most arid region in Colorado, receiving only 180 to 250 mm of precipitation annually on the valley floor. Approximately 2/3 of the annual precipitation occurs from July-September as monsoon rains (Doesken et al. 1984). Mean annual precipitation in the surrounding mountains ranges from 800 to 1500 mm a year, and occurs primarily as winter snow. Snowmelt runoff from the mountains is conveyed to numerous streams that flow over coarse mountain front alluvial fans, recharging the unconfined aquifer that underlies the closed basin. This results in shallow water table depths of 1-5 m across much of the SLV (Cooper et al. 2006). This unconfined aquifer supports over 2400 km<sup>2</sup> of irrigated agriculture, and more than 4850 km<sup>2</sup> of native plant communities that provide domestic livestock forage, wildlife habitat, and soil stabilization.

The study site (Figure 1) is located within the closed basin, near the eastern edge of the SLV between Rito Alto Creek and San Isabel Creek, and approximately 15 km northwest of the town of Crestone. The water table at this site varies from 1 to 1.5 m below the soil surface, and high surface soil salinity exists. The vegetation is dominated by the shrubs greasewood (*Sarcobatus vermiculatus* (Hooker) Torrey) and rubber rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird ssp. *consimilis* (Greene) G.L. Nesom & Baird var. *oreophila* (A. Nelson) G.L. Nesom & Baird), and the grasses alkali sacaton (*Sporobolus airoides* (Torr.) Torr.) and saltgrass (*Distichlis spicata* (L.) Greene). This species assemblage is very common throughout the SLV (Figure 2). These species also occur widely in arid regions of western North America, where *S. vermiculatus* alone occupies approximately 4.8 million hectares (Mozingo 1987). Previous work in the SLV has demonstrated that  $ET_g$  can represent >50% of the total water use of this phreatophyte assemblage (Cooper et al. 2006), and can account for up to 1/3 of the total annual groundwater outflow (RGDSS 2006). *S. vermiculatus* and *E. nauseosa* are winter deciduous  $C_3$  shrubs that have similar phenological patterns, exhibiting high shoot growth in early summer, and flowering in mid-late fall (Donovan et al. 1996). *S. airoides* and *D. spicata* are  $C_4$  perennial grasses that are phenologically similar, but morphologically different. *S. airoides* has a caespitose growth form, while *D. spicata* is strongly rhizomatous. The halophytes *S. vermiculatus*, *S. airoides* and *D. spicata* are well-adapted to the high soil salinity that occurs at shallow groundwater sites throughout the SLV, whereas *E. nauseosa* is only moderately salt-tolerant (Dileanis & Groeneveld 1989). All four species are generally regarded as facultative phreatophytes

(Robinson 1958), able to acquire both groundwater and soil water recharged by precipitation.

### **3. MATERIALS AND METHODS**

#### **3.1 EXPERIMENTAL DESIGN**

In June 2008, I established fifteen 3.7 m x 4.3 m plots in five blocks containing three plots each. All plots included multiple individuals of the four study species. Plots within each block were randomly assigned to receive ambient rainfall (control), or one of two treatments: (1) reduced total rainfall under a rainout shelter (rain out), or (2) increased total rainfall by applying rain captured from shelter roofs (rain addition). Rain out shelter roofs were constructed from clear corrugated polycarbonate sheeting that was 85-90% transparent to photosynthetically active wavelengths of light, and were designed to exclude rainfall (Figure 3a). Shelter roofs were installed at a slight angle that allowed intercepted rainfall to run into gutters that emptied into storage tanks. Rainfall collected in storage tanks was uniformly applied to rain addition plots following natural rain events using 5-gallon watering cans (Figure 3b).

#### **3.2 FIELD AND LABORATORY METHODS**

##### *3.2.1 Soil and Hydrologic Data Collection*

Volumetric water content (VWC) was measured on 3-4 dates during the 2008 and 2009 growing seasons to assess treatment effects on soil layers at 0-15 cm and 15-30 cm depth. On each sampling date I determined VWC for one soil core extracted from each

depth in each plot. Mean VWC for treatments and control were compared using ANOVA to identify significant differences among treatments.

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 minutes, and 15-minute 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. Water table depth was measured manually every 2-3 weeks during the growing seasons in 2008 and 2009. Daily water table depth was also recorded automatically 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*

I measured pre-dawn ( $\psi_p$ ) and mid-day ( $\psi_m$ ) xylem pressure potential on 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. I measured pre-dawn xylem pressure potential from 3:00 to 6:00 hours MST, and made mid-day measurements during cloudless periods between 12:00 and 15:00 hours MST. Within each plot, I collected 3-5 samples from one marked shrub or grass patch on repeated occasions, and averaged these measurements to obtain a plot-level value for each species on each date.

### 3.2.3 Stable Oxygen Isotope Analysis of Plant Water Sources

I 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 total plant water uptake for the four study species. I sampled plant xylem tissues, soil water from 0-15 cm and 15-30 cm depths, and groundwater on 3 dates in 2008 and 2009. I collected fully suberized stem sections from the shrub species, and non-photosynthetic below-ground tissues from the grass species (rhizomes in *D. spicata*, and the bases of culms/crown regions in *S. airoides*). Soil samples were collected at two depths within the active rooting zone, 0-15 cm and 15-30 cm, using a soil coring tool (Giddings, Inc., Windsor, CO). I collected groundwater samples from three monitoring wells on site on each sampling date 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.

I extracted plant and soil waters using the cryogenic vacuum distillation method (Ehleringer & Osmond 1989). The stable oxygen isotope ratio of all water samples was determined by  $\text{CO}_2$  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  $\delta$  notation as follows:

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

where  $R_{sample}$  and  $R_{standard}$  are the molar abundance ratios ( $^{18}\text{O}/^{16}\text{O}$ ) of the sample and standard (Vienna Standard Mean Ocean Water, or 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  $^{18}\text{O}$  and thus has a more negative  $\delta^{18}\text{O}$  value than water in upper soil layers that undergoes evaporation.

### 3.3 STATISTICAL ANALYSIS

The study was established as a split-plot design ( $n = 5$  replicates), where rainfall treatment (rain out, rain addition, control) was the whole-plot factor, and species (*S. vermiculatus*, *E. nauseosa*, *S. airoides*, and *D. spicata*) were sub-plot factors. I 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, I considered ANOVA models with autoregressive, spatial power, and spatial exponential covariance structures, however the model with the lowest 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 that presented a violation of the homogeneity of variance assumption if all species were analyzed together under the same ANOVA structure. 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, I analyzed effects of date, treatment, and their interaction on response variables separately for each of the four species. I compared least-squares means using a Tukey multiple comparisons adjustment to identify significant differences between dates and treatments within a species.

