

AN ABSTRACT OF THE THESIS OF

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Title: Biomass Production and Water Use of Common Plant Species in Owens Valley, California, USA.

Abstract approved:

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This study evaluated biomass production, water-use efficiency (WUE), biomass allocation, and water use characteristics of common plant species in Owens Valley, California, USA. The species studied were the grasses *Distichlis spicata*, *Leymus triticoides*, and *Sporobolus airoides*, the forbs *Glycyrrhiza lepidota*, *Juncus arcticus*, and *Salsola tragus* (annual), the desert shrubs *Artemisia tridentata*, *Atriplex confertifolia*, and *Ericameria nauseosa*, and the riparian shrub *Salix exigua*. Plants of each species were established and grown in 2.4 m X 2.4 m plots in a common garden since 2005. Our first experiment was conducted in 2009 and 2010 and included four monthly summer water treatments: control (no additional water), low (1.3 cm), medium (2.6 cm) and high (3.9 cm). Biomass production and WUE (the amount of water that a plant uses to produce a unit of biomass) were lower in 2009 than in 2010. Water-use efficiency of grasses increased with increasing water application in 2009 but decreased with increasing water application in 2010. The difference between years was attributed to the difference in timing of natural precipitation with higher spring precipitation in 2010. Biomass production and WUE of desert shrubs were not significantly affected by water treatments. Water-use efficiency varied by species; some desert shrubs and the annual *S. tragus* were 13 times more efficient than the

riparian *S. exigua*. Total standing crop and root-to-shoot ratio (RSR) varied by species, but not by watering treatments. Although in general desert shrubs had higher standing crop than herbaceous species, the grass *S. airoides* had the highest standing crop overall. Graminoids had much higher RSR (3 to 6) than the shrubs did (< 1).

Our second experiment was conducted in 2010 using the experimental setting of the first experiment with the objective of determining soil water use and depth of soil water extraction by species. Three monthly watering treatments were applied during the summer months: low (1.3 cm), medium (2.6 cm), and high (3.9 cm). Plant water use was determined by calculating soil water depletion during irrigation cycles using time domain reflectometry (TDR) at two depths (0 - 25 cm and 0 - 50 cm) in vegetated plots. Evaporation was also obtained by water depletion on bare ground plots and subtracted from evapotranspiration to calculate water use. Water use varied by species; those with shallow, fibrous, and rhizomatous root systems such as *J. arcticus* and *L. triticoides* had higher water use than shrubs, including the riparian *S. exigua*. The ratio of deep water (25 - 50 cm) to shallow water (0 - 25 cm) use was 19 to 21 in desert shrubs and 1 to 2 in herbaceous species, indicating that shrubs may be more dependent on groundwater than shallow-rooted species such as grasses. In general, we observed large variability in biomass production, water-use efficiency, biomass allocation, and water-use characteristics among the typical plants of the Owens Valley, which should be considered in land and water management decisions. A potential increase in summer precipitation in the area might favor higher water utilization and higher production of shallow-rooted, high RSR plants such as grasses in detriment of desert shrubs.

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Biomass Production and Water Use of Common Plant Species in Owens
Valley, CA, USA.

by
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Tracie L. Evans, Author

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CONTRIBUTION OF AUTHORS

Additional authors made significant contributions to this thesis. Dr. Ricardo Mata-González contributed to the initial design of the experiments, aided in field sampling methods, data analysis, interpretation and discussion of the data collected, and edited all the chapters. Dr. David Martin contributed to the general design of the study, suggested sampling methods, facilitated field sampling, edited initial study proposal and edited all final chapters. Dr. Terry McLendon contributed to the initial design of the study and edited individual chapters.

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Chapter 1: Introduction

Owens Valley, California, is a narrow (4 - 10 km wide) and closed basin located between the Sierra Nevada Mountains and the White and Inyo Mountains (Elmore et al., 2000; McLendon et al., 2008). The area is dry with annual precipitation between 13 to 17 cm occurring primarily in winter and spring. Despite the low precipitation, groundwater is abundant in the valley (groundwater table 0 – 10 m deep) because of the high recharge from the surrounding mountains. The importance of this valley directly reflects the multiple uses and needs that groundwater is required to support. Los Angeles Department of Water and Power (LADWP) has been diverting water from this region to the city since 1913 (Libecap, 2005; Pataki et al., 2008). Also dependent upon this water system are local township water departments, agriculture producers, and the local economy via tourism.

Vegetation of the area is typical of the Great Basin with plants highly adapted to aridity. However, because of the shallow-aquifer plants can rely on a combination of surface soil water derived from precipitation and groundwater (McLendon et al., 2008; Pataki et al., 2008). An important management goal for the valley groundwater resources is to provide a reliable supply of water to people in California while avoiding adverse effects on the plant communities of the valley floor that rely on it (Or and Groeneveld, 1994).

Recent studies in the Owens Valley have addressed vegetation and groundwater interactions including water table fluctuations and plant responses to nutrient stresses (Elmore et al., 2006; Goedhart and Pataki 2011; Goedhart et al., 2010; Mata-González et al., 2011; McLendon et al., 2008; Naumburg et al., 2005; Pataki et al., 2008), but there is no local information on plant responses to surface soil water variation. In particular, there is no information on vegetation responses to summer water applications. This is important given the projections of some global climate models in which summer precipitation might increase in areas with typical winter-

spring precipitation patterns such as the Great Basin (Anderson and Roads, 2002; Loik, 2007).

Little is known about water-use efficiency, plant production, and water use characteristics of major plant species in the Owens Valley. Water-use efficiency (WUE), expressed as the amount of water that a plant uses to produce a unit of biomass, is an important concept to understand the interactions of water use and carbon gain, which is fundamental in budgeting water resources for the protection of vegetation in a scenario of valley water diversions. Certain species are more economical in arid environments to produce a desired amount of biomass with limited water resources (Kramer and Boyer, 1995). In rangeland communities, drought can lead to severe disruptions in plant populations and ecosystems (Brown, 1995). Therefore, the plant's WUE might play an important role in determining its survival and productivity. Water-use efficiency can be intrinsically different among species because of their specific environmental adaptations, but it can also vary with atmospheric conditions, soil moisture, and soil nutrient conditions (Brown et al., 1995; Hatfield et al., 2001).

Fundamental knowledge is needed on biomass production and root:shoot allocation to better understand carbon pools as affected by changes in available water (Mata-González and Meléndez-González, 2005; Sisson, 1989). It is also important to gain knowledge on the characteristics of water acquisition by plants. Some species might primarily rely on surface water while others may depend on water from deeper sources, which is important to understand surface-subsurface water utilization by plants (Dodd et al., 1998; Pataki et al., 2008). Species-specific information such as that pursued in this study is also essential to improve the functionality of ecosystem models such as EDYS (Childress et al., 2002). The EDYS model simulates changes in soil, water, plant, animal, and landscape components resulting from natural and anthropogenic ecological stressors and has been applied to a variety of ecosystems, management scenarios, and ecological disturbance regimes, including the Owens

Valley (Mata-González et al., 2007; Mata-González et al., 2008 Naumburg et al., 2005).

The specific objectives of this study were:

- To determine water-use efficiency, biomass production, and biomass allocation of common Owens Valley plant species as affected by different levels of soil surface watering applied in the summer.
- To compare soil-water depletion and water-depth uptake characteristics of different Owens Valley species under different amounts of surface watering applied to soil in the summer.

Each of the above objectives constitutes a manuscript in this thesis.

Chapter 2. Biomass production and water-use efficiency of Great Basin plants under different summer watering levels

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Abstract

This two-year study evaluated biomass production, water-use efficiency (WUE), and root-to-shoot ratio (RSR) of ten common plant species in Owens Valley, California. The study included grasses, forbs, desert shrubs, and a riparian shrub. Plants were grown in 5.8 m² plots in a common garden and four watering treatments were applied monthly during the summer: control (no additional water), low (1.3 cm), medium (2.6 cm) and high (3.9 cm). Biomass production and WUE were lower in 2009 than in 2010. Water-use efficiency of grasses increased with increasing watering in 2009 but decreased with increasing watering in 2010. Year differences were related to spring precipitation, which greatly increases vegetation success regardless of water availability in the summer. Desert shrub biomass and WUE were not affected by summer watering. A potential summer precipitation increase in this area would benefit herbaceous plants more than shrubs. Desert shrubs and the annual *Salsola tragus* were 13 times more water-use efficient than the riparian *Salix exigua*. Graminoids had higher RSR (3 to 6) than shrubs (< 1). These results show great variability in biomass production and WUE among the typical plants of the Owens Valley, which should be considered in land and water management decisions.

1. Introduction

Water is a primary limiting resource for plant growth and reproduction in arid environments (Le Houerou et al., 1988). In these environments plants use soil water derived from precipitation and/ or from shallow groundwater if it exists (McLendon et al., 2008). When plants use groundwater the condition of the aquifer influences the characteristics of the vegetation (Mata-González et al., 2011). Because groundwater is often used for multiple purposes, including human consumption, water use by vegetation in shallow-aquifer areas is of direct importance for groundwater management and the convergent needs of urban areas and natural ecosystems.

Owens Valley, California is an arid area with a shallow aquifer (0-10 m) that is a source of water for people and for the vegetation of the area (Goedhart and Pataki, 2011; McLendon et al., 2008). Water has been diverted from the valley for urban uses since 1913 and local in-valley uses are substantial, including local water departments, agriculture, tourism, and state fish hatcheries. An important management goal for the valley groundwater resources is to provide a reliable supply of water to people in California while avoiding adverse effects on the plant communities of the valley floor that rely on it (McLendon et al., 2008). The importance of this valley directly reflects the multiple uses and needs that groundwater is required to support. Similar scenarios exist in other parts of USA (Patten et al., 2008) and the world (Le Maitre et al., 1999; Zhu et al., 2004).

Vegetation on the Owens Valley floor is typical of the Great Basin, with plants highly adapted to arid conditions, but with some species also dependent on water from the shallow aquifer (Naumburg et al., 2005). The Owens Valley also supports stands of important riparian species such as willow (*Salix exigua*). How these plants vary in biomass production, particularly root production, as their available water changes has received little or no attention. Previous information suggests that aboveground and belowground biomass production are differentially affected by changes in available water (Hsiao and Xu, 2000) and that root-to-shoot ratio (RSR) tends to increase under water limitations (Sisson, 1989).

Water-use efficiency (WUE) can be defined as the amount of water used by plants to produce a given amount of biomass (Dwyer and DeGarmo, 1970; Shantz and Piemeisiel, 1927). Plant species were believed to possess specific water requirements for growth, regardless of environmental conditions (Brown, 1995), but it is now accepted that WUE varies with environmental and soil conditions. For example, several desert plants have been shown to become more efficient in water utilization as available water declined (Dwyer and DeGarmo, 1970; Montaña et al., 1988; Toft et al., 1989; Trent et al., 1997). Knowledge of WUE of common plant species in Owens Valley is important to understand the responses of vegetation to fluctuations in

available water and to better explain the relationship between biomass production and water consumption. Water-use efficiency data is also important to improve the functionality of ecological models such as EDYS, which rely on species-specific parameters for better determinations of plant growth and competition (Mata-González et al., 2008; Naumburg et al., 2005).

Recent work in the area has focused on explaining changes in vegetation distribution and cover as affected by depth to water changes (Elmore et al., 2006; Mata-González et al., 2011), determining water sources for vegetation (McLendon et al., 2008), and evaluating plant-stress responses and nutrient cycling (Goedhart and Pataki, 2011; Goedhart et al., 2010). It is increasingly clear that plants in shallow aquifer areas such as the Owens Valley can rely on both groundwater and soil surface water (McLendon et al., 2008), but local studies on plant responses to soil-surface water variation are lacking.

This study focused on plant responses to surface-water additions in late spring and summer. Some climate change scenarios indicate potential alterations in the distribution and seasonality of precipitation in areas such as the Great Basin, where precipitation is normally concentrated in the spring (Anderson and Roads, 2002). This has motivated a number of studies to investigate potential vegetation responses to increasing summer precipitation in the Great Basin (Ehleringer et al., 1991; Loik, 2007; Snyder et al., 2004).

In this study, we analyzed aboveground and belowground production and WUE of a diverse group of important plant species in the Owens Valley under variable watering levels. The goal was to better understand plant responses to changes in simulated summer rainfall (surface watering), which in turn would help to explain the dynamics of surface water/groundwater as determinants of vegetation responses. We hypothesized that in general, for all species, aboveground biomass production and total standing crop would increase and that RSR would decrease with increasing watering levels. We also expected that WUE would increase as watering levels

decreased. However, given the diversity of plant traits represented in our species pool, we expected variable responses among species to our watering treatments.

2. Materials and Methods

2.1. Site Location and Description

The study area was located in Owens Valley, CA, a narrow (4-10 km wide), closed basin valley located between the Sierra Nevada to the west and the White and Inyo Mountains to the east. The climate of the area is characterized by hot and dry summers and cold and relatively moist winters. The area is dry, due to the rain shadow effect from the Sierra Nevada, with annual precipitation between 13-17 cm. Long-term records of weather stations throughout the Owens Valley indicate that 77% of precipitation occurs from November to March, with the remaining 23% occurring from April to October. Despite the low rainfall, groundwater is abundant in the valley floor (water table 0 – 10 m) because of the high recharge from the surrounding mountains.

The project site was located on Los Angeles Department of Water and Power property (LADWP), about 8 km west of Bishop, CA (37° 20' 3.68" N, 118° 18' 23.98" W). The site, with depth to groundwater greater than 6 m, was selected to prevent the water table from being a confounding factor in this surface-water study. Precipitation records for this site were obtained from a weather station located in Bishop, CA. The soil series is a Yermo very gravelly sandy loam, with calcareous, thermic Typic Torriorthents (USDA, 2010) and Haplic Regosols (Calcic, Aridic) (WRB, 2007). The soil texture at 0 – 40 cm depth is loamy sand (80% sand, 16% silt, 4% clay). Bulk density is 1.5 at 0 - 30 cm and 1.6 at 30 - 60 cm. The pH is 8.1, electrical conductivity is 0.4 dS m⁻¹, and organic matter content is 1.4% at the depth of 0 - 40 cm.

2.2. Experimental Procedure

Ten of the most common plant species in the Owens Valley were used for this study (Table 1). Individuals of each species were grown in the field in 2.4 m X 2.4 m

plots as a garden study. Plots were separated by a sheet of 1.3 cm thick laminated wood sheets (plywood) buried to a depth of 1.2 m to minimize between-plot effects and to reduce root proliferation into adjacent plots. Plot establishment began in 2005 and continued through 2008. During this period and throughout the duration of the study plots were irrigated and maintained free of weeds.

Some species were established from locally collected seed, but most were transplanted as young plants from adjacent areas. *Distichlis spicata* and *L. triticoides* are sod-forming, rhizomatous grasses that were established from the center of the plots and achieved 40 – 50% cover inside the plots. *Juncus arcticus* is also a sod forming grass-like plant that was established similar to *D. spicata* and *L. triticoides* and reached 10% cover. *Sporobolus airoides* is a bunchgrass that reached about 25% of cover (four plants). Four plants each of *A. tridentata*, *E. nauseosa*, *G. lepidota*, *A. confertifolia*, and *S. exigua* were planted per plot. *Artemisia tridentata* and *E. nauseosa* established the most successfully. Establishment success varied greatly for the other species. *Atriplex confertifolia* was difficult to establish. Therefore, this species had generally younger individuals than other species in our study. *Salsola tragus* is an annual forb that was established in both years of study using seed (2009) and young plants (2010) from adjacent areas around May. This species was not successfully established in the control plots.

The original experimental design consisted of three treatments (watering levels) with 6 replications (blocks) of each treatment. An additional set of control plots with three replications were included to increase data amplitude. Each treatment X species combination was randomly assigned to a plot. In total, 210 plots were included in this study.

2.3. Treatment Application

Experiments were conducted over two growing seasons, May through September in 2009 and April through August in 2010. Watering treatments were: 1) control, 2) low irrigation, 3) medium irrigation, and 4) high irrigation. The control consisted of no addition of water (other than natural precipitation) during the growing

season. The low irrigation treatment consisted of adding irrigation water to total 1.3 cm of water (irrigation plus precipitation) for the month. If 1.3 cm or more precipitation was received during the month, no irrigation was supplied to the low irrigation treatment plots that month. The amount of total water received by plants either by natural precipitation or irrigation was recorded. The medium irrigation treatment consisted of adding enough water to equal 2 times the moisture received on the low irrigation treatment plots. The high irrigation treatment plots received sufficient irrigation to equal 3 times the moisture received on the low irrigation plots. Irrigation was increased for *J. arcticus*, *L. triticoides*, and *S. exigua* in 2010 because 2009 observations indicated excessive stress and lower than expected biomass production for these species. The low irrigation treatment was increased to 1.9 cm per month while the medium and high irrigation treatments were 2 times and 3 times higher than the low irrigation treatment. We used tap water from Bishop, CA, which was transported to the study site and deposited in large storage tanks. According to the City of Bishop no nitrates and very low amount of total dissolved solids are detected in the water. A water meter (Sensus Invensys SR II positive displacement, Sensus, Raleigh, NC) attached to a water hose and a sprinkler was used to carefully measure the water volume output added at the end of each month during the growing season to every plot.

