

AN ABSTRACT OF THE THESIS OF -

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Abstract approved:

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Desert plant communities are among the most sensitive to changes in soil water conditions. In areas with shallow aquifers, it is important to understand both the effects of groundwater alterations on vegetation and how changes in surface-soil water affect plant water uptake. Studies in arid environments have evaluated the effect of groundwater variation and simulated precipitation on plant production and vegetation condition but it is not clear if plants respond equally to the availability of surface water or groundwater. This study was conducted in a greenhouse to evaluate growth and physiology of three desert graminoids (*Distichlis spicata*, *Leymus triticoides*, and *Juncus arcticus*) as affected by surface water availability (mimicking precipitation) or subsurface water availability (mimicking groundwater). The species of study are amply distributed

in wetlands and open rangelands of western USA and were collected from two sources - of ecological distribution: an area near Bishop, California, and an area near Burns, Oregon. The Bishop, California area has a characteristic shallow aquifer and plants in this area are considered somewhat dependent on groundwater. The Burns, Oregon, area sustains the same species but in a variety of soil moisture conditions. We had two general hypotheses for this study: 1) that the use of surface water is favored over groundwater and 2) that there are ecotypic differences in the response of the species to water availability. The first hypothesis was partially supported by the results of the study, but variability existed among species. However, when all species had equal access to both surface soil water and groundwater plants tended to preferentially use surface water. The second hypothesis was clearly supported by our results. Although the mechanism is not clear, it is possible that an area with periodic and predictable shallow groundwater underlying a dry or saline soil layer, such as the California site, might favor plant ecotypes with high proficiency in water acquisition by deeper roots. Knowledge of water use characteristics of vegetation is essential to provide management guidelines for areas where plants depend on both surface-soil water and groundwater. This study contributed to that knowledge. Further studies on ecotypic variation and an expansion to different species that inhabit areas with shallow aquifers are recommended.

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Physiological Impacts of Groundwater and Surface Water Application on Desert -
Graminoids of Different Geographic Origin -

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Mohamed Abdallah, Author -

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CONTRIBUTION OF AUTHORS -

Additional authors made significant contributions to this thesis. Dr. Ricardo Mata-Gonzalez 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. Jay Noller edited individual chapters.

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Physiological Impacts of Groundwater and Surface Water Application on Desert

Graminoids of Different Geographic Origin

INTRODUCTION:

Desert plant species and communities are highly sensitive to soil water availability because of the controlling role of water on plant physiology and ecosystem processes (Le Houerou et al. 1988; Huxman et al. 2005; Schwinning et al. 2005). Water use characteristics of plants are important for natural resources and water resources management, particularly in water-limited ecosystems (Ogle and Reynolds 2004).

Precipitation and groundwater are the two main natural sources of water for vegetation in arid environments (Chimner and Cooper 2004; McLendon et al. 2008). Because groundwater is often utilized for multiple purposes, including irrigated agriculture and human consumption, water use by vegetation in shallow aquifer areas is of direct significance for groundwater management and the concurrent demands of people and natural environments (Evans et al. 2013).

It is increasingly clear that a shallow aquifer provides additional water for plant growth and may support a greater biomass production than areas with no accessible groundwater (Naumburg et al. 2005; McLendon et al. 2008). Studies in arid environments have evaluated the effect of groundwater variation (Naumburg et al. 2005; McLendon et al. 2008; Mata-Gonzalez et al. 2012) and simulated precipitation on

plant production and vegetation condition (Evans et al. 2013). However, it is not clear if plants respond equally to the availability of surface water or groundwater.

Desert vegetation may use groundwater to varying degrees, either to provide enough water for transpiration and growth through a dry season or for the maintenance of ecosystems in otherwise arid environments (Hatton et al. 1998). In some cases groundwater is so important for plants that the variation in the condition of soil-surface water does not affect their growth or physiology as long as groundwater is present. This was the case with *Tamarix ramosissima*, a plant that often relies on groundwater in China (Xu and Li 2006; Xu et al. 2007). However, evidence also shows that often the use of surface water from precipitation is favored over the use of groundwater, even when the groundwater is available and within reach of plant roots (Nichols 1994; Schulze et al. 1996; Mounsif et al. 2002; McLendon et al. 2008; Brunel 2009; Devitt et al. 2011). For example, a Texas study with *Tamarix gallica*, a plant similar to *T. ramosissima*, showed that variations in gas exchange or stomatal conductance were mainly caused by water availability in the upper soil layers, not by changes in the depth to the water table (Mounsif et al. 2002). In addition, it has been demonstrated that under a constant level of groundwater, an increase in precipitation increases the comparative proportion of total perennial cover supported by precipitation while the proportion of cover supported by groundwater decreases (McLendon et al. 2008). Adiku et al. (2000) suggested if there is a homogeneous water distribution in the soil profile, plant water uptake will be greatest in the section where the root-length-density is also greatest.