## **4. RESULTS**

### **4.1 PRECIPITATION AND DEPTH TO WATER TABLE**

Precipitation patterns differed substantially between 2008 and 2009. Precipitation during the 2008 growing season followed a typical pattern for the study region, with little rainfall in June and early July followed by strong monsoonal flow and precipitation from late July through September (Figures 4-5). Approximately 2/3 of the total annual precipitation occurred in August, including a very large event of 42 mm on August 6, whereas all other daily totals during the study were less than 15 mm. In 2009, the SLV received more late spring and early summer precipitation than average, followed by a drier than average monsoon season (Figures 4-5). More than 2/3 of the total precipitation in 2009 arrived between April and June, when precipitation occurred approximately weekly.

Depth to the water table increased during the summer in both study years. Water table depth below the surface increased from 119 to 143 cm in 2008, and 105 to 150 cm in 2009 (Figure 4). The higher water table in early June 2009 likely created a higher capillary fringe than in 2008.

#### 4.2 TREATMENT EFFECTS ON SOIL VOLUMETRIC WATER CONTENT

In 2008, volumetric water content (VWC) was strongly affected by precipitation in the 0-15 cm soil layer, but remained fairly stable in the 15-30 cm soil layer (Figure 5). Pre-treatment soil VWC in July was 7-8% in the 0-15 cm layer and 13-15% in the 15-30 cm layer, and 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 ( $p \leq 0.0002$ , Figure 5). 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. The only significant treatment effect at this soil depth occurred on August 10 when VWC in rain out plots was 6% lower than control plots ( $p < 0.02$ ).

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 homogenized soil VWC across plots, and no significant treatment differences occurred in either soil layer in July ( $p \geq 0.1$ , all comparisons; Figure 5). From late July through September, most rain events generated insufficient runoff volumes to produce rain addition treatments, and soil drying occurred in the top 15 cm of

soil in all plots. There were no significant differences in mean VWC between treatments in either soil layer in late July ( $p > 0.1$ , all comparisons). On August 29, mean VWC in the 0-15 cm layer was 6% higher in rain addition than rain out plots ( $p = 0.0025$ ), but neither treatment differed significantly from control plots ( $p > 0.1$ , all comparisons). The rain addition treatments increased total growing season precipitation in rain addition plots by 43% (42 mm) in 2008 and 30% (20 mm) in 2009.

#### 4.3 XYLEM PRESSURE POTENTIAL

In both study years, the most significant differences in xylem pressure potential occurred between species (ANOVA;  $253 \leq F \leq 2197$ ,  $p < 0.0001$ ) and dates ( $52 \leq F \leq 289$ ,  $p < 0.0001$ ). Each species responded distinctly to natural and experimental changes in soil water availability. *S. airoides* and *D. spicata* showed the largest increases in  $\Psi_p$  and  $\Psi_m$  following precipitation events that recharged surface soil. *S. vermiculatus*  $\Psi_p$  and  $\Psi_m$  also responded to changes in soil water content, but to a lesser degree than either grass species. *E. nauseosa* maintained a constant  $\Psi$  throughout 2008 and 2009, with little response to seasonal or treatment-induced changes in soil water availability.

In 2008, mean  $\Psi_p$  declined slightly for *S. vermiculatus* during the dry early summer, but there were no differences between control and treatment plants ( $p > 0.10$ , Figure 6). After monsoon rains began in August, mean  $\Psi_p$  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  $\Psi_m$ . In 2009, *S. vermiculatus* mean  $\Psi_p$  and  $\Psi_m$  declined as soil VWC declined from June through September across all plots by an average of 1.4 MPa. There

were no significant differences in mean  $\Psi_p$  or  $\Psi_m$  between treatment and control plants on any date.

*Ericameria nauseosa* xylem pressure potentials were remarkably constant during 2008 and 2009 and did not respond to rainfall treatments or seasonal trends in surface soil water availability (Figure 6). There were no differences in mean  $\Psi_p$  between treatment and control plants in 2008 on any date, except August 9 when  $\Psi_p$  in control plants were 0.1 MPa higher than rain out plants ( $p = 0.02$ ). Mean  $\Psi_m$  also did not differ between treatments on any date in 2008, except September 5 when  $\Psi_m$  in rain out plots was 0.3 MPa higher than in control plots ( $p = 0.008$ ). In 2009, no significant differences occurred among treatments for  $\Psi_p$  or  $\Psi_m$  when averaged over dates ( $p > 0.10$ , 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  $\Psi_p$  and  $\Psi_m$  for both grass species increased slightly, but did not differ between treatment and control plants ( $p > 0.10$ , all comparisons, Figure 6). After the start of the monsoon rains in August, *S. airoides* mean  $\Psi_p$  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*  $\Psi_p$  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  $\Psi_p$  were still over 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  $\Psi_m$  for both grass species in August and September 2008.

Following the wet spring in 2009, *S. airoides* and *D. spicata*  $\Psi_p$  were higher for control and rain addition plants than rain out plants in June ( $p \leq 0.001$ , all comparisons).

Mean  $\Psi_p$  in *S. airoides* control and rain addition plants remained higher than rain out plants for most of the summer except August 11 ( $p \leq 0.001$ , all comparisons), and mean  $\Psi_m$  did not differ between control and treatment plants on most dates. *D. spicata* mean  $\Psi_p$  and  $\Psi_m$  did not differ between treatment and control plants on most dates, but  $\Psi_p$  in rain out plants were 0.8 MPa higher than control plants on August 11 ( $p \leq 0.002$ ), and  $\Psi_m$  were up to 1.3 MPa higher in rain out and rain addition plants than control plants on August 30 ( $p \leq 0.04$ , both comparisons). On average,  $\Psi$  for both grass species declined through the 2009 growing season as soil VWC decreased across all plots. *D. spicata*  $\Psi_m$  dropped from -2.7 MPa to -5.2 MPa, while *S. airoides*  $\Psi_m$  declined from -3.0 MPa to -3.7 MPa.

#### 4.4 STABLE OXYGEN ISOTOPE ANALYSIS

##### 4.4.1 $\delta^{18}O$ of Plant Water Sources

The isotopic signature of groundwater varied little during the 2008 and 2009 growing seasons, with  $\delta^{18}O$  values between -13.8 ‰ and -14.2 ‰ (Figure 7). Mean soil water  $\delta^{18}O$  at 0-15 cm was dynamic, reflecting 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 (Figure 7).

Pre-treatment mean soil water  $\delta^{18}O$  in July 2008 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 ( $p \geq 0.10$ , all comparisons). After August monsoon rainfall, soil water in control and rain addition plots incorporated the isotopic signature of rain water from precipitation events that occurred on August 9 and 10 ( $p = 0.002$ ; rain  $\delta^{18}O = -6.5‰$ ), but was unchanged in rain out plots. In September 2008, soil water in

control and rain addition plots remained 2.2‰ to 2.4‰ more depleted than rain out plots at 0-15 cm, but was isotopically similar in all plots at 15-30 cm depth.