2.4. Aboveground Biomass Sampling

Grasses were clipped to ground level at the beginning of the growing season (spring) in both years to remove the previous-year growth. Grasses were clipped again at the end of the growing season (late summer) to obtain the biomass production during the season. The plant tissue was oven-dried at 68°C for 48 hours. For shrubs, growing season biomass production was determined by estimating standing crop at the beginning and end of the growing season in both years. In order to estimate initial standing crop, parts of representative plants of each species were sampled and clipped. These plant parts were used to visually estimate the size of whole plants in each plot.

Subsequently, the representative plant parts by species were dried, weighed, and used to estimate the weight of whole plants in the plots by extrapolation. A similar procedure has been reported by Mata-González et al. (2002). At the end of the study in 2010, shrubs were harvested to ground level to quantify biomass production and to calculate the relationship between our estimated and harvested biomass. In 2009, the biomass production of *J. arcticus* and *G. lepidota* was also estimated as for shrubs. In 2010, both species were harvested. *J. arcticus* was clipped at ground level the same as grasses to obtain its season biomass production. In both years, the production of the annual *S. tragus* was obtained by harvesting.

Plant cover (percent of ground cover occupied by plants) in each plot was determined by obtaining digital photography from about 2.5 m above ground. Images were printed and the areas occupied by vegetation and bare ground were manually separated and measured with a CID-202 laser area meter (CID Bioscience, Camas, Washington). With cover information, biomass data were converted to square meter basis to have more homogeneous units for species comparison.

Water-use efficiency was determined by dividing the total amount of water received in each plot by the amount of aboveground biomass produced per plot at the end of the summer season (g g^{-1}) (Dwyer and DeGarmo, 1970; Shantz and Piemesisel, 1927). Thus, efficient plants were considered to be requiring less water to produce biomass. Our WUE included both water used in transpiration and water lost by evaporation. In addition to the summer season WUE determined in 2009 and 2010, spring WUE of grasses was determined in 2010. The experimental plots were surveyed early in March and we found that the grasses had not started to re-grow after the 2009 harvest. Then late in April we observed substantial growth which was clipped as we prepared for treatment application initiation. Since the amount of precipitation that those plants had received in March and April was known, their spring WUE was determined.

2.5. Root Sampling

Root sampling was conducted at the end of the 2010 growing season by using an excavator to dig to approximately 1.5 m and extract the soil containing the roots in each plot after the aboveground biomass of all species was harvested. In this study, roots were considered to be any belowground biomass since we clipped at ground level to obtain aboveground biomass. Roots were initially separated from the soil by sifting with 0.5 cm mesh screens and subsequently washed with water to remove the remaining attached soil. Root materials were then oven dried and weighed. Because this process was labor intensive, only three treatment replications and none of the control replications were sampled. Total standing crop was calculated by adding aboveground and belowground biomass.

2.6. Data Analysis

An unbalanced two-way analysis of variance (ANOVA) was used to test differences by watering treatments, species, and years of study. The focus was to compare watering treatments within individual species and years. However, we compared only species when treatments within species were not significantly different in a given year for any variable. Mean comparisons were made by protected LSD at $P < 0.05$. Regression analyses were also used to find potential relationships between some variables at $P < 0.05$.

3. Results

3.1. Precipitation and temperature

During the first year of this study (2009), total precipitation was lower (10.2 cm) than the long term average (16 cm) (Fig. 1). During the second year of the study precipitation was higher (23.6 cm) than the average, mainly because of the large amount of precipitation (13.7 cm) received in December of 2010. However, for our study a key difference between years was the winter and spring precipitation, much

lower in 2009 than in 2010. In terms of temperature both years followed a very similar pattern (data not shown).

3.2. Aboveground biomass production

There was a marked difference in aboveground biomass production between 2009 and 2010. Production in 2010 was nearly twice as great as in 2009 (548 and 280 g/m², respectively) across all species and watering treatments ($P = 0.00$). Grass production generally increased ($P < 0.05$) with increasing watering treatments in both years (Table 2). The exception was *D. spicata* in 2010, as plants in the control treatment were not different ($P > 0.05$) from any of the other treatments. However, growth of grass in response to water addition was different between years. In 2009 the addition of water in the low, medium, and high level treatments resulted in grass production (average of three species) increasing 25, 28, and 47 times respectively, in relation to the production in control plots. In contrast, in 2010 the addition of water in the low, medium, and high level treatments resulted in grass production (average of three species) increasing only two to three times in relation to the production in control plots. In average, the three grasses grown in control plots produced 3% and 68% of the biomass produced in the watered plots in 2009 and 2010, respectively.

Grass species responded differently to watering treatments even in the wet year (2010). *L. triticoides* increased biomass production six-times in the high watering treatment with respect to the control while *S. airoides* increased biomass production two times and *D. spicata* showed no increase (Table 2). Overall, in both years and across the watering treatments, *S. airoides* produced three times more biomass than *D. spicata* and five times more biomass than *L. triticoides*.

There was a strong relationship between estimated and measured shrub biomass in 2010 ($P = 0.00$; $R^2 = 0.86$; Fig. 2). Therefore, we believe the estimated 2009 shrub biomass also followed closely the actual biomass production. In general, desert shrubs had higher biomass production than other species. However, *A. tridentata*, *A. confertifolia*, and *E. nauseosa* showed no significant differences ($P > 0.05$) in biomass production among watering treatments despite some large differences

observed in the field (Table 2). Shrubs were not clearly responsive to watering treatments and were more drought tolerant than grasses. In 2009, the drier year, *A. tridentata* and *A. confertifolia* in control plots produced 35% as much biomass as produced in the watered plots. In 2009 we did not obtain reliable biomass production data for *G. lepidota*, *J. arcticus*, *E. nauseosa*, and *S. exigua* because of the dry conditions of the year and late harvest date (September). *Salix exigua* was completely lost from the control treatment during 2009 and it did not recover during 2010.

Juncus arcticus and *S. exigua* showed a trend of biomass gain related to the increase in watering levels in 2010 (Table 2). *Juncus arcticus* had four times more biomass production in the high-watering treatment than in the control. However, there was no difference between the control and the low and medium watering regimes. Similarly, *S. exigua* had more than six-times more biomass production in the high watering treatment than in the low-watering treatment, but there were no differences between the low-and medium-watering treatments. *Glycyrrhiza lepidota* did not show significant biomass production differences among treatments, in part because of high data variation due to missing replications. However, the general biomass response of this species was similar to that of *J. arcticus* and *S. exigua* in that high biomass resulted from the application of the high water treatment but little differences existed in the other treatments.

Salsola tragus did not successfully establish in the control treatments during either year. In 2009 the biomass production of this species was about three times higher in the high watering treatment compared to the medium-and low-treatments (Table 2). In 2010, production at the medium-watering level was significantly lower than production at the high-and low-watering levels.

3.3. Water-use efficiency

In contrast to biomass production, WUE was less than half ($P = 0.00$) in 2009 ($13,705 \text{ g g}^{-1}$) than in 2010 ($5,609 \text{ g g}^{-1}$) across all species and watering treatments. Although the responses varied by species, water-use efficiency of grasses generally

increased in response to the increase in watering levels in 2009. In contrast, WUE of grasses tended to decrease in response to increases in watering levels in 2010 (Table 3). In both years the WUE of grasses varied linearly ($P = 0.00$) with the variation in water received, but the slope was negative in 2009 and positive in 2010 (Fig. 3).

Spring water-use efficiency in 2010 varied by grass species ($P < 0.05$) (Fig. 4). These water-use efficiencies reflect grass growth stimulated only by natural precipitation from early March to late April and were not influenced by watering treatments. *Distichlis spicata* and *L. triticoides* had similar spring WUE (ca. 900 g g^{-1}) while *S. airoides* was about 30% more efficient. At the end of the 2010 growing season, the WUE of *D. spicata* and *S. airoides* in control plots was two to four times higher than that observed in the spring (Table 3, Fig. 4). In contrast, the WUE of *L. triticoides* at the end of the growing season in control plots was nearly two times lower than that observed in the spring.

Water-use efficiencies of *A. tridentata*, *A. confertifolia*, *E. nauseosa*, *S. exigua* and *G. lepidota* were not significantly affected ($P > 0.05$) by watering treatments (Table 3). *Juncus arcticus* in control plots had higher WUE than in the other watering treatments in 2010. *Salsola tragus* in 2009 was not affected by watering treatments. In 2010 this species had lower- WUE in the medium-watering level with respect to the low watering level, but the low-and high- watering levels were not different.

Water-use efficiency by species showed marked differences (Table 3). *Salix exigua*, *J. arcticus*, and *L. triticoides* were the least efficient species with average values (averaged across watering treatments and the two contrasting years of study) slightly over $20,000 \text{ g g}^{-1}$. *Distichlis spicata*, *S. airoides*, *G. lepidota*, and *A. confertifolia* were intermediate with average efficiency of nearly $6,000 \text{ g g}^{-1}$. The most efficient species were *S. tragus*, *E. nauseosa* and *A. tridentata* with average about $1,500 \text{ g g}^{-1}$.

3.4. Total standing crop and RSR

Total standing crop and RSR were unaffected by moisture levels ($P > 0.05$), but both varied by species ($P < 0.05$). *Salix exigua*, *L. triticoides*, *S. tragus* and *J. arcticus* constituted a group of species with low total standing crop (average 309 g m^{-2}), while in general the desert shrubs had higher total standing crop (Fig. 5). Within the desert shrubs, *A. tridentata* and *A. confertifolia* had about 50% higher total standing crop than *E. nauseosa*. The grass *D. spicata* was (572 g m^{-2}), in-between the low production group and the shrubs. Another grass, *S. airoides*, had the highest total standing crop overall. *S. airoides* produced more than three times the standing crop of *D. spicata* and more than seven times the standing crop of *L. triticoides*.

In general, the graminoids had larger RSR than other species (Fig. 6). *Juncus arcticus* and *S. airoides* had the highest RSR, with belowground biomass more than five times larger than aboveground biomass. The annual *S. tragus* had the lowest RSR, with belowground biomass accounting for less than 10% of aboveground biomass.

4. Discussion

4.1. Aboveground biomass production

The difference in biomass production between years was likely due to precipitation distribution; during 2010 there was more precipitation in spring and winter than during 2009. The April precipitation in 2010 (1.4 cm) was key for the difference because generally in this month plants begin active growth (in our study area). In 2009 there was a similar amount of precipitation in June, but in this month precipitation is much less efficient because of the high temperatures and the typical plant phenology in this area. Plant productivity in desert systems is a direct result of available water at particular points in time and timing differences in rainfall often have large consequences for the subsequent local biological season (Beatley, 1974).

Our watering treatments stimulated grass species growth differently in both years. The increase in grass growth resulting from water addition with respect to the control was much higher in 2009 than in 2010 because grasses in 2009 were more

water limited. In 2010 grasses had more water available in the spring and were less responsive to the addition of water. Similar responses have been reported for other desert grasses (Golluscio et al., 1998). The magnitude of physiological and growth responses to irrigation can be higher in plants that have previously experienced severe stress than in plants that have experienced mild or no stress (Xu et al., 2009). For *D. spicata*, in particular, receiving water after the wet 2010 spring made little difference in plant growth. *Leymus triticoides* had a larger biomass increase in response to watering than the other two grasses, suggesting that this species is more water-limited. In support of this experimental response, it has been reported that *L. triticoides* is usually distributed in microtopographical depressions where water tends to be more abundant (Mata-González et al., 2011). *Sporobolus airoides* was more responsive to water increases than *D. spicata* and less than *L. triticoides*, but overall *S. airoides* biomass production was the highest of the grasses. This is a robust plant that is adapted to arid environments, which offer advantages for forage production and habitat restoration in arid lands (Hickey and Springfield, 1966).

In contrast to grasses, aboveground biomass growth of desert shrubs was not responsive to water additions. Golluscio et al. (1998) reported a similar response in a Patagonian steppe. Similarly, Snyder et al. (2004) found that canopy growth of Great Basin shrubs was not affected by summer irrigation although all shrubs improved their water status and responded physiologically to the treatments. An explanation for the lack of growth response is that shrubs, which usually rely on deeper soil water sources, are not necessarily limited by water in deeper soil layers, even in drier years (Golluscio et al., 1998; Fernandez, 2007). It has been well documented that deep-rooted and woody perennial shrubs are less likely to use surface water from summer precipitation or irrigation than shallow-rooted herbaceous species (Ehleringer et al., 1991; Dodd et al., 1998). Other evidence suggests a complementary explanation. Dwyer and DeGarmo (1970) found in a greenhouse study (where deep roots and shallow roots should make little difference) that shrub production was not affected by different watering regimes, in contrast to grass production which was substantially

affected. Similarly, Mata-González et al. (2001) found no differences in *Atriplex canescens* shoot production grown in a greenhouse study under different water regimes. In general, shrubs are less affected than are grasses by water additions (Golluscio et al., 1998) probably because shrubs are overall less limited by water. This is possible because shrubs generally tend to have lower relative growth rates, lower photosynthetic rates, lower leaf nitrogen concentrations, and lower leaf turnover than grasses (Toft et al., 1989; Carrera et al., 2000). Another possible reason for the lack of response of the desert shrubs to watering in this study is that Great Basin shrubs are more limited by nitrogen than grasses during the summer, even under supplemental irrigation (James et al., 2005).

Juncus arcticus had large biomass production under the high watering treatment but it showed no differences in production from control to medium water levels. This species performs and competes well in wetland areas with high available water by displaying high photosynthesis rates and high water utilization (Svejcar and Riegel, 1998). On the other hand, it is also adapted to dry soils by exerting osmotic adjustment (Sala and Nowak, 1997). *J. arcticus* was less negatively affected by the low water conditions of the control treatment than *L. triticoides* and *S. exigua*, the other species usually found in wetland and riparian conditions in our study area. This dual adaptation of *J. arcticus* to both wetland and dry soil conditions was manifested in our study and previous reports (Mata-González et al., 2011). Similar to *J. arcticus*, *S. exigua* had higher production under the high water treatment, but unlike *J. arcticus*, *S. exigua* could not tolerate the water deficit in the control treatment and the plants did not survive the dry conditions of 2009. *S. exigua* is a common riparian species in western North America that is very sensitive to xylem cavitation and therefore very susceptible to drought stress (Amlin and Rood, 2002).

The annual *S. tragus* responded differently to watering levels between years. In 2009, the year with the dry winter and spring, the high watering treatment greatly increased biomass production with respect to low and medium irrigation. In the wet-spring year (2010) increasing the watering level did not result in significant production

increases, presumably because the plant was not as water limited as in 2009. Even for this annual, which was established in May and irrigated thereafter, the pattern of precipitation distribution in each year determined its productivity and response to watering. The wet winter and spring of 2010 likely resulted in soil water storage which probably diminished water stress for *S. tragus*. Supporting this, Pan et al. (2001) reported that this species typically develops deep roots (1.2 m), which is uncommon in many annuals. It is also possible that nutrients were more available in the 2010 growing season because of the higher available water. However, it is not clear why there was a decrease in production at the medium with respect to the low watering level.

4.2. Water-use efficiency

The low WUE observed in 2009 resulted from the low winter and spring precipitation in relation to 2010. Plants in the spring of 2009 were water-stressed and perhaps nutrient-stressed resulting in poor metabolic efficiency, which carried out the negative effects of the dry spring through the summer. These findings emphasize the importance of winter and spring precipitation in cool desert environments, where summer water availability is less significant (Beatley, 1974). Nevertheless, water addition through the summer benefited some of our species, mainly the herbaceous. This is in agreement with previous findings (Ehlereinger et al., 1991) and emphasizes the benefits to grasslands and pastures under a potential scenario of increasing summer precipitation in the Great Basin.

Two contrasting responses in WUE grasses were observed by year (Fig. 3). In 2009 WUE increased as water application increased while in 2010 WUE decreased as water application increased. In 2009 grass plants were likely severely stressed; control plants produced near zero biomass despite the June precipitation while plants under the watering treatments increased their biomass and their efficiency. In 2010 plants had better water conditions for growth. Spring WUE of grasses in 2010 was 600 to 900 g g⁻¹, much higher than the efficiency observed in grasses at the end of the

previous summer in 2009. Grasses efficiently utilized the available water in the spring of 2010 and although they responded in growth to summer watering, their efficiency greatly decreased through the summer. This pattern was also observed in *J. arcticus*. Two non-conflicting interpretations can be derived from this: 1) the physiology of grasses in our area is greatly affected by spring water conditions and 2) the efficiency of water utilization is low in both extremes of water availability.

The importance of spring growth may be beyond biomass production; studies reported that *D. spicata* had high leaf N concentration and high photosynthesis rates in spring and early summer and that both declined through the summer and early fall (Goedhart et al., 2010; James et al., 2005). The authors attributed such effects to the decline in surface soil N concentrations observed through the summer. Thus, our results suggest that plants would acquire the nutrients that would determine their future summer functioning in the spring because nutrient acquisition through the summer is less feasible.

Efficient water utilization can be restricted in both extremes of water availability (Dwyer and DeGarmo, 1970; Fuller, 1913). On the dry extreme plants may become physiologically impaired and nutrient limited such that water additions only result in minor increases in photosynthesis rates and biomass increases (Chapin, 1991; Chaves et al., 2003). On the wet extreme plants typically increase transpiration rates to a higher extent than photosynthesis or growth rates, resulting in higher water losses and lower efficiency (Toft et al. 1989; Trent et al. 1997). Studies have shown that grasses such as *S. airoides* have lower water requirements under moderate water stress than under no water limitations (Dwyer and DeGarmo, 1970; Montaña et al., 1988). The stomatal control that typically occurs under water limitations is responsible for this effect (Chaves et al., 2003).