However, as the soil profile dries out, water extraction patterns do not show any similarity to root distribution. Adiku et al. (2000) also reported an increased root activity at greater depths when the top sections of the soil become dry.

Desert graminoids are important components of vegetation communities in arid environment subsystems such as wetlands, riparian areas or shallow-aquifer areas (Miller et al. 1982; Svejcar and Riegel 1998; Mata-Gonzalez et al. 2012). Three graminoids were selected for this study: *Distichlis spicata*, *Leymus triticoides* and *Juncus arcticus*. These three species are widely distributed in western North America in a variety of microenvironments (Kemp and Cunningham 1981; Miller et al. 1982; Alpert 1990; Chambers and Linnerooth 2001). Because of this wide distribution, it is possible that the species are physiologically adapted to different local conditions (Kubiske and Abrams 1992). For example, Wan et al. (1995) found that ecotypic variation in water uptake, root growth, and transpiration existed between northern (Idaho) and southern (New Mexico and Texas) populations of *Gutierrezia sarothrae*. However, it has been stated that little information exists related to intraspecific ecotype comparisons of plant water relations and growth (Kubiske and Abrams 1992; Wan et al. 1995).

Differential acquisition of water as a function of soil depth has recently begun to be documented in plants of arid lands. The importance of shallow and deep water may greatly differ by species (Leffler et al. 2004; Mata-Gonzalez et al. 2013). Species that place relatively more importance on acquiring deeper sources of water are more likely to depend on groundwater than species that predominantly rely on surface water

(Evans 2011). A study that evaluated plant growth and photosynthesis demonstrated that the desert shrub *Artemisia tridentata* performed better when water was available in the upper soil layer, whereas a similar desert shrub, *Chrysothamnus nauseosus*, performed better when water was available in lower layers (Leffler et al. 2004). Mata-Gonzalez et al. (2013) found that *D. spicata*, *L. triticoides*, and *J. arcticus* obtained from 1.8 to 2.3 times more water from the 25-50 cm depth than from the 0-25 cm depth. These are low values compared to those obtained (>20) for desert shrubs such as *A. tridentata* or *Atriplex confertifolia* (Mata-Gonzalez et al. 2013) and signify that desert graminoids depend more on surface-soil water than desert shrubs. However, it is not clear if desert graminoids perform differently under different scenarios of depth water availability. Because groundwater is an important source of water in arid environments, understanding the effect of the supply of water from precipitation and from groundwater on plant growth and physiology would help to elucidate better water management strategies in arid ecosystems with shallow aquifers.

The purpose of study was to evaluate growth and physiological responses of the three selected desert graminoids (*D. spicata*, *L. triticoides*, and *J. arcticus*) as affected by surface water availability (mimicking precipitation) or subsurface water availability (mimicking groundwater). The study graminoids have two sources of ecological distribution: an area near Bishop, California and an area near Burns, Oregon. The California ecotypes are distributed in micro-topographical depressions and areas with shallow groundwater whereas the Oregon ecotypes are distributed in a variety of

conditions (see details in Methods). The general research question of this study is how would the supply of groundwater or surface water affect root and shoot biomass production and physiological processes in different ecotypes of desert graminoids? I hypothesized, in general, that the use of surface water is favored over groundwater and that there are ecotypic differences in the response of these species to water availability.

MATERIALS AND METHODS

This study was conducted in the greenhouse facilities of Oregon State University, Corvallis, to allow for adequate environmental control and imposition of water treatments. The temperature inside the greenhouse was maintained at 27 - 28 °C during the day and 10 – 15 °C at night to simulate temperature conditions from the areas where the plants were obtained. This study included three species: *D. spicata*, *J. arcticus*, and *L. triticoides* coming from two locations: the area of Burns, Oregon and the area of Bishop, California. Some growing conditions for both the California and Oregon ecotypes are detailed in Table 1.

D. spicata is a grass distributed in arid soils as well as in wetlands (Kemp and Cunningham 1981; Alpert 1990). The maximum reported root depth of *D. spicata* is 0.7 m (Dahlgren et al. 1997) but it may grow deeper roots (McLendon et al. 2008). *L. triticoides* is a grass that tends to grow in wetlands and low-lying areas whose maximum reported root depth of 1.5 m (Smoliak 1990; Mata-Gonzalez et al. 2012). *J. arcticus* is a rush (family Juncaceae) that is also abundant in wetland areas (Mata-Gonzalez et al.