Soil water was more isotopically depleted in early July 2009 than early July 2008 (Figure 7), likely reflecting the input of cold spring precipitation and the influence of a higher water table in 2009. After three weeks of soil drying, soil water at 0-15 cm was up to 2.2‰ more enriched in all plots in late July ( $p = 0.05$ ), while soil water signatures at 15-30 cm did not change between July dates ( $p > 0.1$ ). Soil water was more enriched in  $^{18}\text{O}$  by late August at both depths, due primarily to further soil drying ( $p \leq 0.03$ , both comparisons). The largest isotopic differences between soil layers in 2009 occurred on August 29 (mean soil water  $\delta^{18}\text{O} = -2.0\text{‰}$  at 0-15 cm, and  $-9.1\text{‰}$  at 15-30 cm).

#### 4.4.2 $\delta^{18}\text{O}$ of Plant Xylem Water

Differences in mean xylem water  $\delta^{18}\text{O}$  between the four study species were highly significant in 2008 and 2009 (ANOVA,  $134 < F < 207$ ,  $p < 0.0001$ , both years; Figure 8). *S. airoides* and *D. spicata* xylem water was significantly enriched in  $^{18}\text{O}$  relative to *S. vermiculatus* and *E. nauseosa* throughout both growing seasons ( $p < 0.01$ , all comparisons). Across all plots, *S. airoides* and *D. spicata* had similar xylem water isotopic signatures on most dates. Mean xylem water signatures of *S. vermiculatus* and *E. nauseosa* differed during 2008 but not during 2009.

Pre-treatment xylem water  $\delta^{18}\text{O}$  in 2008 was similar in all plots within a species ( $p \geq 0.10$ , all comparisons), except for *S. airoides*, which were slightly more depleted in rain addition than control plots ( $p = 0.04$ ). During July 2008 there were no differences in mean xylem  $\delta^{18}\text{O}$  between *S. vermiculatus* and *E. nauseosa* ( $p = 0.50$ ), and xylem water

in both shrubs was isotopically similar to groundwater (Figure 8). Xylem water signatures in *S. airoides* and *D. spicata* were significantly enriched relative to both shrubs ( $p < 0.001$ , all comparisons; Figure 8), and were similar to soil water in the upper 30 cm. After August rains occurred, mean xylem water  $\delta^{18}\text{O}$  for both *S. airoides* and *D. spicata* was  $-6.8\text{‰}$ , which was nearly identical to the  $\delta^{18}\text{O}$  of rain-derived soil water in both upper layers. In September, grass xylem water  $\delta^{18}\text{O}$  values remained very similar to surface soil water  $\delta^{18}\text{O}$  values. *S. vermiculatus* xylem water  $\delta^{18}\text{O}$  was  $2.4\text{‰}$  more enriched than *E. nauseosa* in August ( $p = 0.0001$ ) and  $4.5\text{‰}$  more enriched in September ( $p < 0.0001$ ). *S. vermiculatus* xylem water became more isotopically similar to soil water during the monsoon period, while *E. nauseosa* xylem water  $\delta^{18}\text{O}$  remained most like groundwater and did not change over the 2008 growing season ( $p > 0.9$ ).

In early July 2009, xylem  $\delta^{18}\text{O}$  did not differ between shrub ( $p > 0.9$ ) or between grass species ( $p > 0.9$ ), but was  $4.6\text{-}5.2\text{‰}$  more enriched in grasses than shrubs ( $p < 0.0001$ , all comparisons). Mean xylem water  $\delta^{18}\text{O}$  in both grasses closely followed soil water  $\delta^{18}\text{O}$  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 as surface soil water enrichment increased in late 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  $4.8\text{‰}$  more depleted than control and rain addition plants ( $p < 0.0001$ ), suggesting more incorporation of soil water from 15-30 cm. Xylem water signatures in both shrub species were very similar to groundwater by late August. *S. vermiculatus* mean xylem water  $\delta^{18}\text{O}$  did not vary 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 all been described as phreatophytes (Robinson 1958, Sorenson et al. 1991, Nichols 1994), yet their water relations and water acquisition patterns varied considerably. Natural seasonal and experimentally driven changes in near surface soil water availability had a larger influence on  $\Psi$  in *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 2008. Due to variations in water acquisition strategy and physiological sensitivity between these species, persistent changes in summer rainfall patterns will differentially affect grasses and shrubs (Lin et al. 1996; Schwinning et al. 2005b; Peters et al. 2010). This could directly influence basin-scale vegetation composition and consumptive use of groundwater by native vegetation in the SLV and similar arid regions.

### 5.1 RESPONSE OF PLANT WATER RELATIONS TO PRECIPITATION

Seasonal and experimentally altered changes in soil water content affected water relations in *S. vermiculatus*, indicating that this species responds to growing season precipitation. *S. vermiculatus*  $\Psi_p$  and  $\Psi_m$  increased in 2008 after monsoon rainfall events recharged surface soil layers in the control and rain addition plots. However, because the

2009 monsoon season produced little rain, its  $\Psi$  declined steadily through the summer in all plots. Thus, although *S. vermiculatus* is capable of groundwater acquisition, its water status improves in response to precipitation-recharged soil water in the upper 30 cm. Romo & Haferkamp (1989) observed a similar  $\Psi$  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 measured for *S. vermiculatus* in the SLV during two years with very different precipitation patterns are similar to those reported at other western U.S. locations, suggesting that this species functions similarly in regions with and without monsoon rains (Sorenson et al. 1991, Donovan et al. 1996, Trent et al. 1997, Sperry & Hacke 2002).

*Ericameria nauseosa*, in contrast to *S. vermiculatus*, maintained consistent  $\Psi_p$  and  $\Psi_m$  within each growing season and between years, despite large differences in soil water availability. *E. nauseosa* was the only study species for which  $\Psi$  was unaffected by experimental rain addition or exclusion. This is consistent with previous work in the Great Basin and Owens Valley, California indicating that the  $\Psi$  of mature *E. nauseosa* plants changed little during the growing season (Ehleringer et al. 1991, Flanagan et al. 1992, Donovan & Ehleringer 1994, Goedhart et al. 2010). However, these regions have a winter-dominated precipitation regime and lack consistent monsoon driven summer precipitation. In the SLV and other areas where the precipitation regime is monsoon-dominated, *E. nauseosa*  $\Psi$  might be expected to respond to predictable late summer rain (Williams & Ehleringer 2000), but surprisingly, this species appears to function similarly under a wide range of precipitation regimes across the western U.S. (Lin et al. 1996).

*Sporobolus airoides* and *Distichlis spicata* exhibited similar  $\Psi$  patterns in

response to soil water availability. After monsoon rainfall began in 2008, mean  $\Psi_m$  for both species was higher in rain addition than rain out plants, yet the magnitude of mid-day responses was relatively small. However,  $\Psi_p$  for both species in the control and rain addition plots was 1.4 - 2.0 MPa higher than in rain out plots. Acquisition of rain-recharged soil water allowed these grass species to recover overnight from very low daytime xylem potentials, while grasses in the rain out plots experienced continuous water stress. During 2009, when there was little summer rain, both grass species had an overall decline in mean  $\Psi$  as soil VWC decreased across all treatments.