There was large variation in the water-use efficiency of shrubs among the watering treatments, but no significant differences. A similar response was reported by Dwyer and DeGarmo (1970) for shrubs grown in greenhouse conditions under different irrigation regimes. Interestingly, in the same study those authors did find

differences in water-use efficiency of grasses related to differences in irrigation treatments. So, as previously discussed, it appears that shrubs are more variable in their response to water and less responsive to watering differences than grasses.

Salsola tragus did not show consistent trends in water-use efficiency associated with watering treatments. However, a marginal trend was observed in 2010 in which *S. tragus* was most efficient at the low water treatment than at higher watering levels (Table 3). Dwyer and Wolde-Yohannis (1971) showed that *Salsola kali*, also known as *S. tragus*, became more water efficient as available water was experimentally reduced in a greenhouse study. However, other reports have shown that this annual weed is highly variable and complex in its responses to available water, timing of precipitation, and other environmental variables (Beatley, 1974).

As expected, *S. exigua*, *J. arcticus* and *L. triticoides*, species that are usually distributed in wetlands and riparian corridors were the least efficient species in our study, utilizing 3 - 13 times more water for production than desert shrubs and grasses (Table 3). In the Owens Valley, *J. arcticus* is usually found in shallow groundwater areas (less than 1.5 m from the surface) and *L. triticoides* is mostly distributed in microtopographical depressions where water is more abundant (Mata-González et al., 2011). *Glycyrrhiza lepidota* is a C₃ plant usually found in wetlands, but its average water requirements were comparable to those of *S. airoides*, *D. spicata*, and *A. confertifolia*, which are drought tolerant, C₄ species. On the other extreme, the annual C₄ *S. tragus* and the desert shrubs *A. tridentata* and *E. nauseosa* had lowest water requirements overall. *Salsola tragus* is considered an efficient exotic weed that can outcompete native species especially under low soil water conditions (Allen, 1982; Dwyer and Wolde-Yohannis, 1971). *Artemisia tridentata* is generally considered drought tolerant but not necessarily efficient in water use compared to plants of similar environments (DeLucia and Schlesinger, 1991; Toft et al., 1989). However, Evans and Black (1993) pointed out that while *A. tridentata* has high water requirements in the spring it tends to be efficient during the summer when reproductive growth occurs. Our study extended throughout the summer and we did not distinguish between

vegetative and reproductive growth, but, overall, because of its high production (Table 2), *A. tridentata* was highly efficient in water use. *Ericameria nauseosa* is generally considered less tolerant to drought and equally efficient in water use than *A. tridentata* (Leffler et al., 2004; Mata-González et al., 2011).

4.3. Total standing crop and RSR

The lack of effect of the watering treatments on standing crop and RSR was unexpected, but the observations that standing crop can be less variable than annual biomass production (Kelly and Walker, 1976) helps to explain these results. Root-to-shoot ratios have been found to increase with decreasing available water (Sisson, 1989), but other reports have found no effect of water availability on RSR (Osorio et al., 1998), as observed in our study.

The riparian shrub *S. exigua* had lower standing crop than the desert shrubs, likely because it was limited by soil moisture and did not have access to groundwater (Amlin and Rood, 2002). The standing crop of *S. exigua* was not different from that of other typical wetland plants, *L. triticoides* and *J. arcticus*, even though these are herbaceous plants of lower stature. The annual *S. tragus* achieved a standing crop similar to the riparian/wetland species of the study. However, the standing crop of *S. tragus* was mainly concentrated aboveground (Fig. 6) while *L. triticoides* and *J. arcticus* had three to six times more biomass belowground than aboveground. Other researchers have reported low RSR for *S. tragus* (Dwyer and Wolde-Yohannis, 1971) and usually annual species have lower RSR than perennial species (Monaco et al., 2003). Surprisingly, the highest standing crop overall was observed in the grass *S. airoides*. This is a grass with high forage production (Hickey and Springfield, 1966) and yet its biomass is five times larger belowground than aboveground. This is an attractive native species to promote carbon sequestration while enhancing habitat suitability and forage base for herbivores.

The desert shrubs of our study had low RSR (< 1), similar to reports elsewhere (Wallace et al., 1974). In our study, roots were obtained to a depth of 1.5 m and

therefore our method was not able to recover deeper roots that can be found in desert shrubs. However, more than 95% of the root biomass in shrubs like *A. tridentata* may be found at the 0 - 1.5 m depth (Sturges and Trlica, 1978). In contrast to shrubs, the graminoids of our study had RSR of 3 to 6. Similarly, Köchy and Wilson (2000) reported several studies in which grasses had RSR of 6 while shrubs had RSR near 1. Because grasses tend to accumulate large pools of carbon belowground, grasslands and pastures are attractive biomes to favor carbon sequestration.

5. Summary

The response of plants to our watering treatments varied in the two years of study. In general, in 2009 plants produced less biomass and had lower water-use efficiency than in 2010. This was likely the result of different rainfall distribution in both years. In 2009 precipitation was lower in winter and spring than in 2010. Apparently this difference in precipitation made plants more efficient throughout the summer in 2010. In general, grasses increased production as a result of the increase in watering levels in both years, but the growth response to water addition with respect to the control was higher in 2009, the year plants were more stressed. Water-use efficiency of grasses linearly increased in 2009 but decrease in 2010 with the increase in water received, an opposite effect.

Desert shrub growth was not significantly affected by watering in both years likely because these shrubs were either not water limited or unable to obtain the additional water that was supplied through the summer. The lack of response of shrubs to summer watering has been reported in the Great Basin and other similar arid areas of the world (Ehleringer et al., 1991; Golluscio et al., 1998; Snyder et al. 2004). We concur with previous research suggesting that under the global change scenario of increasing summer precipitation in the Great Basin, herbaceous species would be better positioned to compete in the community than desert shrubs.

Our hypothesis that water-use efficiency would increase with the decreasing watering levels was only corroborated in 2010 and mainly for herbaceous species. But,

confirming our hypothesis, water-use efficiency varied greatly by species. Plants with highest water requirements, those traditionally considered wetland and riparian species, did utilize up to 13 times more water to produce a unit of aboveground biomass than plants with the lowest requirements, some desert shrubs and the annual *S. tragus*. Therefore, water use and biomass production would vary greatly in plant communities across the Owens Valley and this should be considered on planning allocation of water resources to vegetation.

Contrary to our expectation total standing crop and RSR were not influenced by watering treatment, but both variables varied by species. In general, desert shrubs achieved higher standing crop and lower RSR than herbaceous species. However, the grass *S. airoides* had the highest standing crop overall, mainly because its high root production ($RSR > 5$). *Sporobolus airoides* came across as an interesting species for several reasons: 1) it produces high amount of aerial biomass (forage), 2) it does so with relatively high water use efficiency, and 3) it can store large amounts of carbon belowground. Therefore, this is a species that offers great advantages from the production point of view as well as from conservation and environmental perspectives.

References

- Allen, E.D., 1982. Water and nutrient competition between *Salsola kali* and two native grass species (*Agropyron smithii* and *Bouteloua gracilis*). *Ecology* 63, 732-741.
- Amlin, N.M., Rood, S.B., 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands* 22, 338-346.
- Anderson, B.T., Roads, J.O., 2002. Regional simulation of summertime precipitation over the southwestern United States. *Journal of Climate* 15, 3321–3342.
- Beatley, J.C., 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55, 856-863.
- Brown, R.W., 1995. The water relations of range plants: Adaptations to water deficits, in: Bedunah, D.J., Sosebee, R.E., (Eds.), *Wildland Plants: Physiological Ecology and Development Morphology*. Society for Range Management, Denver, Colorado, USA, pp. 291-413.
- Carrera, A.L., Sain, C.L., Bertiller, M.B., 2000. Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. *Plant and Soil* 224:185–193.
- Chapin, E.S., 1991. Effects of multiple environmental stresses on nutrient availability and use, in: Mooney, H.A., Winner, W.E., Pell, E.J., (Eds.), *Response of plants to multiple stresses*. Academic Press, San Diego, California, USA, pp. 68-88.
- Chaves, M.M., Maroco, J.P., Pereira, J.S., 2003. Understanding plant response to drought: From genes to the whole plant. *Functional Plant Biology* 30, 239–264.
- DeLucia, E.H., Schlesinger, W.H., 1991. Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology* 72, 51-58.

- Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life forms in a shortgrass steppe community. *Oecologia* 117, 504-512.
- Dwyer, D.D., DeGarmo, H.C., 1970. Greenhouse productivity and water-use efficiency of selected desert shrubs and grasses under four soil-moisture levels. Bulletin 570. New Mexico State University, Agriculture Experiment Station. Las Cruces, NM, USA.
- Dwyer, D.D., Wolde-Yohannis, K., 1971. Germination, emergence, water use, and production of Russianthistle (*Salsola kali* L.). *Agronomy Journal* 64, 52-55.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. *Oecologia* 8, 430-434.
- 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.
- Evans, R.D., Black, R.A., 1993. Growth, photosynthesis, and resource investment for vegetative and reproductive modules of *Artemisia tridentata*. *Ecology* 74, 1516-1528.
- Fernandez, R.J., 2007. On the frequent lack of response of plants to rainfall events in arid areas. *Journal of Arid Environments* 68, 688–691.
- Fuller, G.D., 1913. Water requirement of plants. *Botanical Gazette* 56, 514-515.
- 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.
- Goedhart C.M., Pataki, D.E., 2011. Ecosystem effects of groundwater depth in Owens Valley, California. *Ecohydrology* 4, 458-468.
- Golluscio, R.A., Sala, O.E., Lauenroth, W.K., 1998. Differential use of large summer rainfall events by shrubs and grasses: A manipulative experiment in the Patagonian steppe. *Oecologia* 115, 17–25.

- Hickey, W.C., Springfield, H.W., 1966. Alkali sacaton: its merits for forage and cover. *Journal of Range Management* 19, 71-74.
- Hsiao, T.C., Xu, L.K., 2000. Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. *Journal of Experimental Botany* 51, 1595–1616.
- James, J.J., Richards, J.H., 2005. Plant N capture from pulses: Effects of pulse size, growth rate, and other soil resources. *Oecologia* 145, 113–122.
- Kelly, R.D., Walker, B.H., 1976. The effects of different forms of land use on the ecology of a semi-arid region in south-eastern Rhodesia. *Journal of Ecology* 64, 553-576.
- Köchy, M., Wilson, S.D., 2000. Competitive effects of shrubs and grasses in prairie. *Oikos* 91, 385-395.
- Leffler, J.A., Ivans, C.Y., Ryel, R.J., Caldwell, M.M., 2004. Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow vs. deep soil water in a glasshouse experiment. *Environmental and Experimental Botany* 15, 9-19.
- Le Houerou, H.N., Bingham, R.L., Skerbek, W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15, 1–18.
- Le Maitre, D.C., Scott, D.F., Colvin, C., 1999. A review of information on interactions between vegetation and groundwater. *Water SA* 25, 137–151.
- Loik, M.E., 2007. Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecology*, 191, 95–108.
- Mata-González, R., Meléndez-González, R., Martínez-Hernández, J.J., 2001. Aerial biomass and elemental changes in *Atriplex canescens* and *A. acanthocarpa* as affected by salinity and soil water availability, in: McArthur, E.D., Fairbanks, D.J. (Comps.), *Shrubland Ecosystem Genetics and Biodiversity: Proceedings*

- RMRS-P-21. U.S.D.A. Forest Service Rocky Mountain Research Station, Ogden, UT, USA, pp. 308–311.
- Mata-González, R., Sosebee, R.E., Wan, C. 2002. Physiological impacts of biosolids application in desert grasses. *Environmental and Experimental Botany* 48, 139-148.
- Mata-González, R., Hunter, R.G., Coldren, C.L., McLendon, T., Paschke, M. 2008. A comparison of modeled and measured impacts of resource manipulations for control of *Bromus tectorum* in sagebrush steppe. *Journal of Arid Environments* 72, 836-846.
- Mata-González, R., McLendon, T., Martin, D.W., Trlica, M.J., Pearce, R., 2011. Vegetation as affected by groundwater depth and microtopography in a shallow aquifer area of the Great Basin. *Ecohydrology* In press, doi:10.1002/eco.196.
- McLendon, T., Hubbard, P.J., Martin, D.W., 2008. Partitioning the use of precipitation- and groundwater-derived moisture by vegetation in an arid ecosystem in California. *Journal of Arid Environments* 72, 986-1001.
- Monaco, T.A., Johnson, D.A., Norton, J.M., Jones, T.A., Connors, K.J., Norton, J.B., Redinbaugh, M.B., 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management* 56, 282–290.
- Montaña, C., Floret, C., Cornet, A. 1988. Water use efficiency and biomass production of two perennial grasses from the Chihuahuan Desert (Mexico). In: *Range Management Society of India (Ed.), Third International Rangeland Congress Abstracts Vol. 1. Range Management Society of India, New Dehli*, pp. 240-243.
- Naumburg, E., Mata-González, R., Hunter, R.G., McLendon, T., Martin, D.W., 2005. Phreatophytic vegetation and groundwater fluctuations: A review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. *Environmental Management* 35, 726-740.

- Osório, J., Osório, M.L., Chaves, M.M., Pereira, J.S. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. *Tree Physiology* 18 (6), 363-373.
- Pan, W.L., Young, F.L., Bolton, R.P., 2001. Monitoring Russian thistle (*Salsola iberica*) root growth using a scanner-based, portable mesorhizotron. *Weed Technology* 15, 762–766.
- Patten, D.T., Rouse, L., Stromberg, J.C., 2008. Isolated spring wetlands in the Great Basin and Mojave Deserts, USA: Potential response of vegetation to groundwater withdrawal. *Environmental Management* 41, 398–413.
- Sala, A., Nowak, R.S., 1997. Ecophysiological responses of three riparian graminoids to changes in the soil water table. *International Journal of Plant Sciences* 158, 835–843.
- Shantz, H.L., Piemeisel, L.N., 1927. The water requirement of plants at Akron, Colorado. *Journal of Agricultural Research* 34, 1093-1190.
- Sisson, W.B., 1989. Carbon balance of *Panicum coloratum* during drought and non-drought in the northern Chihuahuan Desert. *Journal of Ecology* 77, 799–810.
- Snyder, K.A., Donovan, L.A., James, J.J., Tiller, R.L., Richards, J. H., 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia* 141, 325-334.
- Sturges, D.L., Trlica, M.J., 1978. Root weights and carbohydrate reserves of big sagebrush. *Ecology* 59, 1282-1285.
- Svejcar, T., Riegel, G.M., 1998. Spatial pattern of gas exchange for montane moist meadow species. *Journal of Vegetation Science* 9, 84–94.
- Toft, N.L., Anderson, J.E., Nowak, R.S., 1989. Water use efficiency and carbon isotope composition of plants in a cold desert environment. *Oecologia* 80, 11-18.
- Trent, I.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.

- Wallace, A., Bamberg, S.A., Cha, J.W., 1974. Quantitative studies of perennial plants in the Mojave Desert. *Ecology* 55, 1160–1162.
- USDA, 2010. Keys to Soil Taxonomy. Natural Resources Conservation Service, US Department of Agriculture, Washington D C.
- WRB, 2007. World Reference Base for Soil Resources, World Soil Resources Report, Vol. 103; FAO: Rome, 2007.
- Xu, Z.Z, Zhou, G.S., Shimizu, H., 2009. Are plant growth and photosynthesis limited by pre-drought following rewatering in grass? *Journal of Experimental Botany* 60, 3737-3749.
- Zhu, Y., Wua, Y., Drake, S., 2004. A survey: Obstacles and strategies for the development of ground-water resources in arid inland river basins of western China. *Journal of Arid Environments* 59, 351–367.

Tables

Table 1. Plant species included in the study.

Species	Life form	Life cycle
<i>Distichlis spicata</i> L. Greene	Grass	Perennial
<i>Leymus triticoides</i> (Buckley) Pilg.	Grass	Perennial
<i>Sporobolus airoides</i> (Torr.) Torr.	Grass	Perennial
<i>Glycyrrhiza lepidota</i> Pursh	Forb	Perennial
<i>Juncus arcticus</i> Willd ¹ .	Forb	Perennial
<i>Salsola tragus</i> L.	Forb	Annual
<i>Artemisia tridentata</i> Nutt.	Shrub	Perennial
<i>Atriplex confertifolia</i> (Torr. & Frem.) S. Wats.	Shrub	Perennial
<i>Ericameria nauseosa</i> (Pall. ex Pursh) G.L. Nesom & Baird ²	Shrub	Perennial
<i>Salix exigua</i> Nutt.	Shrub/tree	Perennial

¹Previously known as *Juncus balticus*; ²Previously known as *Chrysothamnus nauseosus*

Table 2. Aerial biomass production (g m^{-1}) by species, year of study, and watering treatment in Owens Valley, CA. Species are ordered from more to less productive according to their average production across years and watering treatments.