2012). The typical root depth of *J. arcticus* is 0.4 m (Manning et al 1989) but it might grow roots up to 1.3 m (Sala and Nowak 1997). These species have several things in common 1) a creeping rhizomatous root system, 2) adaptation to wetlands or shallow-groundwater areas, 3) distribution in low-lying areas, and 4) high water requirements (Mata-Gonzalez et al. 2012; Evans et al. 2013).

Table 1. Habitat characteristics of the three species and ecotypes used in this study.

	Ecotypes	
	Bishop, California	Burns, Oregon
Species	Typical habitat	
<i>Distichlis spicata</i>	Shallow groundwater conditions, low lying areas	Open rangeland, no apparent groundwater access
<i>Leymus triticoides</i>	Shallow groundwater conditions, low lying areas	Temporally flooded lake area
<i>Juncus arcticus</i>	Shallow groundwater conditions, low lying areas	Temporally flooded riparian area

Plants from the California site were obtained from areas with sandy loam to loam soils, with saline soil surface, and groundwater typically present at 0.9 to 1.5 m depth (Natural Resources Conservation Service 2002). Plants from the Oregon site were

collected from sites without apparent groundwater (*D. spicata*) and from areas subjected to periodic river flooding (*J. arcticus*) or lake flooding (*L. triticoides*).

Plants of the different ecotypes were collected from the field in their areas of origin and transported to the greenhouse at Oregon State University. Plants were grown in plastic pots (25 cm height by 25 cm upper diameter) containing commercial growing medium for eight months to promote the growth of healthy individuals with strong roots and adapted to the greenhouse conditions. After this adaptation period, plants were transplanted to new pots that contained a mix of soil from river bank deposits and sand (7:3). The soil mix was analyzed at the Central Analytical Laboratory of Oregon State University. The soil mix had a pH of 6.7, a nitrate concentration of 11 ppm, an organic matter content of 1.3% and electrical conductivity of 0.5 mS cm^{-1} . The characteristic water retention curve of the soil mix was determined at the Soil Physics Laboratory of Oregon State University (Fig. 1). The water retention curve was developed using pressure plate data fitted to the van Genuchten soil hydraulic model (Bittelli and Flury 2009). The soil mix had a field capacity (-0.03 MPa) of 24% soil volumetric water content and a permanent wilting point (-1.5 MPa) of 0.05% soil volumetric water content.

The pots were arranged in a split-root apparatus (Wan et al. 2000) (Fig. 2, Fig A1) in which an upper pot was placed on top of a lower pot containing the same substrate (soil mix). Twenty holes (5 mm in diameter) were drilled at the bottom of the upper container to allow root penetration. Ten to 15 roots for each plant in each container

were manually forced to pass from the upper container to the lower container to ensure that roots were growing in both compartments. As a precaution against capillary movement of water between pots, a 1-cm layer of gravel was placed on top of the lower container. The edges of the lower container were covered with aluminum foil to minimize evaporation losses, but were uncovered to allow irrigation of the lower pot according to the treatments.

Plants were well-watered in the split-root apparatus for about one month in order to promote root establishment in both compartments. Subsequently, irrigation treatments started. Irrigation treatments were 1) top container wet and bottom container dry (TWBD), 2) top container dry and bottom container wet (TDBW), and 3) top container wet and bottom container wet (TWBW). The wet condition was obtained by watering to approximately achieve field capacity while the dry condition was achieved by not irrigating. This experiment simulated three situations that plants with access to groundwater might face: 1) available water from precipitation that penetrates surface (0-25 cm) soil layers but no access to groundwater in subsurface layers (deeper than 25 cm), 2) no access to precipitation water on the surface but access to groundwater in subsurface layers, and 3) access to both precipitation on the surface and groundwater on subsurface layers.

The three irrigation treatments were obtained by adding or restricting water to the top and bottom compartments for approximately three weeks until achieving the water levels desired by treatment. These water levels were maintained for two weeks

by replenishing water as needed. A four-week period of observations during which water was not replenished, was initiated. During the first week, the soil surface was covered to eliminate evaporation. During the following three weeks the soil surface of the top container was uncovered to allow evaporation but the soil surface (surrounding edge) of the bottom container was maintained covered with aluminum foil. During weeks 2, 3, and 4, plant and soil experimental evaluations were conducted.