The highly significant responses of *D. spicata* and *S. airoides*  $\Psi$  to natural seasonal and experimentally controlled soil water dynamics suggest that roots involved in water acquisition are concentrated in upper soil layers. This is in contrast to *S. vermiculatus* and especially *E. nauseosa*. In the Owens Valley, *D. spicata*  $\Psi_p$  was more responsive to changes in surface soil water than the co-occurring phreatophytic shrubs *S. vermiculatus* and *Atriplex torreyi* (Goedhart et al. 2010). Thus, despite the presence of shallow water tables at my SLV study site and in the Owens Valley, the water relations of *D. spicata* and *S. airoides* are tightly coupled with near surface soil water availability.

Plant responses to the experimental precipitation treatments differed in a strong (2008) versus a weak (2009) monsoon year. In 2008, the  $\Psi$  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  $\Psi$  in these species. The rain addition treatment did not significantly increase  $\Psi$  over control plots for any species, suggesting that a modest short term increase in rainfall (130-150% of growing season total) may not dramatically affect plant water relations for these species. In contrast to 2008, atypical wet spring conditions

and subsequent soil dry-down during the usually wet monsoon period overwhelmed treatment effects in 2009 and resulted in a seasonal  $\Psi$  decline in *S. vermiculatus*, *S. airoides* and *D. spicata*. High soil VWC likely persisted during the wet spring period due to cooler temperatures and lower evaporative demand, relative to later in the summer. As a result,  $\Psi$  in all species were higher in June 2009 than at any other time during the study.

## 5.2 $\delta^{18}\text{O}$ OF PLANTS AND WATER SOURCES

Differences between groundwater and soil water  $\delta^{18}\text{O}$  signatures allowed me 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, and varied little between dates due to minimal evaporative enrichment. In both years, early summer soil water  $\delta^{18}\text{O}$  derived from winter and spring precipitation was continuously modified by evaporative enrichment and monsoon rain inputs. Mean soil water  $\delta^{18}\text{O}$  at 0-15 cm was highly variable between dates, while soil water  $\delta^{18}\text{O}$  varied less at 15-30 cm but was likely influenced by both precipitation recharge and capillary rise of groundwater on some dates (Chimner & Cooper 2004).

Water acquisition patterns of *S. vermiculatus* and *E. nauseosa* differed by year. During the dry early summer of 2008, *S. vermiculatus* primarily used groundwater, however as monsoon rain events recharged soil, its uptake of soil water increased. Thus, although *S. vermiculatus* can persist largely on groundwater, as it did during 2009, it can also respond rapidly to acquire near surface soil water, as it did in 2008.

*Ericameria nauseosa* utilized primarily groundwater during both 2008 and 2009, even when soil water was abundant. *E. nauseosa* plants acquired a much lower

proportion of soil water in control and rain addition plots than *S. vermiculatus* during the 2008 monsoon season. Chimner and Cooper (2004) found that both *S. vermiculatus* and *E. nauseosa* utilized groundwater in early summer and soil water recharged by monsoon rain in late summer in the SLV, but that study occurred in areas with deeper water tables. In most areas of the Owens Valley and Great Basin *E. nauseosa* does not take up summer rain (Ehleringer et al. 1991, Flanagan & Ehleringer 1991, Flanagan et al. 1992, Donovan & Ehleringer 1994). It is surprising that even in regions with a strong summer monsoon regime, including the SLV and the southern Colorado Plateau, *E. nauseosa* acquires little rain recharged soil water (Lin et al. 1996).

In contrast with the shrub species, both *S. airoides* and *D. spicata* acquired water almost entirely from the upper 30 cm of the soil profile on all sample dates and used little or no groundwater. Grasses in control and rain addition plots acquired water from both sampled soil layers, while those in rain out plots utilized a larger proportion of soil water from the 15-30 cm layer. *D. spicata* plants in the Owens Valley also accessed shallow soil water, in contrast with neighboring shrub species that used groundwater (Pataki et al. 2008, Goedhart et al. 2010, Goedhart & Pataki 2010). However, Elmore et al. (2006) used satellite imagery to determine that the cover of both *S. airoides* and *D. spicata* was affected more by variations in groundwater depth than summer precipitation at Owens Valley sites with water tables < 2.5 m. At my SLV study site, *S. airoides* and *D. spicata* do not function as phreatophytes, although they may use groundwater in locations with fine-grained soil textures where the water table is < 1 m below the ground surface. Because groundwater consumption for both grass species is minimal at deeper groundwater sites, they may have little influence on the regional groundwater budget.

Differences in physiological adaptations among the four study species may explain why they vary in their use of summer monsoon rain, which can represent 50-70% of the total annual precipitation in the SLV (Doesken et al. 1984). In addition to assumed differences in functional rooting depth (Sperry & Hacke 2002, Pataki et al. 2008), these four species vary in drought and salt tolerance. *E. nauseosa* is more susceptible to xylem cavitation (Hacke et al. 2000, Sperry & Hacke 2002) and leaf cell dehydration (Dileanis & Groeneveld 1989) than most co-occurring shrub species in its range including *S. vermiculatus*, which may explain its strong groundwater dependence and consistently high  $\Psi$ . 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, James et al. 2006). The dramatically lower  $\Psi$  measured in rain out plants in 2008 and all plots in the dry late summer of 2009 likely reflect osmotic adjustments in these three species, all of which acquired surface soil water at least periodically. Thus, *S. vermiculatus*, *S. airoides*, and *D. spicata* may be better adapted to exploit monsoon-driven soil moisture pulses, while *E. nauseosa* appears to invest more resources into accessing a deeper, more stable water source. Recognition of these contrasting water use patterns will inform predictions of how this plant community may respond to changes in precipitation.

### 5.3 IMPLICATIONS FOR PLANT COMMUNITY COMPOSITION AND GROUNDWATER USE

All four study species were previously considered to be phreatophytes that largely used groundwater in the SLV. My results demonstrate that a broad range of water acquisition strategies exist for these four species, which dominate the native vegetation of the SLV. The two grass species are almost entirely dependent on summer rain water, while *E. nauseosa* is almost entirely groundwater-dependent, and *S. vermiculatus* is more opportunistic in its exploitation of available water. Therefore, an increase in summer rainfall could improve the water status of both grass species as well as *S. vermiculatus*. Increases in  $\Psi$  may not necessarily result in increased growth, particularly if they do not coincide with high growth periods in species that are phenologically constrained (Snyder et al. 2004, Schwinning et al. 2005b). However, favorable water status is likely to encourage the survival of shallow-rooted grasses (Schwinning et al. 2005b). A moderate, short duration increase in summer rainfall as simulated by the rain addition treatment may not change current plant water acquisition strategies or alter plant community composition and  $ET_g$ . However, a larger or longer duration increase in rainfall could favor grasses and inhibit shrub expansion (Pockman & Small 2010), and may allow plants to increase root abundance in shallow soil layers. Conversely, a decrease in summer rainfall would increase water stress in grass species, which could reduce their net primary production and cover. A decline in grass production would reduce forage availability for livestock, which would be detrimental to a major land use in the SLV. More extreme or extended summer drought could force grasses beyond critical water stress thresholds, leading to plant mortality (Schwinning et al. 2005b). Reduced grass

cover may allow gradual shrub expansion (Schlesinger et al. 1990, Elmore et al. 2003), particularly for clonal species such as *S. vermiculatus*, and result in vegetation that is increasingly dominated by shrubs.