Species	Year	Watering treatment			
		Control	Low	Medium	High
		(g m ⁻¹)			
<i>Atriplex confertifolia</i>	2009	81 a	181 a	206 a	235 a
	2010	690 a	435 a	875 a	848 a
<i>Artemisia tridentata</i>	2009	115 a	443 a	221 a	371 a
	2010	374 a	413 a	492 a	348 a
<i>Ericameria nauseosa</i>	2009	NA	NA	NA	NA
	2010	191 a	405 a	189 a	413 a
<i>Sporobolus airoides</i>	2009	2 a	121 b	128 bc	205 c
	2010	265 a	320 ab	399 bc	445 c
<i>Salsola tragus</i>	2009	NA	57 a	64 a	189 b
	2010	NA	337 a	254 b	465 a
<i>Salix exigua</i>	2009	NA	NA	NA	NA
	2010	NA	33 a	68 a	191 b
<i>Juncus arcticus</i>	2009	NA	NA	NA	NA
	2010	40 a	49 a	79 a	160 b
<i>Glycyrrhiza lepidota</i>	2009	NA	NA	NA	NA
	2010	38 a	53 a	69 a	150 a
<i>Distichlis spicata</i>	2009	4 a	18 ab	28 b	53 c
	2010	132 ab	107 a	121 a	155 b
<i>Leymus triticoides</i>	2009	0 a	8 a	10 a	25 b
	2010	21 a	83 b	92 b	121 b

*Different letters following an average indicate differences ($P < 0.05$) between watering treatments within a given species and year. NA = data not available.

Table 3. Water-use efficiency (g g^{-1}) by species, growing season (year), and watering treatments in Owens Valley, CA. Water-use efficiency represents grams of water received divided by grams of aerial biomass produced in each plot per season. Species are ordered from higher to lower water requirements (less efficient to more efficient species) averaged across years and watering treatments.

Species	Year	Watering treatment			
		Control	Low	Medium	High
(g g ⁻¹)					
<i>Salix exigua</i>	2009	NA	NA	NA	NA
	2010	NA	52,520 a	17,599 a	9,564 a
<i>Juncus arcticus</i>	2009	NA	NA	NA	NA
	2010	1,403 a	29,328 b	25,946 b	17,032 b
<i>Leymus triticoides</i>	2009	NA	53,879 a	30,736 a	17,625 a
	2010	1,641 a	2,312 a	4,420 b	4,913 b
<i>Distichlis spicata</i>	2009	29,996 a	8,606 b	9,918 b	10,048 b
	2010	236 a	1,157 b	1,925 c	2,428 c
<i>Sporobolus airoides</i>	2009	30,924 a	2,476 b	3,754 b	3,776 b
	2010	256 a	662 b	1,074 c	1,448 d
<i>Glycyrrhiza lepidota</i>	2009	NA	NA	NA	NA
	2010	1,626 a	5,594 a	8,009 a	4,313 a
<i>Atriplex confertifolia</i>	2009	2,894 a	6,794 a	10,873 a	8,330 a
	2010	200 a	2,334 a	1,673 a	2,041 a
<i>Salsola tragus</i>	2009	NA	3,132 a	5,031 a	2,624 a
	2010	NA	386 a	1,556 b	814 ab
<i>Ericameria nauseosa</i>	2009	NA	NA	NA	NA
	2010	466 a	2,787 a	1,637 a	942 a
<i>Artemisia tridentata</i>	2009	298 a	314 a	1,782 a	992 a
	2010	105 a	311 a	399 a	1,216 a

*Different letters following an average indicate differences ($P < 0.05$) between watering treatments within a species and year. NA = data not available.

Figures

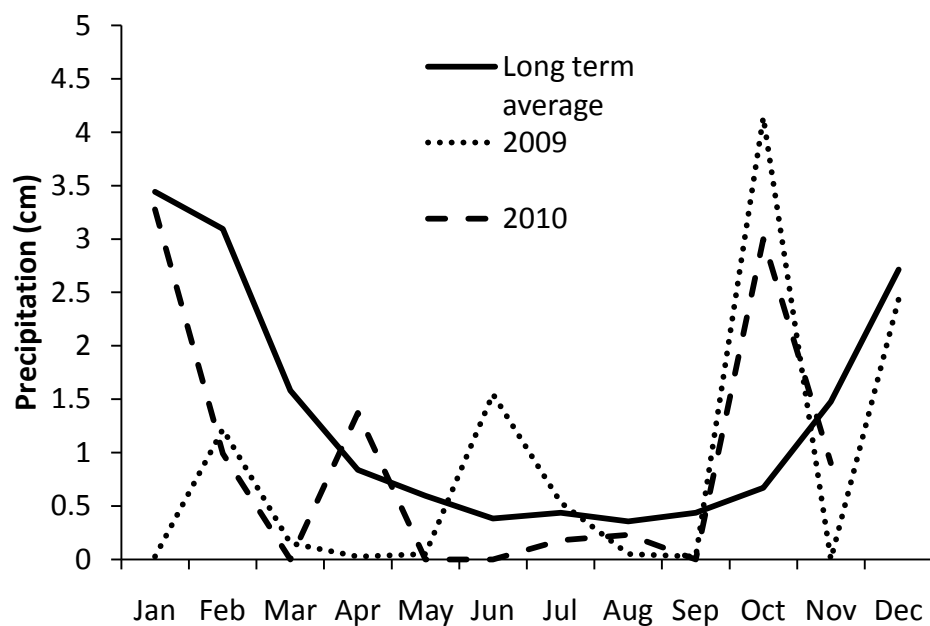


Figure 1. Monthly precipitation of the study area in the two years of study, 2009 and 2010, and the long-term average (1931 - 2009). Data obtained from a weather station located 8 km from the study area in Bishop, CA. Precipitation of December of 2010 (13.7 cm) was omitted in the graph for clarity purposes.

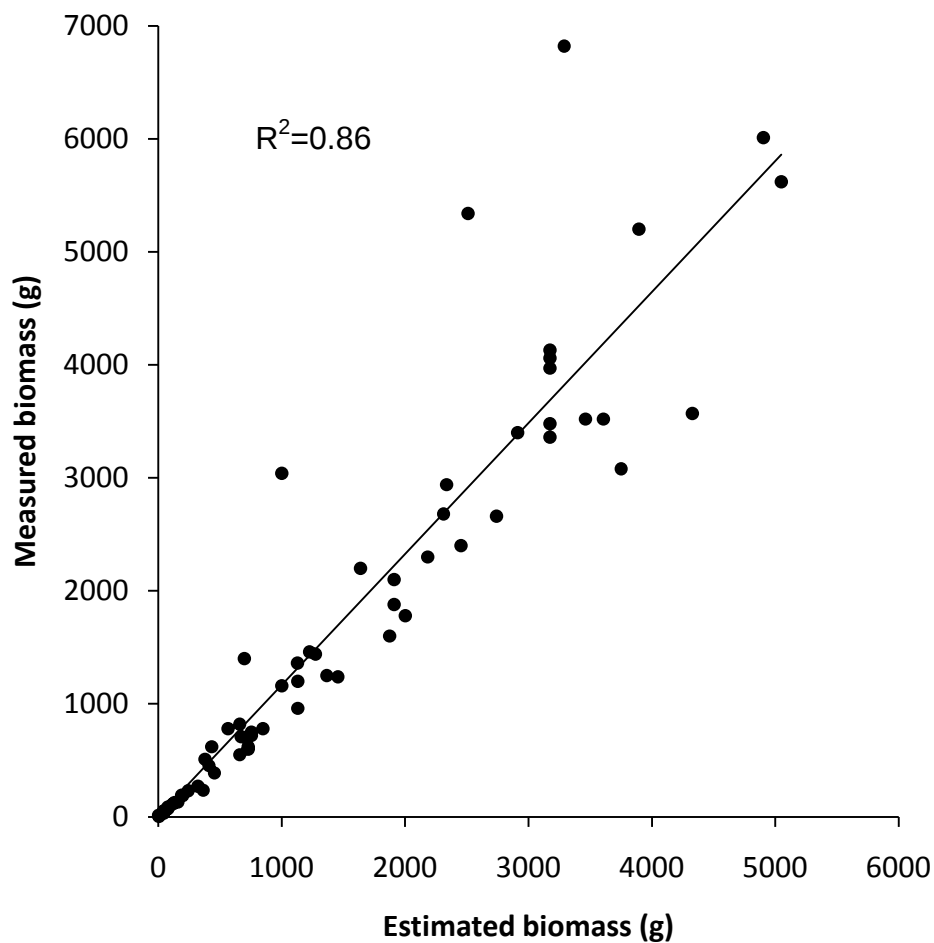


Figure 2. Relationship between weighed and estimated biomass of different shrub species in Owens Valley, CA. The species included are *Artemisia tridentata*, *Atriplex confertifolia*, *Ericameria nauseosa*, and *Salix exigua*. $Y = 1.159X + 6.856$; $P = 0.00$.

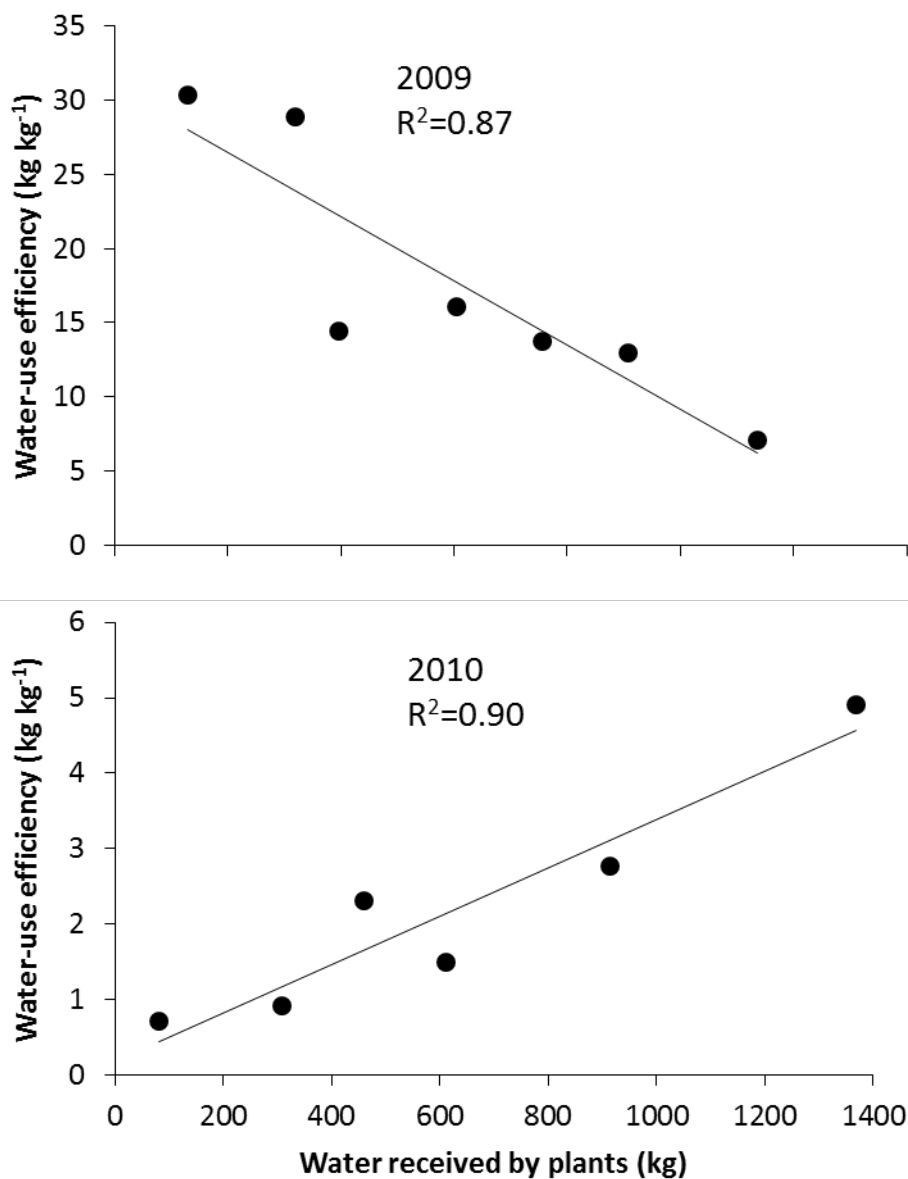


Figure 3. Water-use efficiency (kg kg⁻¹) of grasses in two different years as affected by amount of water received. Water-use efficiency represents kg of water received divided by kg of aerial biomass produced per plot. The grasses included are *Distichlis spicata*, *Leymus triticoides*, and *Sporobolus airoides*. For 2009 $Y = -0.022X + 30.80$; $P = 0.00$. For 2010 $Y = 0.003X + 0.19$; $P = 0.00$.

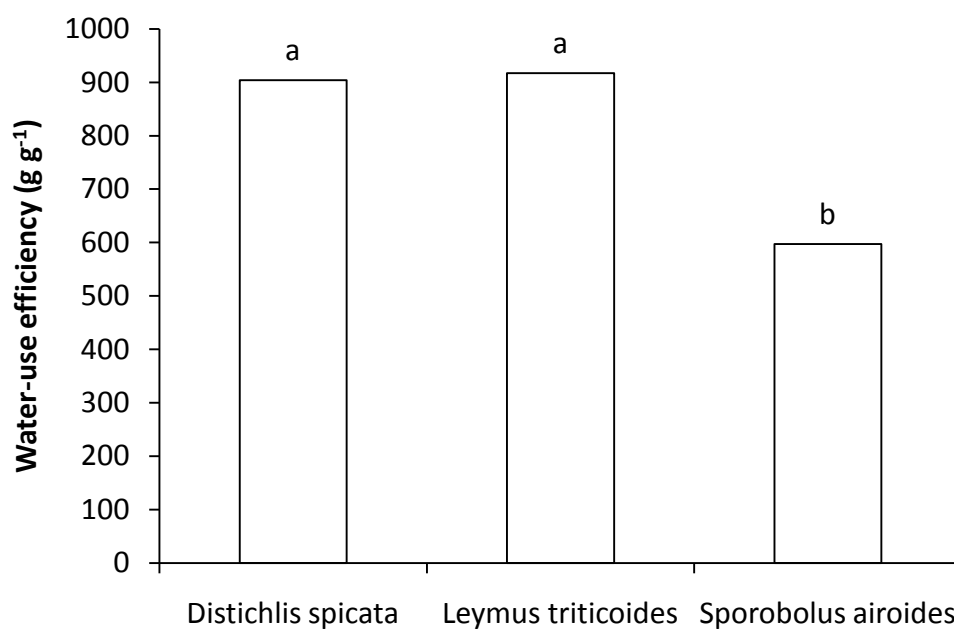


Figure 4. Spring water-use efficiency (g g⁻¹) of the three grasses of the study. These averages reflect water-use efficiency of plants from early March to late April. Water-use efficiency represents grams of water received divided by grams of aerial biomass produced per plot. Different letters above columns indicate significant differences between species at $P < 0.05$.

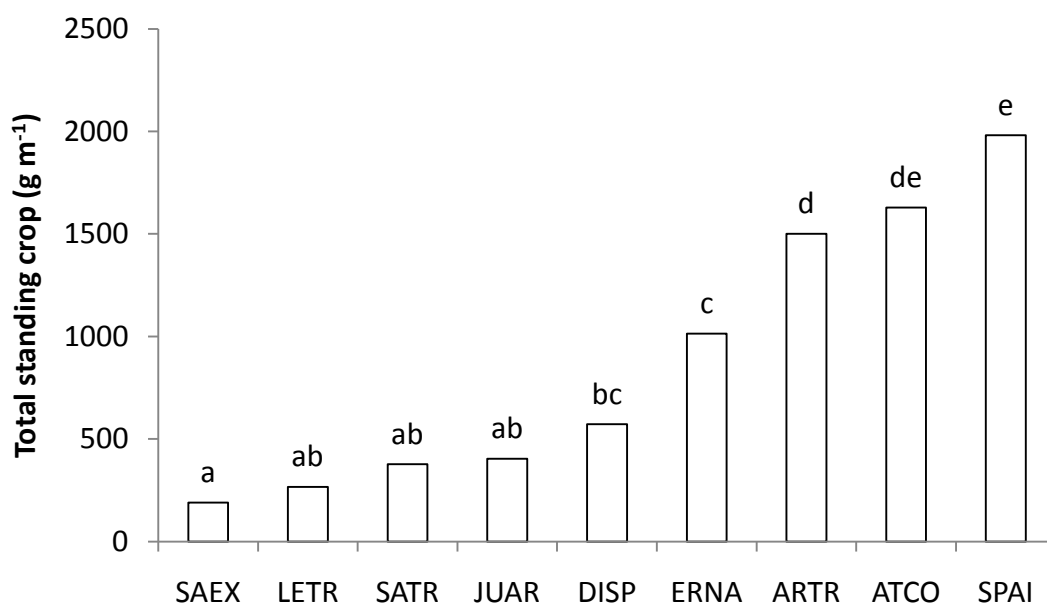


Figure 5. Total standing crop (g m^{-1}), including aboveground and belowground biomass, by species averaged across watering treatments at the end of the 2010 growing season. Species key: SATR, *Salsola tragus*; ARTR, *Artemisia tridentata*; ATCO, *Atriplex confertifolia*; ERNA, *Ericameria nauseosa*; SAEX, *Salix exigua*; LETR, *Leymus triticoides*; DISP, *Distichlis spicata*; SPAI, *Sporobolus airoides*; and JUAR, *Juncus arcticus*. Data was not obtained for *Glycyrrhiza lepidota*. Different letters above columns indicate significant differences between species at $P < 0.05$.