Changes in SLV growing season precipitation could produce several different outcomes for phreatophyte community composition, each associated with different effects on  $ET_g$ . Cover of the rain-dependent *S. airoides* and *D. spicata* may increase or decrease with rainfall, but these species do not contribute greatly to  $ET_g$  at sites where the maximum water table depth is >1 m. 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 across sites with similar characteristics in the SLV. However, an increase in *S. vermiculatus* and/or *E. nauseosa* abundance due to a loss of grass cover could result in a large increase in basin-scale  $ET_g$ , which may alter the balance of groundwater available to sustain regional agriculture and other human uses in the SLV.

Climate models indicate that in addition to growing season precipitation changes, the SLV and many similar intermountain basins could experience changes in winter precipitation patterns. Snow water equivalent, which is strongly correlated with depth of snowpack, has decreased significantly over the past 30-50 years across mountainous regions in the western U.S. (Barnett et al. 2008, McCabe & Wolock 2009). In Colorado's high elevation mountains, snow water equivalent has been less sensitive to increasing winter temperatures during this period (Hamlet et al. 2005, CWCB 2008). However, as air temperatures continue to rise, a reduction in mountain winter snowpack is likely (Mote et al. 2005, CWCB 2008). Declining snowpack in the Sangre de Cristo and San

Juan Mountains could reduce the recharge of SLV aquifers, which could lower water tables (Wurster et al. 2003) and impose water stress on phreatophytic shrubs (Charles 1987, Sorenson et al. 1991). In addition, because many SLV plant species require a winter snowmelt soil moisture pulse to initiate growth in spring, changes in the amount and timing of snowmelt could have a strong influence on plants in this region. Research on the Colorado Plateau has suggested that changes in winter precipitation would have a greater effect on plant community composition than a shift in summer precipitation (Gebauer et al. 2002, Schwinning et al. 2005b). The uncertain impacts of changing summer and winter precipitation regimes in the SLV will have a large role in determining the future vegetation composition and  $ET_g$ , and hydrologic models must account for such plant-climate feedbacks.

## **6. CONCLUSION**

Phreatophytes dominate the vegetation of many arid basins with shallow aquifers in the western U.S., and can have a substantial influence on regional water budgets through groundwater evapotranspiration ( $ET_g$ ). In the SLV, native phreatophyte communities occupy close to 50% of the total land area, and  $ET_g$  from these communities accounts for nearly 1/3 of the total annual groundwater outflow (RGDSS 2006). As human demand for dependable water supplies grows, accurate estimates of groundwater use by phreatophyte communities are increasingly critical for sustainable groundwater management in arid basins.  $ET_g$  rates are likely to change as 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  $ET_g$  at large spatial scales. This study demonstrated that water relations and water acquisition patterns varied markedly among native phreatophytes in the SLV in response to seasonal and experimental changes in precipitation, suggesting that these species will differ in their sensitivity to forecast changes in climate. Water relations in the grass species *S. airoides* and *D. spicata* were tightly coupled to rain-recharged surface soil water, and isotopic evidence showed that both grass species depend almost entirely on growing season rainfall, despite the presence of shallow groundwater. Thus, *S. airoides* and *D. spicata* do not function as phreatophytes at the study site. In contrast, *E. nauseosa* acquired little or no 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 decline in water table depth. Persistent changes in precipitation patterns may cause a shift in plant community composition and affect basin-scale groundwater use under future climate conditions. The effects of these 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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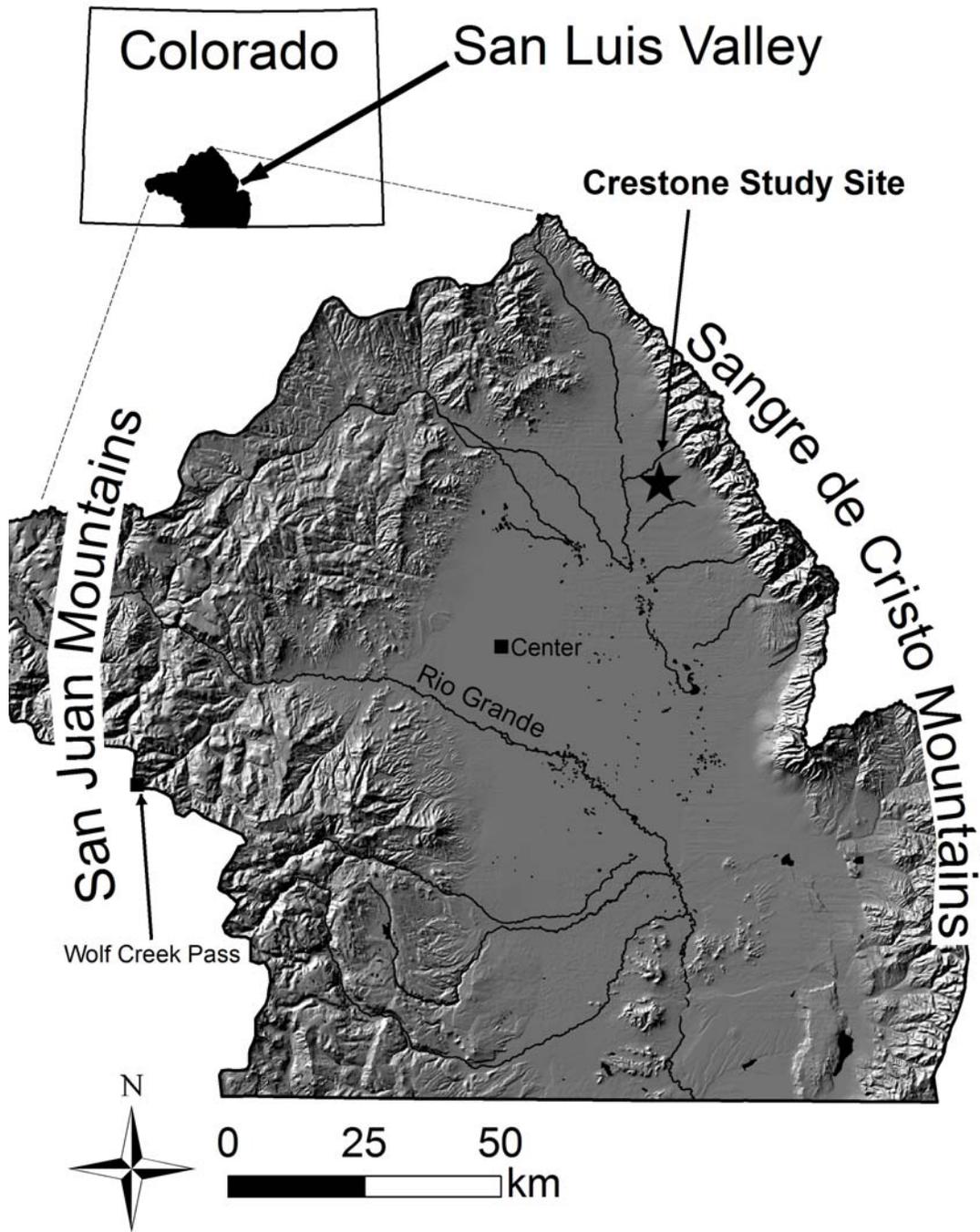
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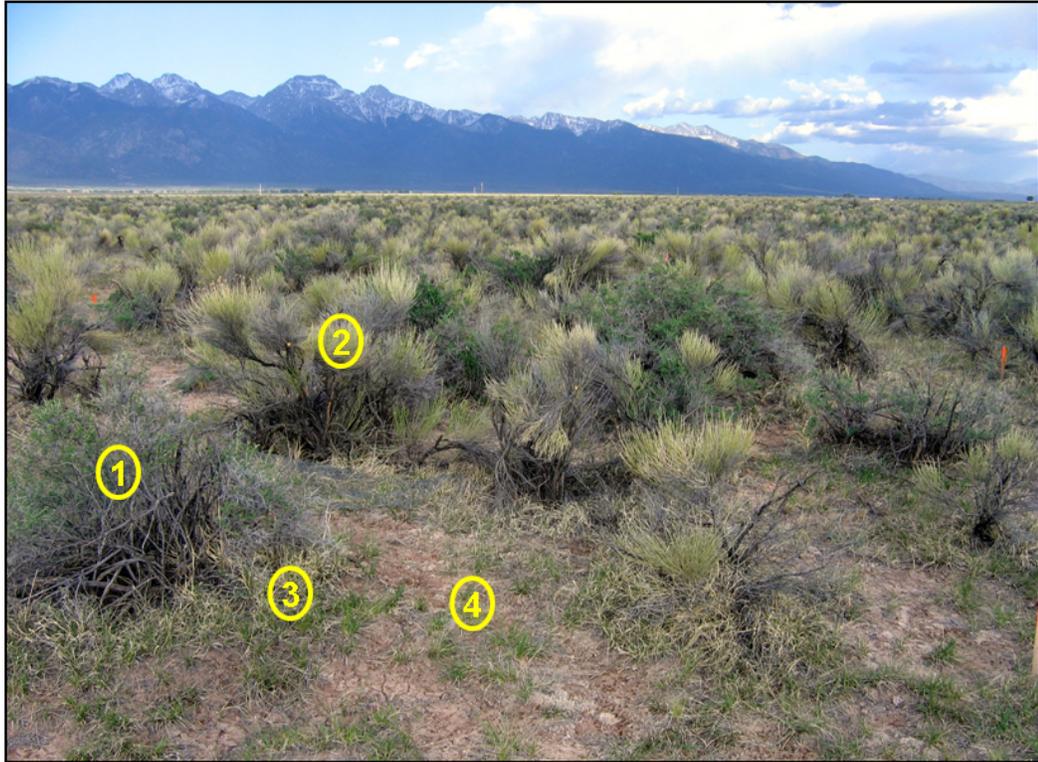
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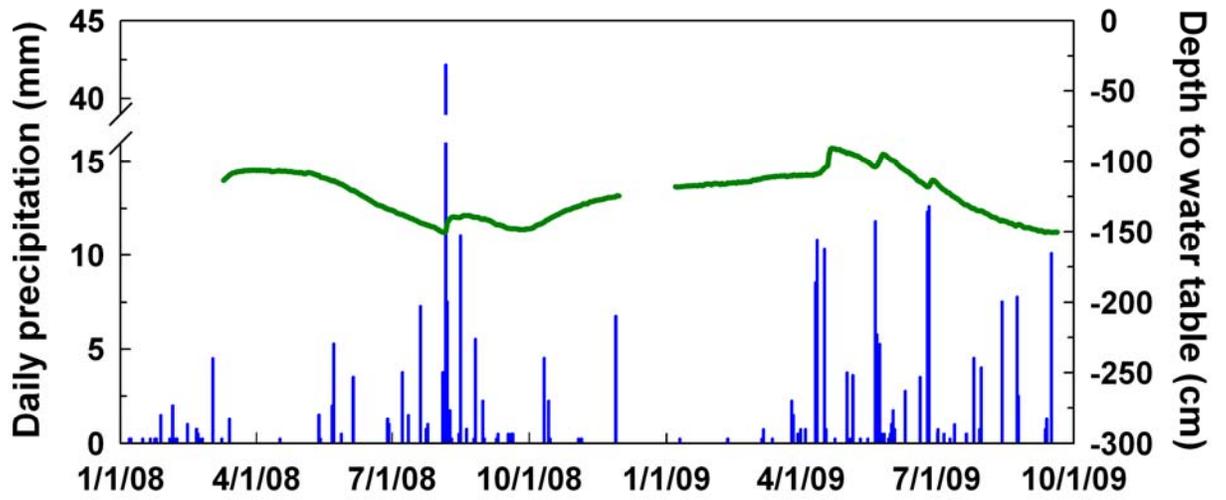
**Figure 1.** Location of the Crestone study site and the San Luis Valley, Colorado.