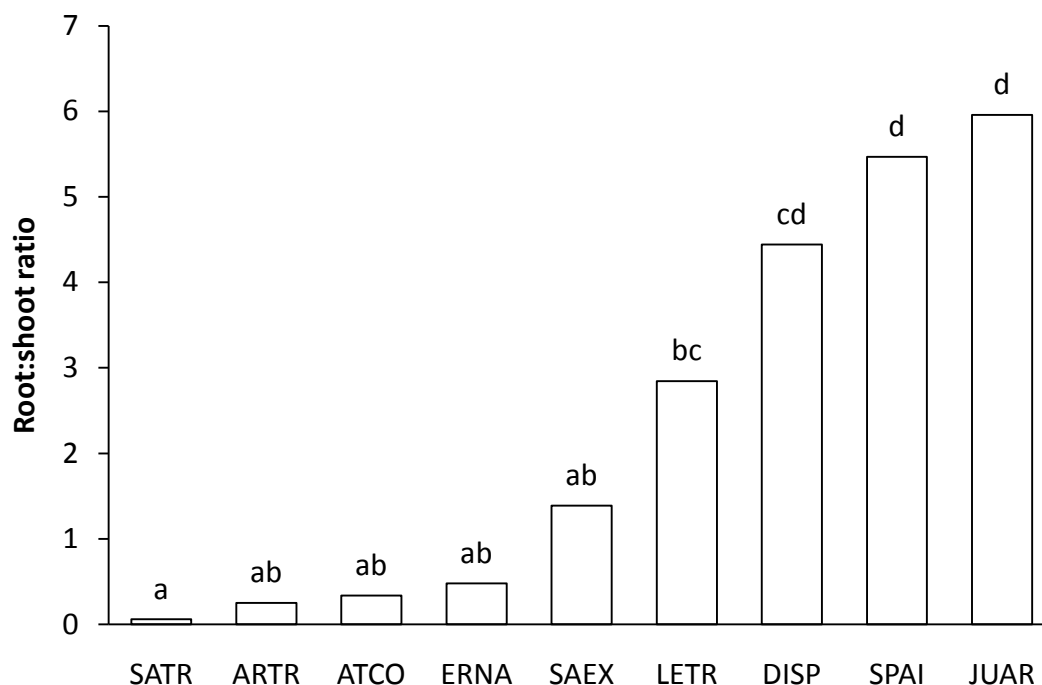


Figure 6. Root:shoot ratio (RSR) by species averaged across watering treatments at the end of the study in 2010. Species key: SATR, *Salsola tragus*; ARTR, *Artemisia tridentata*; ATCO, *Atriplex confertifolia*; ERNA, *Ericameria nauseosa*; SAEX, *Salix exigua*; LETR, *Leymus triticoides*; DISP, *Distichlis spicata*; SPAI, *Sporobolus airoides*; and JUAR, *Juncus arcticus*. Data was not obtained for *Glycyrrhiza lepidota*. Different letters above columns indicate significant differences between species at $P < 0.05$.

Water use characteristics of Great Basin plants under different summer watering levels

T. L. Evans, R. Mata-González, D. W. Martin, T. McLendon

Abstract

We examined water use of common plants in the Owens Valley, California. The species studied were the grasses *Distichlis spicata*, *Leymus triticoides*, and *Sporobolus airoides*, the forbs *Glycyrrhiza lepidota*, *Juncus arcticus*, and *Salsola tragus* (annual), the desert shrubs *Artemisia tridentata*, *Atriplex confertifolia*, and *Ericameria nauseosa*, and the riparian shrub *Salix exigua*. Three water treatments were applied monthly: low (1.3 cm), medium (2.6 cm), and high (3.9 cm) during the summer months. Plant water use was determined by calculating soil water depletion during irrigation cycles using time domain reflectometry (TDR) at two depths (0 - 25 cm and 0 - 50 cm) in vegetated plots. Evaporation amounts were also obtained from bare ground plots and subtracted from evapotranspiration to calculate water use. Water use varied by species; those with shallow, fibrous, and rhizomatous root systems such as *J. arcticus* and *L. triticoides* had higher water use than shrubs, including the riparian *S. exigua*. A potential increase in summer precipitation in the area might favor water utilization by shallow-rooted plants with high root-to-shoot ratio. Shrubs relied more on deeper water sources than herbaceous species, implying that shrubs can be more dependent on groundwater than grasses.

1. Introduction

Owens Valley, CA is an arid environment with a shallow aquifer due to runoff from the surrounding Sierra Nevada Mountains. Vegetation in this area is typical of the Great Basin, with plants highly adapted to arid conditions, but also dependent to some degree on water from the shallow aquifer (McLendon et al., 2008; Naumburg et al., 2005; Goedhart and Pataki, 2011). Plants in this region are drought tolerant and some may suffer from minor biomass loss to considerable dieback during extended periods without groundwater (Naumburg et al., 2005). It is increasingly clear that plants in shallow aquifer areas such as the Owens Valley can rely on both groundwater and topsoil water (McLendon et al., 2008), but studies on plant use of topsoil water are lacking.

This study focused on water-use characteristics of plants during the summer because some climate change models suggest potential alterations to the distribution and seasonality of precipitation in areas such as the Great Basin, where precipitation is normally concentrated in the spring (Anderson and Roads, 2002). This has motivated a number of studies to investigate potential vegetation responses to increasing summer precipitation in the Great Basin (Ehleringer et al., 1991; Loik, 2007; Snyder et al., 2004; Gillespie and Loik, 2004).

Summer precipitation events differ from winter and spring precipitation events. Summer events normally do not go deep into the soil column (Sala and Lauenroth, 1982) and depending on the evaporative demand and water event size the summer precipitation water can be present in the soil column from a few hours to weeks (Sala et al., 1981). In contrast, winter and spring precipitation events are characterized as gentle rains that allow deeper penetration due to the reduced evaporation and transpiration losses that are possible under cooler temperatures (Caldwell, 1985). Phenology also plays an important role on a plant's ability to utilize summer precipitation; shallow active roots will enable the plant to use this water source (Donovan and Ehleringer, 1994) but some studies have found that certain deep-rooted species have inactive shallow root systems in the summer, therefore surface water is

not utilized (Ehleringer et al., 1991; Flanagan and Ehleringer, 1991). While rooting distribution indicates the soil volume potentially available for plant use, actual uptake is dependent on root activity in soil areas where the moisture is available (Donovan and Ehleringer, 1994).

Different techniques have been used in arid regions such as the Owens Valley to estimate landscape-level evapotranspiration, including remote sensing, micrometeorological techniques, and transpiration coefficient methods (Mata-González et al., 2005; Steinwand et al., 2006). Leaf-level transpiration has also been commonly determined by porometry (Groeneveld and Warren, 1992). However, water use at the scale of individual plants has not been studied in the Owens Valley. Water use of individual plants is important to predict plant water relations as affected by competition and to evaluate effects of available water on species populations (Wan et al., 1993a; Wan et al., 1993b).

The objective for this study was to determine water-use characteristics of ten dominant species of the Owens Valley at different soil depths in response to simulated rainfall applications in the summer. We determined water use as the amount of soil water depleted by plants over time using time domain reflectometry. Given the diversity of plant characteristics involved in the species of this study we hypothesized that 1) plant water use will vary among species, 2) species would rely on different proportions of shallow and deeper soil water, and 3) plant water use and soil evaporation would increase with increasing water applications. Information on this topic should be useful to better understand plant water utilization and to incorporate better practices of groundwater management that protect vegetation.

2. Site Description and Methods

2.1. Site Location and Description

The study area was located in Owens Valley, CA, which has a climate characterized by hot and dry summers and cold and relatively moist winters. The area receives between 13 - 17 cm of annual precipitation, with 77% of it occurring from

November to March and 23% from April to October. Despite the low rainfall, groundwater is abundant in the valley because of the high recharge from the surrounding mountains. The water table in the valley floor is between 0 to 10 m deep (McLendon et al., 2008). The project site (37° 20' 3.68" N, 118° 18' 23.98" W) was located on Los Angeles Department of Water and Power (LADWP) property, about 8 km west of Bishop, CA (Fig. 1). This site, which has groundwater depth in excess of 6 m, was selected to prevent groundwater from being a confounding factor. It was abandoned agricultural land dominated by weedy annual species prior to the implementation of this project. Precipitation data for this site was obtained from a weather station located in Bishop, CA. The project site is located on a Yermo very gravelly sandy loam soil series. Soils of this type are calcareous, thermic Typic Torriorthents (USDA, 2010) and Haplic Regosols (Calcic, Aridic) (WRB, 2007). The texture of the soil (0 – 40 cm depth) is Loamy Sand (80% sand, 16% silt, 4% clay). The bulk density for 0-30 cm depth is 1.5 and for 30-60 cm depth is 1.6. The average pH is 8.1, the electrical conductivity is 0.4 dS m⁻¹, and the organic matter content is 1.4% at the depth of 0 - 40 cm.

2.2. Experimental Procedure

Ten of the most abundant plant species in the Owens Valley were used for this study (Table 1). Plants of individual species were grown in the field in a common garden in 2.4 m X 2.4 m plots. Plots were separated by a sheet of 1.3 cm thick plywood buried to a depth of 1.2 m to reduce the possibility of one treatment affecting another and to reduce root proliferation into adjacent plots.

Plot establishment began in 2005 and evaluations for this experiment were conducted during the summer of 2010. Some species were established from locally collected seed, but most were transplanted as young plantlets from adjacent areas. *D. spicata* and *L. triticoides* are sod-forming, rhizomatous grasses that were established from the center of the plots and achieved 40% – 50% cover inside the plots. *J. arcticus* is also a sod forming grass-like plant that was established similar to *D. spicata* and *L.*

triticoides and reached 10% cover. *S. airoides* is a bunchgrass that was established by planting four plants per plot and reached about 25% of cover. Four plants of each of *A. tridentata*, *E. nauseosa*, *G. lepidota*, *A. confertifolia*, and *S. exigua* were planted per plot. *Artemisia tridentata* and *E. nauseosa* established the most successfully but establishment success varied greatly for the other species. *Salsola tragus* is an annual forb that was established using plantlets from adjacent areas in May. This species was not successfully established in the control plots. During the period of establishment and throughout the experiment the plants were irrigated and maintained free of weeds to ensure maximum establishment. The experimental design consisted of three treatments (watering levels) with 6 replications (blocks) of each treatment. Each treatment X species combination was randomly assigned to a plot and each block contained all the treatments.

2.3. Treatment Application

The three water treatments simulated different amounts of summer rainfall. They were: 1) low, 2) medium, and 3) high. The low irrigation treatment consisted of adding enough water to the plots to account for 1.3 cm of water including irrigation and the natural precipitation that the plots might have received during the month. If 1.3 cm or more of precipitation was received during the month, no irrigation was supplied to the low irrigation treatment plots that month. The amount of total water received by plants either by natural precipitation or irrigation was recorded. The medium irrigation treatment consisted of adding enough water to equal 2 times the moisture received on the low irrigation treatment plots. The high irrigation treatment plots received sufficient irrigation to equal 3 times the moisture (precipitation and irrigation) received on the low irrigation plots. We used tap water from Bishop, CA, which was transported to the study site and deposited in large storage tanks. According to the City of Bishop, this water complies with the primary drinking water standards established by USEPA, has very low levels of salinity and total dissolved solids, and an undetected concentration of nitrates. A water meter (Sensus Invensys

SR II positive displacement, Sensus, Raleigh, NC) attached to a water hose and a sprinkler head was used to carefully measure the water volume output onto every plot.

2.4. Soil Moisture Measurements

Soil volumetric water content was monitored by time domain reflectometry (TDR) (Topp and Davis, 1985) during the summer of 2010. Stainless steel paired rods of 3.2 mm in diameter were used as TDR probes. Parallel pairs of rods, 5 cm apart, were vertically inserted to a depth of 25 cm and 50 cm in each plot. In plots containing shrubs and forbs the rods were placed underneath the plant canopy, close to the main trunk of one of the plants per plot. In plots containing grasses the rods were placed near the center of the grass sward. TDR readings were obtained with a Tektronix1502C TDR cable tester (Tektronix, Beaverton, OR) connected to the rods as in Wan et al. (1993b). The TDR pulse readings were converted to a dielectric constant (K) and volumetric water content (Q) was calculated using an empirical equation $Q = -0.053 + 0.0292K - 0.00055K^2 + 0.0000043K^3$ (Topp et al., 1980). The volumetric water content information obtained with the TDR was adjusted against water content attained gravimetrically as in Wan et al. (1993b).

Soil volumetric water content was measured in each plot from early June to late August before and after each irrigation period (monthly). This information illustrated how much soil water was lost to evapotranspiration one month after the water treatments were applied. Rods were also installed at the same depths in plots containing no plants to monitor water content change (evaporation) with no plant involvement. The evaporation plots were replicated within the same blocks as the vegetative plots. Plant water use (soil water depletion) was calculated by subtracting the soil water content obtained about one month following irrigation to the initial water content obtained one day after irrigation in the vegetative plots.

The calculated water use (evapotranspiration) was corrected by subtracting the amount of water evaporated during the same period obtained for the bare ground plots (Stroosnijder, 1987; Sturges, 1977). The water use reported here is the average of two

soil water depletion periods, June to July and July to August. Our soil water depletion approach to estimate plant water use assumes that soil water losses were due to transpiration and evaporation and that water seepage was negligible (Sturges 1977). For this we measured initial soil water content 24 hours after applying the watering treatments, after most downward water movement had occurred and field capacity has been reached, especially in sandy soils (Brady and Weil, 1996; Stroosnijder, 1987). The ratio of deep water use to shallow water use was calculated in each plot as:

$$\frac{\text{Deep water use (0 - 50 cm)} - \text{Shallow water use (0 - 25 cm)}}{\text{Shallow water use (0 - 25 cm)}}$$

Plants were harvested to ground level in late August to determine aboveground standing crop. Following that, root standing crop was determined by using an excavator digging to approximately 1.5 m to extract the soil cores containing the roots in each plot. In this study, roots were considered to be any belowground biomass since we clipped at ground level to obtain aboveground biomass. Roots were initially separated from the soil by sifting with 0.5 cm mesh screens and subsequently washed with water to remove the remaining attached soil. Root materials were then oven dried and weighed. Because this process was labor intensive, only three treatment replications were sampled. Root-to-shoot ratio (RSR) was calculated as belowground standing crop / aboveground standing crop.

2.5. Description of Analysis

A two-way analysis of variance (ANOVA) was used to test differences by watering treatments and species. Significant differences between treatments and species were determined by LSD at $P < 0.05$. Regression analyses were also used to find potential relationships between some variables at $P < 0.05$.

3. Results

The interaction of species and water treatments was not significant ($P > 0.05$), but water use significantly differed by both species and water treatments. In general, the three grasses of the study, *S. airoides*, *D. spicata*, and *L. triticoides*, as well as *J. arcticus* obtained more water from the 0 - 25 cm depth than the shrubs and forbs (Fig. 1). Water use at this depth was not significantly different among shrubs and forbs ($P > 0.05$), but unexpectedly, in plots occupied by the desert shrubs *E. nauseosa*, *A. confertifolia* and *A. tridentata* there was a small net water gain instead of water depletion. With respect to their differences in water use at the 0 - 50 cm depth plant species can be grouped into three general categories: species with high water use (*D. spicata*, *L. triticoides* and *J. arcticus*), species with intermediate water use (*S. tragus*, *S. exigua*, and *S. airoides*) and species with low water use (*E. nauseosa*, *A. confertifolia*, *A. tridentata*, and *G. lepidota*). Species with high water use utilized in average two times more water than species with intermediate water use and 11 times more water than those with low water use.

Plant water use significantly varied ($p < 0.05$) by watering treatment regardless of species (Fig. 2). As the watering levels increased, plant water use from the 0 - 50 cm depth increased. In contrast, as the watering levels increased plant water use at the 0 - 25 cm depth decreased. Therefore, water extraction from the 0 - 50 cm depth was 12 times higher than from the 0 - 25 cm depth in plants under the high watering treatment, while in plants under the medium watering treatment it was 3.5 times higher and in plants under the low watering treatments it was only 0.57 times higher.

The ratio of deep water (25 - 50 cm) to shallow water (0 - 25 cm) use by the different species was investigated (Fig. 3). All the species in the study used more deep water than shallow soil water. *S. airoides* had the lowest ratio (1.3) indicating that this species used similar amounts of water from shallow and deep sources. *Sporobolus airoides*, *G. lepidota*, *J. arcticus*, *L. triticoides*, and *D. spicata* had similar low ratios (1 - 2). *S. exigua*, *S. tragus* and *E. nauseosa* showed intermediate ratios (4 - 7), while

the desert shrubs *A. confertifolia* and *A. tridentata* had the highest ratios (19 - 21) indicating high reliance on deeper water sources.

The volumetric soil water lost to evaporation in bare ground plots increased with increasing irrigation treatments at both depths (Fig. 4). In average, water lost from 0 - 25 cm was 85% of water lost from 0-50 cm. Therefore, although most evaporation losses came from the surface layer, 15% of losses from evaporation came from below 25 cm.

Water use by plants from 0 to 50 cm depth, the whole soil layer investigated in the study, was not correlated ($P > 0.05$) to aboveground biomass by species (data not shown). However, soil water use was linearly correlated ($P < 0.05$; $R^2 = 0.53$) with the RSR displayed by species.