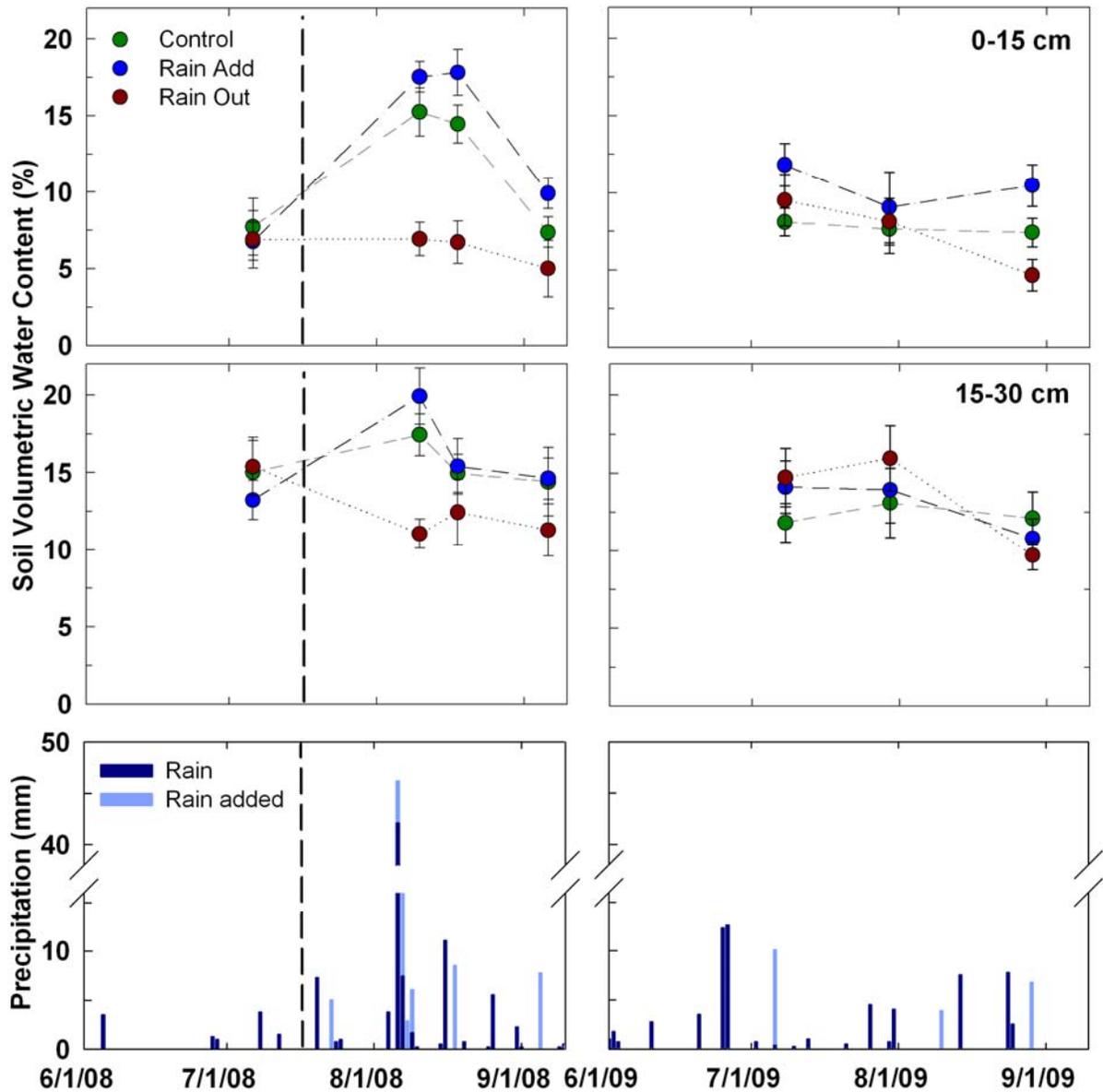
**Figure 2.** Native phreatophyte communities occupy over 4850 km<sup>2</sup> in the San Luis Valley, Colorado. These include the shrubs (1) *Sarcobatus vermiculatus* and (2) *Ericameria nauseosa*, and the grasses (3) *Sporobolus airoides*, and (4) *Distichlis spicata*.



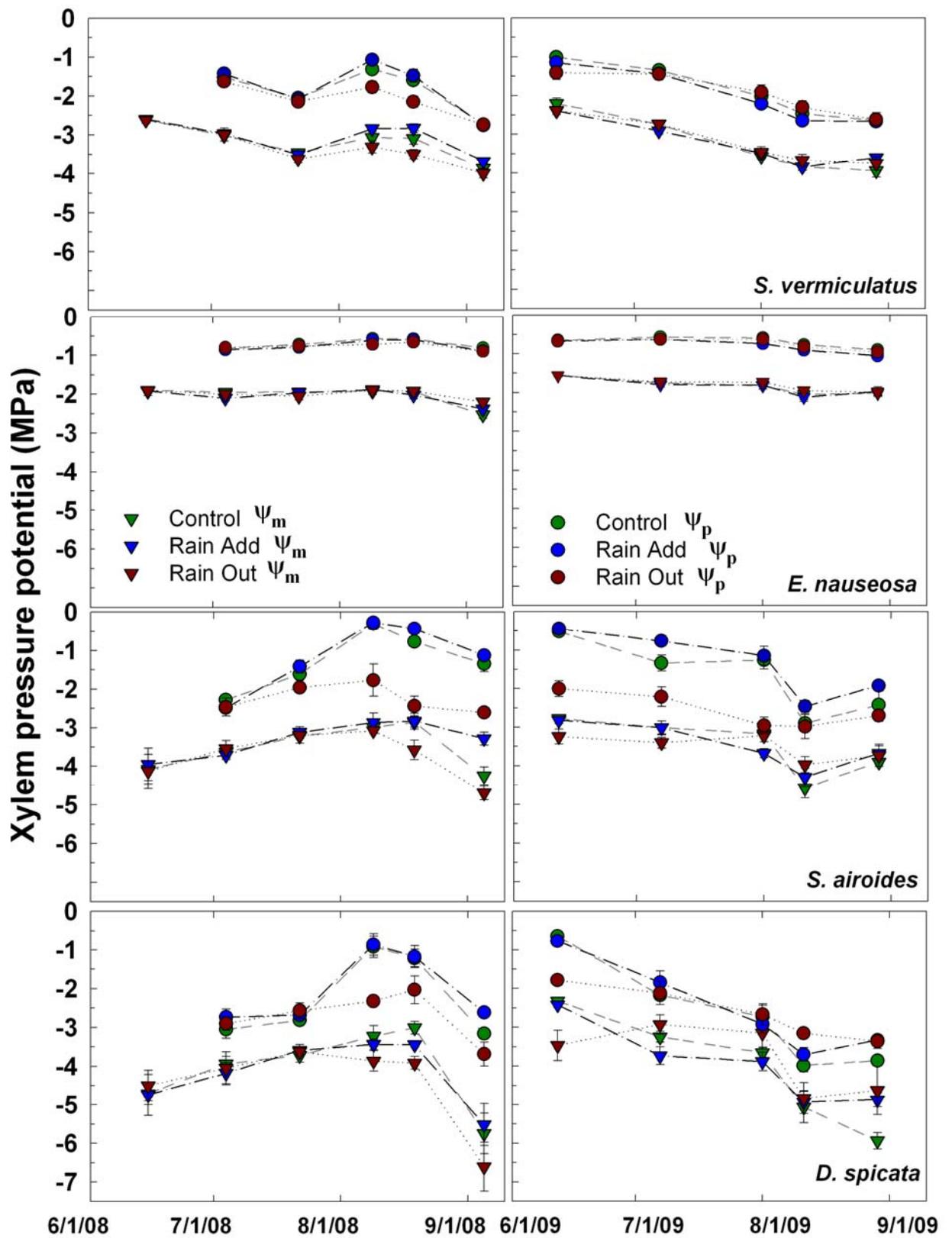
**Figure 3.** The rainfall manipulation experiment compared control plots receiving ambient rainfall with one of two treatments, (a) decreased rainfall using rain-out shelters and (b) increased rainfall through addition of rain captured by shelter roofs.