4. Discussion

The variation in water use by species was expected given the diversity of plant characteristics represented in our species pool. *J. arcticus*, *L. triticoides*, and *D. spicata* used the most water at both soil depths. *J. arcticus* is a wetland species that has high transpiration rates and performs well when high water is available (Svejcar and Riegel, 1998). *Leymus triticoides* is usually distributed in microtopographical depressions where water tends to be more abundant (Mata-González et al., 2011). *Distichlis spicata* is known to occupy wet, but not flooded soils adjacent to marshes and lagoons (Zengel et al., 1995) and shallow groundwater areas in the Owens Valley (Mata-González et al., 2011). *Leymus triticoides* and *J. arcticus* extracted more water than *S. exigua*, a well known riparian species with high water requirements (Amlin and Rood, 2001). This shows the high capacity of fibrous and rhizomatous root systems such as those of *L. triticoides* and *J. arcticus* to obtain water when it is highly available.

Also expected was that the desert shrubs, *A. tridentata*, *E. nauseosa*, and *A. confertifolia*, used the least amount of water. In general, desert shrubs are deep-rooted species that grow mostly in the spring, when most precipitation occurs and roots are

more active (Branson et al., 1976; Caldwell, 1985; Sperry and Hacke, 2002). These species use little soil water in late summer even after the occasional rainfall pulses (Ehleringer et al., 1991; Evans and Black, 1993). However, our TDR sensors only accounted for soil moisture down to 50 cm and it is likely that we did not account for all the water that plants acquired. For example, *A. tridentata* is considered a deep-rooted species that obtains about 80% of its water from 0 - 60 cm depth and the other 20% from 60 - 120 cm during May to September (Sturges, 1977). *Ericameria nauseosa* tends to rely on deeper water sources due to its less developed and less functional lateral roots close to the soil surface (Groeneveld and Crowley, 1988; Donovan and Ehleringer, 1994) and so it is likely that our method underestimated its water use. However, our method was useful because it considered water extraction from relatively shallow sources which mimics the potential shallow soil water distribution of summer rainfall.

Surface soil moisture (0 - 25 cm) was not depleted by the desert shrubs (*A. tridentata*, *A. confertifolia*, and *E. nauseosa*). On the contrary, there was a small gain in surface soil water amount. This was unexpected, but potentially explained by the hydraulic lift phenomenon, which has been reported in *A. tridentata* (Richards and Caldwell, 1987) and *E. nauseosa* (Donovan et al., 2003; Leffler et al., 2004). A rigorous test of hydraulic lift is outside the scope of this study, but it is a possibility that justifies further investigation.

Plants extracted more water from 0 - 50 cm as the watering levels increased, which is expected since transpiration usually responds positively to increases in available water (Patrick et al., 2007; Wan et al., 1993a). However, the decline in water use from the 0 – 25 cm depth as watering levels increased was unexpected. It is possible that deeper roots exert more of the water extraction than shallow roots in soils with high available water because deeper, nonsuberized roots tend to have higher hydraulic conductance than suberized shallow roots (Wan et al., 1994). Also, it is possible that root growth was concentrated in areas with more constant or high soil moisture as it has been observed in some desert species (Wilcox et al., 2004). If so,

plants under the high watering treatments perhaps had more deeper roots (25 – 50 cm) than shallow roots (0 – 25 cm), which might have facilitated water withdrawal from the relatively deeper sources.

The ratio of deep water (25-50 cm) to shallow water (0-25 cm) use differed greatly by species. In general, deep-rooted shrubs utilized more deep water than shallow-rooted grasses and forbs. This has been previously observed by Pataki et al. (2008) in the Owens Valley and other researchers elsewhere (Dodd et al., 1998). *Ericameria nauseosa* used significantly less deep water than *A. tridentata* and *A. confertifolia*, but it is likely that *E. nauseosa* utilized significant amounts of water from sources deeper than 50 cm, which we did not monitor (Leffler et al., 2004; McLendon et al., 2008). With shrubs relying highly on deeper water sources it is expected that they can depend on groundwater more regularly than grasses as noted by Pataki et al. (2008). Grasses on the other hand can be relatively more responsive to summer rainfall than shrubs because of their shallower roots (Ehleringer et al., 1991).

The annual *S. tragus* obtained seven times more water from the 25 -50 cm depth than from 0 – 25 cm depth, substantially depending on deeper water than grasses and other forbs. *Amphiachyris dracunculoides*, an annual forb native to the southern Great Plains also withdrew more water than grasses from a depth of 75 cm (Yoder et al., 1998). Grasses and forbs, especially those with fibrous and rhizomatous root systems are highly adapted to compete for surface water, but are at a disadvantage competing for deeper water sources (Wan et al., 1993c; Mata-Gonzalez et al., 2011). *Salsola tragus* can rapidly develop deep roots early after emergence to compete for deeper water resources (Pan et al., 2001).

Salix exigua obtained four times more water from the 25 – 50 cm depth than from the 0 – 25 cm depth. Yet, its ratio of deep to shallow water uptake was lower than that of desert shrubs and not significantly different from that of the grasses *L. triticoides* and *D. spicata*. Given its riparian habit, *S. exigua* may rely primarily on relatively shallow roots rather than on deeper roots as desert shrubs do (Amlin and Rood, 2002). Even compared to other riparian shrubs such as *Populus* spp., *S. exigua*

has high water requirements and a non-plastic root system that does not easily adapt or grow in response to water table declines or water shortages (Amlin and Rood, 2001).

Evaporation amounts increased along with watering treatments. This was expected given that evaporation rate is controlled by atmospheric conditions, surface soil wetness, and moisture transport towards the surface soil layer (Kondo et al., 1990). However, evaporation losses occurring from subsurface soil layers, beyond 25 cm, were unexpected. It is often considered in simulation models that the maximum depth of the surface soil layer subject to evaporation is 10 to 15 cm (Burt et al., 2005). Our watering might have facilitated water transfer from subsurface layers to the soil surface because upward water transfer of this type can occur as an evaporation front (Boulet et al., 1997).

Water extraction by plants was not associated with aboveground standing crop, which was unusual because transpiration is commonly correlated with leaf area variation (Vertessy et al., 1995). One reason for this lack of correlation was that desert shrubs, species with large aboveground standing crop in our study, also had low summer water use (Fig. 1). Interestingly, water extraction was linearly and positively correlated to RSR. High RSR species in our study were those with shallow and fibrous rooting systems such as *J. arcticus*, *D. spicata*, *L. triticoides* and *S. airoides*. Preferential allocation of root biomass over shoot biomass has been shown to be associated with the plant's ability to take up soil resources (Lloret et al., 1999). Specifically, summer water utilization may be favored in those species with shallow root systems (Schwinning and Ehleringer, 2001)

5. Summary

Water use varied by species. Herbaceous species with shallow, fibrous, and rhizomatous root systems such as *J. arcticus*, *L. triticoides*, and *D. spicata* had higher water use than desert shrubs. These herbaceous species had also higher water use than the riparian *S. exigua*, which indicates the competitive advantage conferred by fibrous and shallow roots in situations of abundant soil surface water. Under the scenario of

increasing summer precipitation in areas such as the Great Basin water utilization might be highly favored in grasses and forbs with shallow roots, perhaps in detriment of deeper rooted woody species. Deep-rooted shrubs relied more on deeper water sources than shallow-rooted herbaceous species. This is in agreement with the reports indicating that shrubs may rely on groundwater more constantly than grasses (Pataki et al., 2008). A consequence to this scenario could also favor invasive annual grasses that utilize summer precipitation. Summer plant water use in the Owens Valley can be positively correlated with the RSR of plants since in this area high RSR species are also those with shallow root systems.

References

- Amlin, N. A., Rood S.B., 2001. Inundation tolerances of riparian willows and cottonwoods. *Journal of the American Water Resources Association* 37, 1709–1720.
- Amlin, N.M., Rood, S.B., 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands* 22, 338-346.
- Anderson, B.T., Roads, J.O., 2002. Regional simulation of summertime precipitation over the southwestern United States. *Journal of Climate* 15, 3321–3342.
- Boulet, G., Raud, I., Vauclin, M., 1997. Study of the mechanisms of evaporation under arid conditions using a detailed model of the soil–atmosphere continuum. Application to the EFEDA I experiment. *Journal of Hydrology* 193, 114–141.
- Brady, N.C., Weil, R.R., 1996. The nature and properties of soils. Prentice Hall, Upper Saddle River, New Jersey.
- Branson, F.A., Miller, R.F., McQueen, I.S., 1976. Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. *Ecology* 57, 1104-1124.
- Burt, C.M., Mutziger, A.J., Allen, R.G., Howell, T.A., 2005. Evaporation research: review and interpretation. *Journal of Irrigation and Drainage Engineering* 131, 37–58.
- Caldwell, M. M., 1985. Cold deserts. B. F. Chabot and H. A. Mooney, editors. *Physiological ecology of North American plant communities*. Chapman and Hall, New York, New York, USA. pp 198–212.
- Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life forms in a shortgrass steppe community. *Oecologia* 117, 504-512.
- Donovan, A., Ehleringer, J.R., 1994. Water Stress and Use of Summer Precipitation in a Great Basin Shrub Community. *Functional Ecology* 8 (3), 289-297.

- Donovan, L.A., Richards, J.H., Linton, M.J., 2003. Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. *Ecology* 84(2), 463-470.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. *Oecologia* 8, 430-434.
- Evans, R.D., Black, R.A., 1993. Growth, photosynthesis, and resource investment for vegetative and reproductive modules of *Artemisia tridentata*. *Ecology* 74, 1516-1528.
- Flanagan, L.B., Ehleringer, J.R., 1991. Stable isotope composition of stem and leaf water applications to the study of plant water use. *Functional Ecology* 5, 270-277.
- Gillespie, I.G., Loik, M.E., 2004. Pulse events in Great Basin Desert shrublands: physiological responses of *Artemisia tridentata* and *Purshia tridentata* seedlings to increased summer precipitation. *Journal of Arid Environments* 59, 41-57.
- Groeneveld D.P., Crowley, D.E., 1988. Root system response to flooding in three desert shrub species. *Functional Ecology* 2, 491-497.
- Groeneveld, D.P., Warren, D.C., 1992. Evapotranspiration measurements of native vegetation, Owens Valley, California, June 1986. U.S. Geological survey. Water-Resources investigations Report 91-4159. Sacramento, CA USA.
- Kondo, J., Saigusa, N., Sato, T., 1990. A parameterization of evaporation from bare soil surfaces. *Journal of Applied Meteorology* 29, 385-389.
- Leffler, J.A., Ivans, C.Y., Ryel, R.J., Caldwell M.M., 2004. Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow- vs. deep-soil water in a glasshouse experiment. *Environmental and Experimental Botany* 51(1), 9-19.
- Lloret, F., Casanovas, C., Penuelas, J., 1999. Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Functional Ecology* 13, 210-216.

- Loik, M.E., 2007. Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecology* 191, 95–108.
- Mata-Gonzalez, R., McClendon, T., Martin, D., 2005. The inappropriate use of transpiration coefficients (K_c) to estimate evapotranspiration in arid ecosystems: a review. *Arid Land Research and Management* 19, 285–295.
- Mata-González, R., McLendon, T., Martin, D.W., Trlica, M.J., Pearce, R., 2011. Vegetation as affected by groundwater depth and microtopography in a shallow aquifer area of the Great Basin. *Ecohydrology* In press, doi:10.1002/eco.196.
- McLendon, T., Hubbard, P.J., Martin, D.W., 2008. Partitioning the use of precipitation- and groundwater-derived moisture by vegetation in an arid ecosystem in California. *Journal of Arid Environments* 72, 986–1001.
- Naumburg, E., Mata-González, R., Hunter, R.G., McLendon, T., Martin, D.W., 2005. Phreatophytic vegetation and groundwater fluctuations: A review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. *Environmental Management* 35, 726–740.
- Pan, W.L., Young, F.L., Bolton, R.P., 2001. Monitoring Russian thistle (*Salsola iberica*) root growth using a scanner-based, portable mesorhizotron. *Weed Technology* 15, 762–766.
- Pataki, D.E., Billings, S.E., 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.
- Patrick, L., Cable, J., Potts, D., Ignace, D., Barron-Gafford, G., Griffith, A., Alpert, H., Gestel, N.V., Robertson, T., Huxman, T.E., Zak, H., Loik, M.E., Tissue, D., 2007. Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO_2 and H_2O in a sotol grassland in Big Bend National Park, Texas. *Oecologia* 151, 704–718.

- Richards, J.H., Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73, 486-489.
- Sala, O.E., Lauenroth, W.K., Parton, W.J., Trlica, M.J. 1981. Water status of soil and vegetation in a shortgrass steppe. *Oecologia* 48, 327-331.
- Sala, O.E., Lauenroth, W.K. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia* 53, 301-304.
- Schwinning, S., Ehleringer, J.R., 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* 89, 464-480.
- Snyder, K.A., Donovan, L.A., James, J.J., Tiller, R.L., Richards, J. H., 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia* 141, 325-334.
- 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.
- Stroonsnijder, L., 1987. Soil evaporation: test of a practical approach under semi-arid conditions. *Netherlands Journal of Agricultural Science* 35, 417-426.
- Sturges, D.L. 1977. Soil water withdrawal and root characteristics of Big Sagebrush. *The American Midland Naturalist* 98(2), 257-274.
- Svejcar, T., Riegel, G.M., 1998. Spatial pattern of gas exchange for montane moist meadow species. *Journal of Vegetation Science* 9, 84-94.
- Topp, G.C., Davis, J.L., Annan, A.P. 1980. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. *Water Resource Research* 16, 574-582.
- Topp, G.C., Davis, J.L. 1985. Measurements of soil water content using time-domain reflectometry. *Soil Science of America Journal* 49, 19-24.

- USDA, 2010. Keys to Soil Taxonomy. Natural Resources Conservation Service, US Department of Agriculture, Washington D C.
- Vertessy, R.A., Benyon, R.G., O'Sullivan, S.K., Gribben P.R., 1995. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology* 15,559-567.
- Wan, C., Sosebee, R.E., McMichael, B.L., 1993a. Broom snakeweed responses to drought: photosynthesis, conductance, and water-use efficiency. *Journal of Range Management* 46, 355–359.
- Wan, C., Sosebee, R.E., McMichael, B.L., 1993b. Growth, photosynthesis, and stomatal conductance in *Gutierrezia sarothrae* associated with hydraulic conductance and soil water extraction by deep roots. *International Journal of Plant Sciences* 154, 144–151.
- Wan, C., R. E. Sosebee, McMichael. B.L., 1993c. Soil water extraction and photosynthesis in *Gutierrezia sarothrae* and *Sporobolus cryptandrus*. *Journal of Range Management* 46, 425–430.
- Wan, C., Sosebee, R.E., McMichael, B.L., 1994. Hydraulic properties of shallow vs. deep lateral roots in a semiarid shrub (*Gutierrezia sarothrae*). *American Midland Naturalist* 131, 120–127.
- Wilcox CS, Ferguson JW, Fernandez GCJ, Nowak RS. 2004. Fine root growth dynamics of four Mojave Desert shrubs as related to soil moisture and microsite. *Journal of Arid Environments* 56: 129-148.
- WRB, 2007. World Reference Base for Soil Resources, World Soil Resources Report, Vol. 103; FAO: Rome.
- Yoder C.K., Boutton T.W., Thurow T.L., Midwood A.J., 1998. Differences in soil water use by annual broomweed and grasses. *Journal of Range Management* 51, 200–206.
- Zengel, S.A., Meretsky, V.J., Glenn, E.P., Felger, R.S., Ortiz, D. 1995. Cienega de Santa Clara, a remnant wetland in the Rio Colorado delta (Mexico): vegetation distribution and the effects of the water flow reduction. *Ecological Engineering* 4, 19-36.

Tables

Table 1. Plant species included in the study.

Species	Life form	Life cycle
<i>Distichlis spicata</i> L. Greene	Grass	Perennial
<i>Leymus triticoides</i> (Buckley) Pilg.	Grass	Perennial
<i>Sporobolus airoides</i> (Torr.) Torr.	Grass	Perennial
<i>Glycyrrhiza lepidota</i> Pursh	Forb	Perennial
<i>Juncus arcticus</i> Willd ¹ .	Forb	Perennial
<i>Salsola tragus</i> L.	Forb	Annual
<i>Artemisia tridentata</i> Nutt.	Shrub	Perennial
<i>Atriplex confertifolia</i> (Torr. & Frem.) S. Wats.	Shrub	Perennial
<i>Ericameria nauseosa</i> (Pall. ex Pursh) G.L. Nesom & Baird ²	Shrub	Perennial
<i>Salix exigua</i> Nutt.	Shrub/tree	Perennial

¹Previously known as *Juncus balticus*; ²Previously known as *Chrysothamnus nauseosus*;

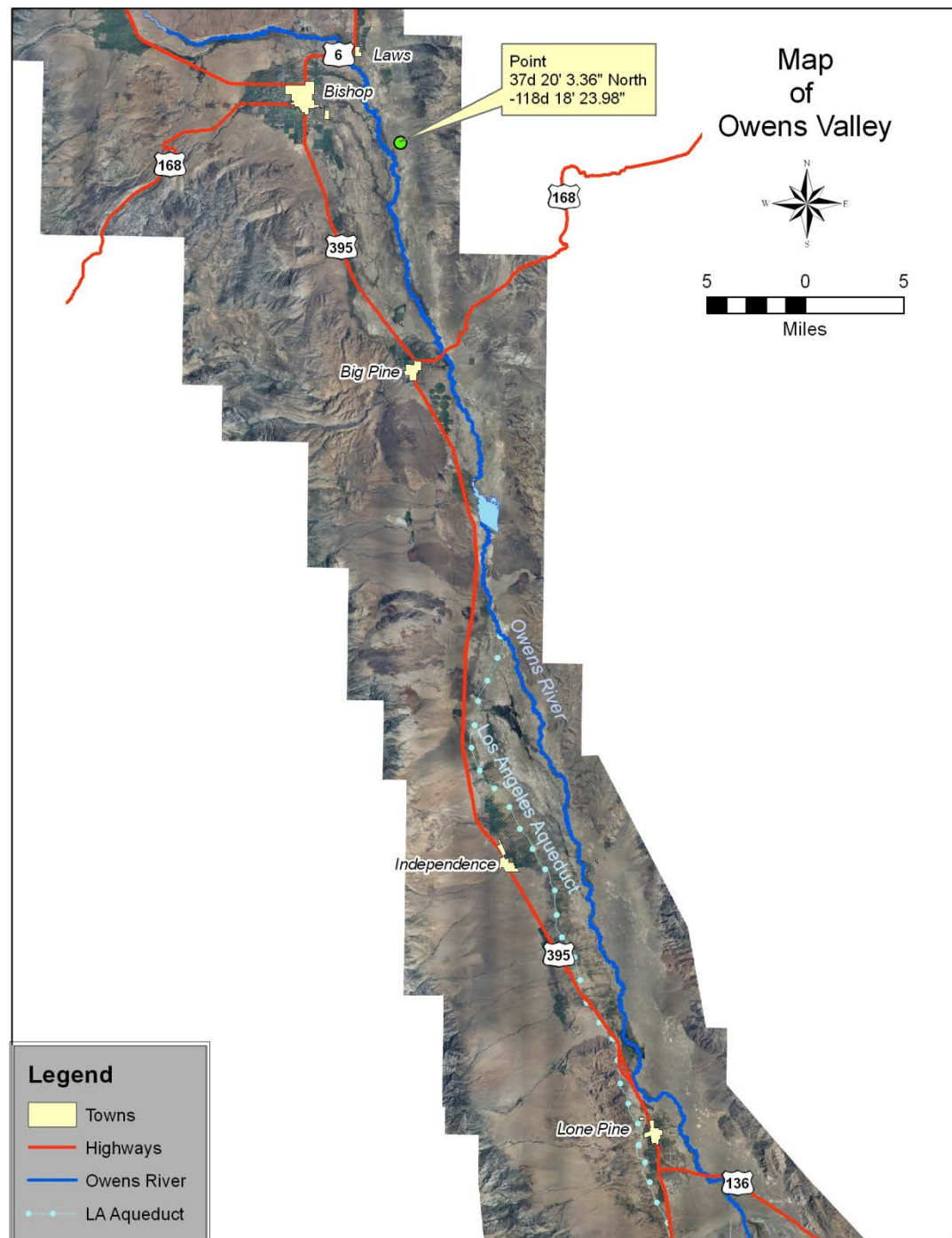


Figure 1. A map of Owens Valley, CA showing the location of the project study site.

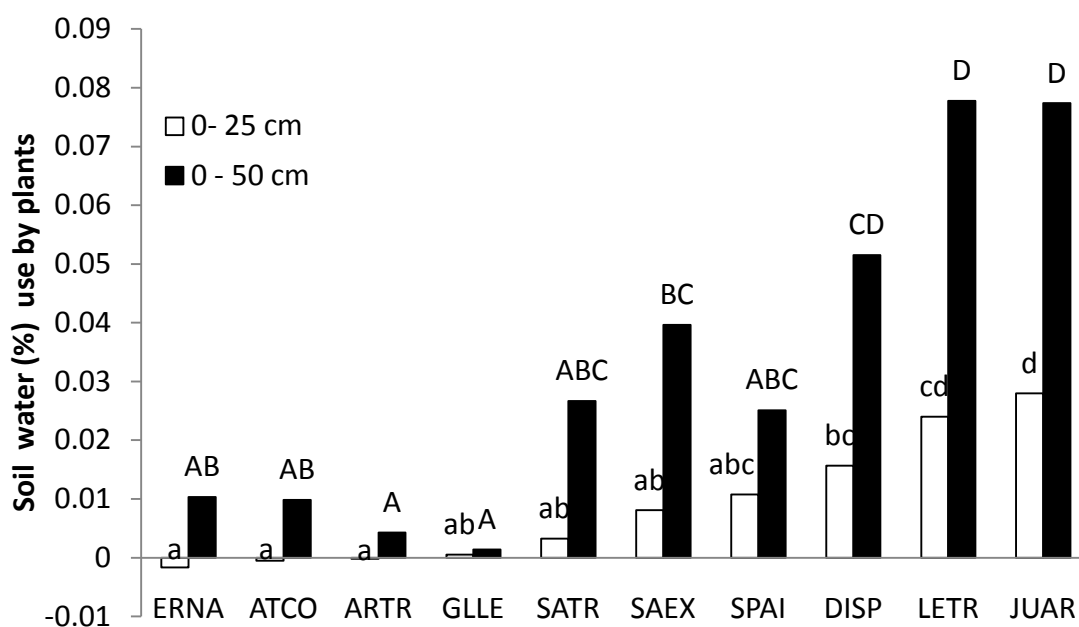


Figure 2. Volumetric soil water (%) used by different Owens Valley, CA species from two different soil depths: 0-25 cm and 0-50 cm. Different lowercase letters indicate differences in soil water used from the 0-25 cm depth among species. Different uppercase letters indicate differences in soil water used from the 0-50 cm depth among species.

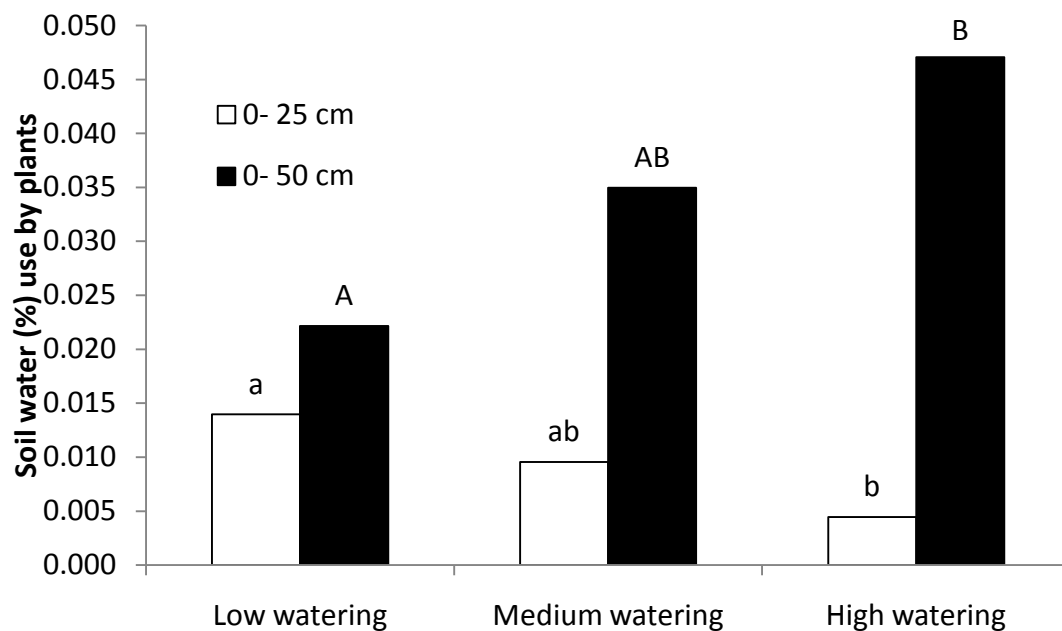


Figure 3. Volumetric soil water (%) used by Owens Valley, CA plants irrigated at three different rates from two different soil depths: 0-25 cm and 0-50 cm. Different lowercase letters indicate differences in soil water use from the 0-25 cm depth among plants watered at different levels. Different uppercase letters indicate differences in soil water use from the 0-50 cm depth among plants watered at different levels.

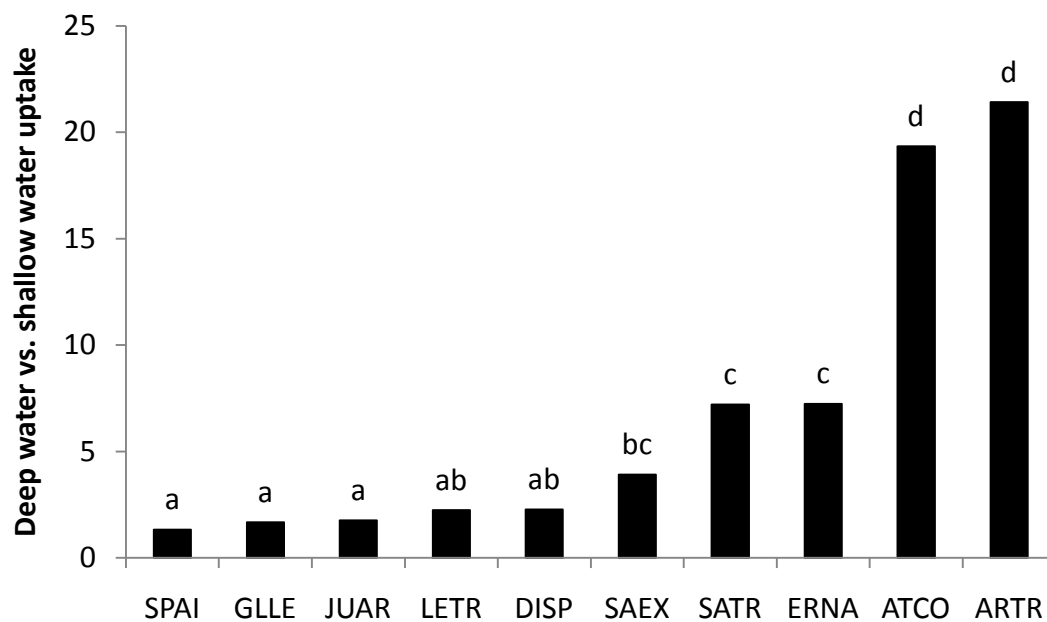


Figure 4. Deep water (25-50 cm)/shallow water (0-25cm) uptake ratio of different species in Owens Valley, CA. Different letters indicate differences in ratio among species.

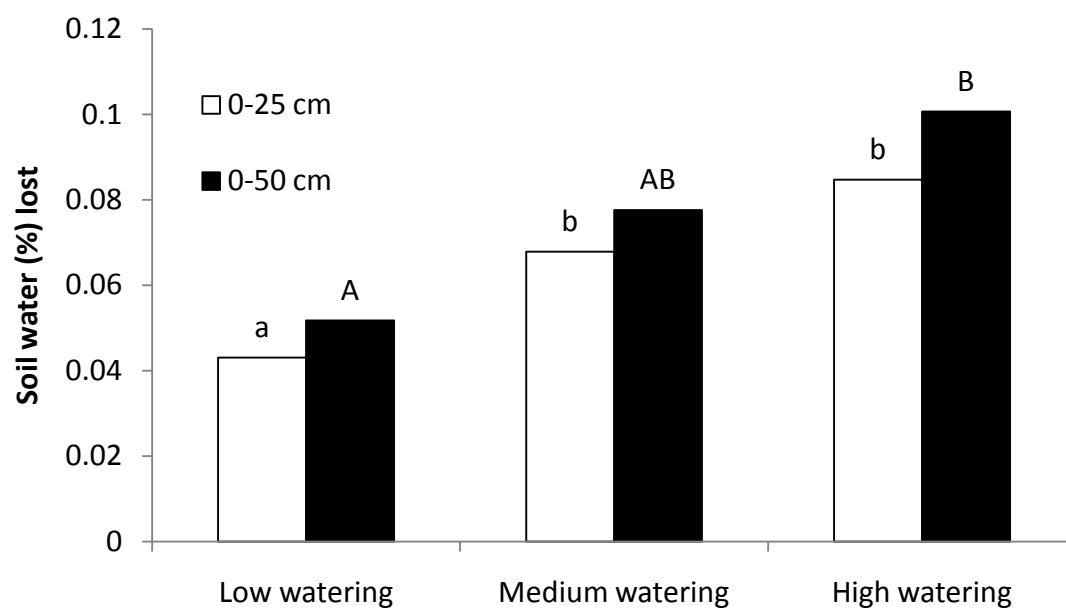


Figure 5. Average monthly volumetric soil water (%) lost to evaporation in plots watered at three different rates from two different soil depths: 0-25 cm and 0-50 cm. The averages involved two months: July and August. Different lowercase letters indicate differences from the 0-25 cm depth among plants watered at different levels. Different uppercase letters indicate differences in soil water use from the 0-50 cm depth among plants watered at different levels. On average, water lost from the 0-25 cm depth was 85% of water lost from the 0-50 cm depth.

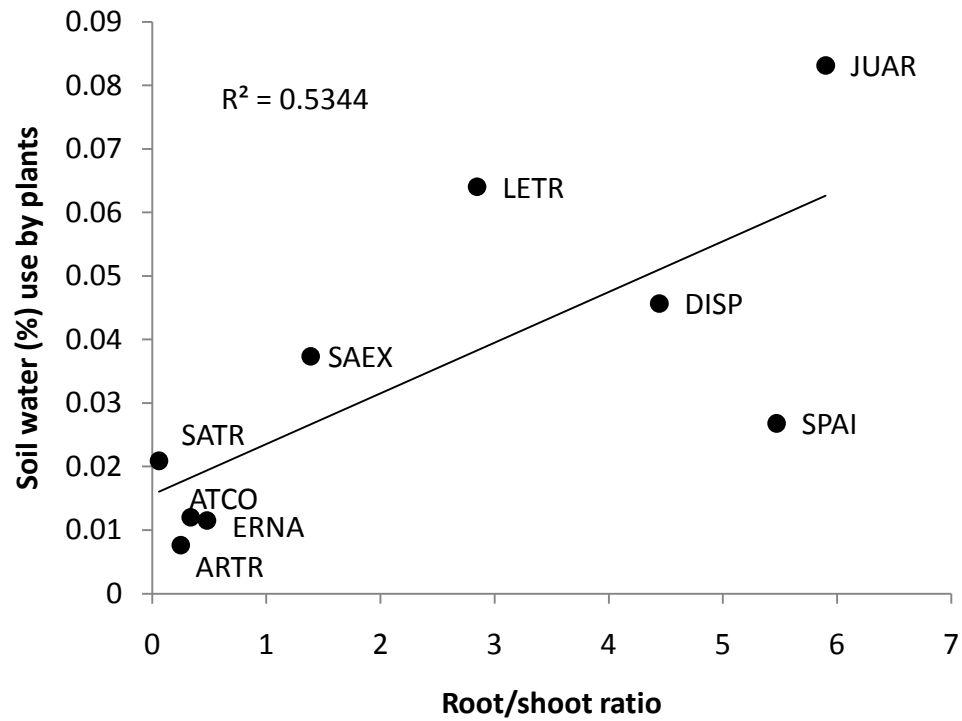


Figure 6. Volumetric soil water (%) used by different species in the Owens Valley as related to their root: shoot ratio. Relationship was significant ($P < 0.05$).

Chapter 4: General Conclusions

Plant responses to summer watering varied by year; in 2010 plants produced more biomass and had higher water-use efficiency than in 2009. This was attributed to the higher winter and spring precipitation that occurred in 2010 prior to the application of our watering treatments. In general, grasses increased production as a result of the increase in watering levels in both years, but the growth response to water addition with respect to the control was higher in 2009 than in 2010. Water-use efficiency of grasses linearly increased in 2009 but decreased in 2010 with the increase in water received.

Desert shrub growth and water use efficiency were not significantly affected by watering in both years, likely because these shrubs were either not water limited or unable to obtain the additional water that was supplied through the summer.

I hypothesized that water-use efficiency would decrease with the increasing watering levels but this was only corroborated in 2010 and mainly for herbaceous species. Summer water-use efficiency varied greatly by species and it was affected by the initial spring condition of the plants.

Contrary to my expectation total standing crop and RSR did not vary by watering treatment, but varied by species. In general desert shrubs achieved higher standing crop and lower RSR than herbaceous species.

Plants with highest water requirements, those traditionally considered wetland and riparian species, utilized up to 13 times more water to produce a unit of aboveground biomass than plants with the lowest requirements such as desert shrubs and the annual *S. tragus*.

I observed large variation in summer water use by species. Herbaceous species with shallow, fibrous, and rhizomatous root systems such as *J. arcticus* and *L. triticoides* had higher water use than shrubs, including the riparian *S. exigua*. This suggests a competitive advantage conferred by fibrous and shallow roots in situations of abundant soil surface water. Summer plant water use in the Owens Valley can be

positively correlated with the RSR of plants since in this area high RSR species are also those with shallow root systems.

In general, deep-rooted shrubs relied more on deeper water sources than shallow-rooted herbaceous species. This was expected and confirms previous reports (Pataki et al., 2008) indicating that shrubs may rely on groundwater more constantly than grasses.