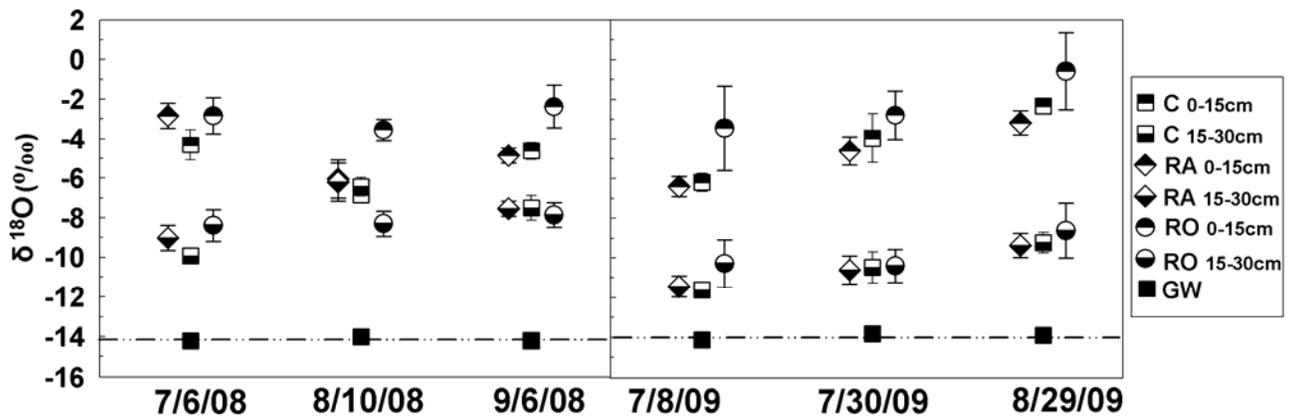
**Figure 4.** Daily precipitation (vertical blue bars) and depth to water table (green line) recorded at the study site in 2008 and 2009.



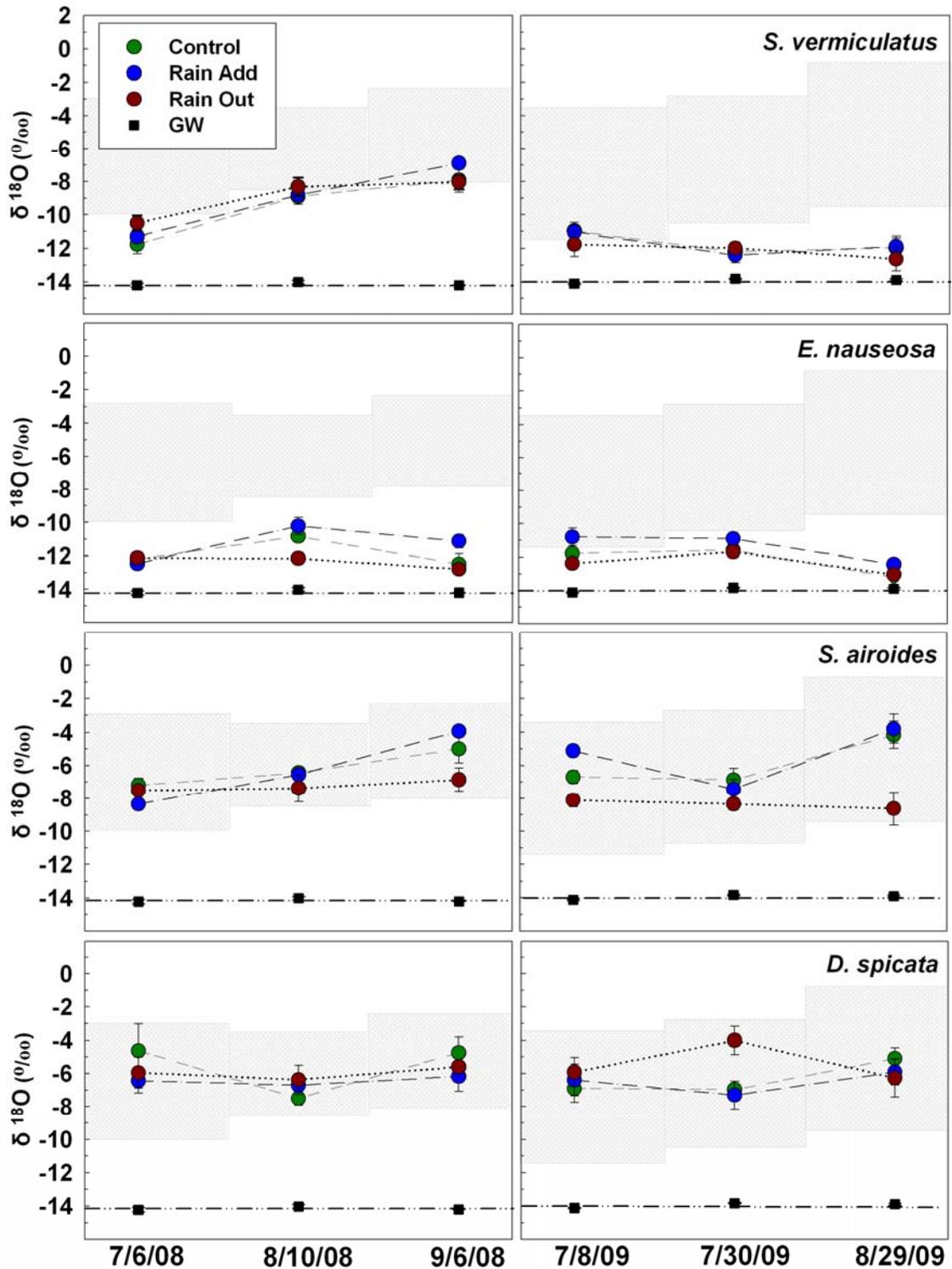
**Figure 5.** Mean ( $\pm 1$  SE) volumetric soil water content for control and treatment plots in 2008 (left column) and 2009 (right column) for the 0-15 cm (upper panels) and 15-30 cm (middle panels) soil layers. Daily precipitation for June-September (dark blue bars) and rain additions (pale blue bars) are shown as stacked bars in the lowest panel. The dashed vertical line separates pre- and post-treatment periods.



**Figure 6.** Mean ( $\pm 1$  SE) pre-dawn ( $\Psi_p$ ) and mid-day ( $\Psi_m$ ) xylem pressure potentials for plants in control and treatment plots in 2008 (left column) and 2009 (right column).



**Figure 7.** 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 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.



**Figure 8.** Mean plant xylem oxygen isotope composition ( $\delta^{18}\text{O}$ ,  $\pm 1$  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  $\delta^{18}\text{O}$  values are indicated by black squares, and the range of soil water  $\delta^{18}\text{O}$  values for all treatments are shown by shaded regions behind plant xylem  $\delta^{18}\text{O}$  values.