Additional soil water in the summer may favor herbaceous species over desert shrubs. We concur with previous research (Ehleringer et al., 1991) suggesting that under the global change scenario of increasing summer precipitation in the Great Basin, herbaceous species would be better positioned to compete in the community than desert shrubs.

The species-specific information obtained in this study can be used in ecological simulation models such as EDYS, which is comprehensive, mechanistically based, and spatially explicit (Childress and McLendon, 1999). EDYS has been applied in ecological evaluations, land management decision making, environmental planning, revegetation and restoration design analysis, and for watershed management by federal and state agencies, municipal and water authorities, and corporations. This model has been used in the Owens Valley to project vegetation responses to fluctuating groundwater (Naumburg et al., 2005) and it may be further used to elucidate potential vegetation responses to changes in surface and groundwater resulting from future climate changes and water management practices.

Water use, biomass production, and conversion efficiency vary greatly in plant communities across the Owens Valley and this should be considered on planning the allocation of water resources to vegetation. This study can assist in a better understanding of the interconnectedness of soil, water, and vegetation as well as the plant utilization of surface water and groundwater. Our study analyzed plant responses to water applications when the plants were out of contact with groundwater. We suggest that future studies focus on examining plant responses to surface soil

water applications in the presence of available groundwater to try to better replicate the field conditions and interactions of vegetation in the Owens Valley.

Comprehensive Bibliography

- Allen, E.D., 1982. Water and nutrient competition between *Salsola kali* and two native grass species (*Agropyron smithii* and *Bouteloua gracilis*). *Ecology* 63, 732-741.
- Amlin, N. A., Rood S.B., 2001. Inundation tolerances of riparian willows and cottonwoods. *Journal of the American Water Resources Association* 37, 1709–1720.
- Amlin, N.M., Rood, S.B., 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. *Wetlands* 22, 338-346.
- Anderson, B.T., Roads, J.O., 2002. Regional simulation of summertime precipitation over the southwestern United States. *Journal of Climate* 15, 3321–3342.
- Beatley, J.C., 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55, 856-863.
- Boulet, G., Raud, I., Vauclin, M., 1997. Study of the mechanisms of evaporation under arid conditions using a detailed model of the soil–atmosphere continuum. Application to the EFEDA I experiment. *Journal of Hydrology* 193, 114–141.
- Brady, N.C., Weil, R.R., 1996. The nature and properties of soils. Prentice Hall, Upper Saddle River, New Jersey.
- Branson, F.A., Miller, R.F., McQueen, I.S., 1976. Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. *Ecology* 57, 1104-1124.
- Brown, R.W., 1995. The water relations of range plants: Adaptations to water deficits, in: Bedunah, D.J., Sosebee, R.E., (Eds.), *Wildland Plants: Physiological Ecology and Development Morphology*. Society for Range Management, Denver, Colorado, USA, pp. 291-413.
- Burt, C.M., Mutziger, A.J., Allen, R.G., Howell, T.A., 2005. Evaporation research: review and interpretation. *Journal of Irrigation and Drainage Engineering* 131, 37–58.

- Caldwell, M. M., 1985. Cold deserts. B. F. Chabot and H. A. Mooney, editors. Physiological ecology of North American plant communities. Chapman and Hall, New York, New York, USA. pp 198–212
- Carrera, A.L., Sain, C.L., Bertiller, M.B., 2000. Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. *Plant and Soil* 224:185–193.
- Chapin, E.S., 1991. Effects of multiple environmental stresses on nutrient availability and use, in: Mooney, H.A., Winner, W.E., Pell, E.J., (Eds.), Response of plants to multiple stresses. Academic Press, San Diego, California, USA, pp. 68-88.
- Chaves, M.M., Maroco, J.P., Pereira, J.S., 2003. Understanding plant response to drought: From genes to the whole plant. *Functional Plant Biology* 30, 239–264.
- Childress, W.M., Coldren, C.L., McLendon, T., 2002. Applying a complex, general ecosystem model (EDYS) in large scale land management. *Ecol. Model.* 153, 97–108.
- DeLucia, E.H., Schlesinger, W.H., 1991. Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology* 72, 51-58.
- Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life forms in a shortgrass steppe community. *Oecologia* 117, 504-512.
- Donovan, A., Ehleringer, J.R., 1994. Water Stress and Use of Summer Precipitation in a Great Basin Shrub Community. *Functional Ecology* 8 (3), 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.
- Donovan, L.A., Richards, J.H., Linton, M.J., 2003. Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. *Ecology* 84(2), 463-470.

- Dwyer, D.D., DeGarmo, H.C., 1970. Greenhouse productivity and water-use efficiency of selected desert shrubs and grasses under four soil-moisture levels. Bulletin 570. New Mexico State University, Agriculture Experiment Station. Las Cruces, NM, USA.
- Dwyer, D.D., Wolde-Yohannis, K., 1971. Germination, emergence, water use, and production of Russianthistle (*Salsola kali* L.). *Agronomy Journal* 64, 52-55.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. *Oecologia* 8, 430-434.
- 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.
- Elmore, A.J., Mustard, J.F., Manning, S.J, Lobell, D.B. 2000. Quantifying vegetation change in semiarid environments: Precision and accuracy of spectral mixture analysis and the normalized difference vegetation index. *Remote Sensing of Environment*. 73: 87-102.
- Evans, R.D., Black, R.A., 1993. Growth, photosynthesis, and resource investment for vegetative and reproductive modules of *Artemisia tridentata*. *Ecology* 74, 1516-1528.
- Fernandez, R.J., 2007. On the frequent lack of response of plants to rainfall events in arid areas. *Journal of Arid Environments* 68, 688–691.
- Flanagan, L.B., Ehleringer, J.R., 1991. Stable isotope composition of stem and leaf water applications to the study of plant water use. *Functional Ecology* 5, 270-277.
- Fuller, G.D., 1913. Water requirement of plants. *Botanical Gazette* 56, 514-515.
- Gillespie, I.G., Loik, M.E., 2004. Pulse events in Great Basin Desert shrublands: physiological responses of *Artemisia tridentata* and *Purshia tridentata* seedlings to increased summer precipitation. *Journal of Arid Environments* 59, 41–57.

- 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.
- Goedhart C.M., Pataki, D.E., 2011. Ecosystem effects of groundwater depth in Owens Valley, California. *Ecohydrology* 4, 458–468.
- Golluscio, R.A., Sala, O.E., Lauenroth, W.K., 1998. Differential use of large summer rainfall events by shrubs and grasses: A manipulative experiment in the Patagonian steppe. *Oecologia* 115, 17–25.
- Groeneveld, D.P., Warren, D.C., 1992. Evapotranspiration measurements of native vegetation, Owens Valley, California, June 1986. U.S. Geological survey. Water-Resources investigations Report 91-4159. Sacramento, CA USA.
- Hatfield, J. L., Sauer, T.J., Prueger, J.H., 2001. Managing soils to achieve greater water use efficiency: A review. *Agronomy Journal* 93, 271–280.
- Hickey, W.C., Springfield, H.W., 1966. *Alkali sacaton*: its merits for forage and cover. *Journal of Range Management* 19, 71–74.
- Hsiao, T.C., Xu, L.K., 2000. Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. *Journal of Experimental Botany* 51, 1595–1616.
- James, J.J., Richards, J.H., 2005. Plant N capture from pulses: Effects of pulse size, growth rate, and other soil resources. *Oecologia* 145, 113–122.
- Kelly, R.D., Walker, B.H., 1976. The effects of different forms of land use on the ecology of a semi-arid region in south-eastern Rhodesia. *Journal of Ecology* 64, 553–576.
- Köchy, M., Wilson, S.D., 2000. Competitive effects of shrubs and grasses in prairie. *Oikos* 91, 385–395.
- Kondo, J., Saigusa, N., Sato, T., 1990. A parameterization of evaporation from bare soil surfaces. *Journal of Applied Meteorology* 29, 385–389.
- Kramer, P.J., and Boyer, J.S., 1995. Water relationships of plant and soils. Academic Press, San Diego.

- Leffler, J.A., Ivans, C.Y., Ryel, R.J., Caldwell M.M., 2003. Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow- vs. deep-soil water in a glasshouse experiment. *Environmental and Experimental Botany* 51(1), 9-19.
- Leffler, J.A., Ivans, C.Y., Ryel, R.J., Caldwell, M.M., 2004. Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow vs. deep soil water in a glasshouse experiment. *Environmental and Experimental Botany* 15, 9-19.
- Le Houerou, H.N., Bingham, R.L., Skerbek, W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15, 1–18.
- Le Maitre, D.C., Scott, D.F., Colvin, C., 1999. A review of information on interactions between vegetation and groundwater. *Water SA* 25, 137–151.
- Lloret, F., Casanovas, C., Penuelas, J., 1999. Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Functional Ecology* 13, 210–216.
- Libecap, G.D., 2005. The myth of Owens Valley. Regulation.
- Loik, M.E., 2007. Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecology*, 191, 95–108.
- Mata-González, R., Meléndez-González, R., Martínez-Hernández, J.J., 2001. Aerial biomass and elemental changes in *Atriplex canescens* and *A. acanthocarpa* as affected by salinity and soil water availability, in: McArthur, E.D., Fairbanks, D.J. (Comps.), *Shrubland Ecosystem Genetics and Biodiversity: Proceedings RMRS-P-21*. U.S.D.A. Forest Service Rocky Mountain Research Station, Ogden, UT, USA, pp. 308–311.
- Mata-González, R., Sosebee, R.E., Wan, C. 2002. Physiological impacts of biosolids application in desert grasses. *Environmental and Experimental Botany* 48, 139-148.

- Mata- González, R., McClendon, T., Martin, D., 2005. The inappropriate use of transpiration coefficients (K_c) to estimate evapotranspiration in arid ecosystems: a review. *Arid Land Research and Management* 19, 285–295.
- Mata-González, R., Hunter, R.G., Coldren, C.L., McLendon, T., Paschke, M. 2008. A comparison of modeled and measured impacts of resource manipulations for control of *Bromus tectorum* in sagebrush steppe. *Journal of Arid Environments* 72, 836-846.
- Mata-González, R., McLendon, T., Martin, D.W., Trlica, M.J., Pearce, R., 2011. Vegetation as affected by groundwater depth and microtopography in a shallow aquifer area of the Great Basin. *Ecohydrology* In press, doi:10.1002/eco.196.
- McLendon, T., Hubbard, P.J., Martin, D.W., 2008. Partitioning the use of precipitation- and groundwater-derived moisture by vegetation in an arid ecosystem in California. *Journal of Arid Environments* 72, 986-1001.
- Monaco, T.A., Johnson, D.A., Norton, J.M., Jones, T.A., Connors, K.J., Norton, J.B., Redinbaugh, M.B., 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management* 56, 282–290.
- Montaña, C., Floret, C., Cornet, A. 1988. Water use efficiency and biomass production of two perennial grasses from the Chihuahuan Desert (Mexico). In: *Range Management Society of India (Ed.), Third International Rangeland Congress Abstracts Vol. 1. Range Management Society of India, New Dehli, 240-243.*
- Naumburg, E., Mata-González, R., Hunter, R.G., McLendon, T., Martin, D.W., 2005. Phreatophytic vegetation and groundwater fluctuations: A review of current research and application of ecosystem response modeling with an emphasis on Great Basin vegetation. *Environmental Management* 35, 726-740.
- Or, D., Groeneveld, D.P., 1994. Stochastic estimation of plant-available soil water under fluctuating water table depths. *Journal of Hydrology* 163, 43-64.

- Osório, J., Osório, M.L., Chaves, M.M., Pereira, J.S. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. *Tree Physiology* 18 (6), 363-373.
- Pan, W.L., Young, F.L., Bolton, R.P., 2001. Monitoring Russian thistle (*Salsola iberica*) root growth using a scanner-based, portable mesorhizotron. *Weed Technology* 15, 762–766.
- Pataki, D.E., Billings, S.E., 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.
- Patten, D.T., Rouse, L., Stromberg, J.C., 2008. Isolated spring wetlands in the Great Basin and Mojave Deserts, USA: Potential response of vegetation to groundwater withdrawal. *Environmental Management* 41, 398–413.
- Patrick, L., Cable, J., Potts, D., Ignace, D., Barron-Gafford, G., Griffith, A., Alpert, H., Gestel, N.V., Robertson, T., Huxman, T.E., Zak, H., Loik, M.E., Tissue, D., 2007. Effects of an increase in summer precipitation on leaf, soil, and ecosystem fluxes of CO₂ and H₂O in a sotol grassland in Big Bend National Park, Texas. *Oecologia* 151, 704-718.
- Richards, J.H., Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73, 486-489.
- Sala, A., Nowak, R.S., 1997. Ecophysiological responses of three riparian graminoids to changes in the soil water table. *International Journal of Plant Sciences* 158, 835–843.
- Sala, O.E., Lauenroth, W.K., Parton, W.J., Trlica, M.J. 1981. Water status of soil and vegetation in a shortgrass steppe. *Oecologia* 48, 327-331.
- Sala, O.E., Lauenroth, W.K. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia* 53, 301-304.
- Schwinning, S., Ehleringer, J.R., 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* 89, 464–480.

- Shantz, H.L., Piemeisel, L.N., 1927. The water requirement of plants at Akron, Colorado. *Journal of Agricultural Research* 34, 1093-1190.
- Sisson, W.B., 1989. Carbon balance of *Panicum coloratum* during drought and non-drought in the northern Chihuahuan Desert. *Journal of Ecology* 77, 799–810.
- Snyder, K.A., Donovan, L.A., James, J.J., Tiller, R.L., Richards, J. H., 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia* 141, 325-334.
- 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.
- Stroonsnijder, L., 1987. Soil evaporation: test of a practical approach under semi-arid conditions. *Netherlands Journal of Agricultural Science* 35, 417–426.
- Sturges, D.L. 1977. Soil water withdrawal and root characteristics of Big Sagebrush. *The American Midland Naturalist* 98(2), 257-274.
- Sturges, D.L., Trlica, M.J., 1978. Root weights and carbohydrate reserves of big sagebrush. *Ecology* 59, 1282-1285.
- Svejcar, T., Riegel, G.M., 1998. Spatial pattern of gas exchange for montane moist meadow species. *Journal of Vegetation Science* 9, 84–94.
- Toft, N.L., Anderson, J.E., Nowak, R.S., 1989. Water use efficiency and carbon isotope composition of plants in a cold desert environment. *Oecologia* 80, 11-18.
- Topp, G.C., Davis, J.L., Annan, A.P. 1980. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. *Water Resource Research* 16, 574–582.
- Topp, G.C., Davis, J.L. 1985. Measurements of soil water content using time-domain reflectometry. *Soil Science of America Journal* 49, 19-24.

- Trent, I.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.
- USDA, 2010. Keys to Soil Taxonomy. Natural Resources Conservation Service, US Department of Agriculture, Washington D C.
- Vertessy, R.A., Benyon, R.G., O’Sullivan, S.K., Gribben P.R., 1995. Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. Tree Physiology 15,559-567.
- Wallace, A., Bamberg, S.A., Cha, J.W., 1974. Quantitative studies of perennial plants in the Mojave Desert. Ecology 55, 1160–1162.
- Wan, C., Sosebee, R.E., McMichael, B.L., 1993a. Broom snakeweed responses to drought: photosynthesis, conductance, and water-use efficiency. Journal of Range Management 46, 355–359.
- Wan, C., Sosebee, R.E., McMichael, B.L., 1993b. Growth, photosynthesis, and stomatal conductance in *Gutierrezia sarothrae* associated with hydraulic conductance and soil water extraction by deep roots. International Journal of Plant Sciences 154, 144–151.
- Wan, C., R. E. Sosebee, McMichael. B.L., 1993c. Soil water extraction and photosynthesis in *Gutierrezia sarothrae* and *Sporobolus cryptandrus*. Journal of Range Management 46, 425–430.
- Wan, C., Sosebee, R.E., McMichael, B.L., 1994. Hydraulic properties of shallow vs. deep lateral roots in a semiarid shrub (*Gutierrezia sarothrae*). American Midland Naturalist 131, 120–127.
- Wilcox, C.S., Ferguson, J.W., Fernandez, G.C.J., Nowak, R.S., 2004. Fine root growth dynamics of four Mojave Desert shrubs as related to soil moisture and microsite. Journal of Arid Environments 56: 129-148.
- WRB, 2007. World Reference Base for Soil Resources, World Soil Resources Report, Vol. 103; FAO: Rome.

- Xu, Z.Z, Zhou, G.S., Shimizu, H., 2009. Are plant growth and photosynthesis limited by pre-drought following rewatering in grass? *Journal of Experimental Botany* 60, 3737-3749.
- Yoder, C.K., Boutton T.W., Thurow, T.L., Midwood, A.J., 1998. Differences in soil water use by annual broomweed and grasses. *Journal of Range Management* 51, 200–206.
- Zengel, S.A., Meretsky, V.J., Glenn, E.P., Felger, R.S., Ortiz, D., 1995. Cienega de Santa Clara, a remnant wetland in the Rio Colorado delta (Mexico): vegetation distribution and the effects of the water flow reduction. *Ecological Engineering* 4, 19-36.
- Zhu, Y., Wua, Y., Drake, S., 2004. A survey: Obstacles and strategies for the development of ground-water resources in arid inland river basins of western China. *Journal of Arid Environments* 59, 351–367.