Throughout the experimental period, soil volumetric water content was monitored in both the upper and lower containers by time domain reflectometry (TDR) using a pair of stainless steel probes (3.2 mm in diameter) inserted horizontally in the middle of the pots. The probes were 18 cm long and were separated 5 cm from each other. TDR readings were obtained with a Tektronix1502C TDR cable tester (Tektronix, Beaverton, OR) connected to the probes as in Wan et al. (1993). The TDR pulse readings were converted to a dielectric constant (K), which was used to calculate volumetric water content (Q) using the following empirical equation from Topp et al. (1980)

$$Q = -0.053 + 0.0292K - 0.00055K^2 + 0.0000043K^3.$$

The volumetric water content data obtained with the TDR were adjusted against gravimetrically attained water content as in Wan et al. (1993).

Following TDR measurements, soil water depletion was calculated as the difference between initial and final soil water content after the three weeks of measurements. This variable indicates the magnitude of evapotranspiration in the top pot and the magnitude of transpiration in the lower pot since the lower pot was not

subject to evaporation losses. We did not measure the proportion of evaporation and transpiration in top containers; we expected that water depletion would largely represent transpiration because we were measuring water content at a depth of 12.5 cm where evaporation should be lower than closer to the surface and because our species tend to have large transpiration-to-evaporation rates (Mata-Gonzalez et al. 2013).

Pre-dawn leaf water potential in all plants was measured with a pressure chamber (AMS Instrumental, Corvallis, OR) for three leaves of every plant (Doescher et al. 1997). Photosynthesis and transpiration were measured in all plants using a portable photosynthesis system (Li-Cor 6400, Li-Cor, Inc, Lincoln, NE) with a supplemental light source (Li-Cor 6400-02, Li-Cor, Inc., Lincoln, NE) to prevent stomatal closure caused by chamber orientation, transient clouds, or shadows in the greenhouse. The photosynthetically active radiation (PAR) was set at $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ with the supplemental light source to represent ambient light inside the greenhouse (Leffler et al. 2004). Measurements were taken on representative leaves of each plant and repeated three times. Each species was measured on a different day to shorten the period of time needed to complete the measurements.

At the end of week 4 and after completion of the physiological measurements, plant shoots were cut to ground level and collected in paper bags. Roots were collected from the top and bottom containers by carefully removing soil and sifting by hand and

placed in paper bags. The paper bags containing shoots and roots were oven-dried at 68 °C for 48 hours and weighed (Evans et al. 2013).

The experiment was arranged as a factorial (3 watering treatments, 3 species, 2 ecotypes, and 5 replications) for a total of 90 experimental units (each consisting of a split-root apparatus containing a single plant). The physical arrangement of the experimental units in the greenhouse followed a randomized design. Differences among ecotypes and water distribution treatments were determined by analysis of variance (ANOVA). Means were separated with protected Fisher's least significant difference at $P < 0.05$. All analyses were performed with SPSS statistical software (SPSS Inc. 2000)

RESULTS

Juncus arcticus

Biomass

The water distribution treatments produced significant differences ($P < 0.05$) in aboveground mass in the California ecotype but not in the Oregon ecotype (Fig. 3). In the California ecotype, aboveground mass was greatest in plants with water in both compartments (TWBW), followed by plants with water only in lower pot (TDBW) and least in plants with water only in top pot (TWBD). With respect to top root mass, the treatments affected ($P < 0.05$) the Oregon ecotype but not the California ecotype. In the Oregon ecotype, the treatments with low pot watering (TDBW and TWBW) produced greater mass than the treatment with only top irrigation (TWBD). Bottom root mass in both ecotypes was significantly ($P < 0.05$) and similarly affected by treatments. Treatments with irrigation in the lower pot (TDBW and TWBW) produced greater mass than the treatment with only top irrigation (TWBD).

Soil volumetric water content

Top soil water declined ($P < 0.05$) through the weeks of measurements for both ecotypes in treatments with top irrigation (TWBW and TWBD), but remained largely unchanged in the treatment with dry top (TDBW) (Fig. 4). The rate of decline in soil

water content through time was approximately constant for both TWBW and TWBD in both ecotypes. Bottom soil water content declined through the weeks of measurements for the treatments with bottom pot irrigation (TDBW and TWBW), but only in the California ecotype. An unexpected increase in water content was observed in the TWBD treatment for both ecotypes, although only in the Oregon ecotype was that statistically significant.

Soil water depletion

Soil water depletion from the top container was similarly affected by the water distribution treatments in both ecotypes (Fig. 5). As expected, the two treatments with top irrigation (TWBD and TWBW) had greater (7 - 8 times) top soil water depletion than the treatment without top irrigation (TDBW). Also, as expected, the two treatments with bottom irrigation (TDBW and TWBW) had greater bottom soil water depletion than the treatment with no bottom irrigation (TWBD). However, an unexpected result was that the treatment with only top irrigation (TWBD) produced negative depletion or a net gain in soil water in both ecotypes. In general, water depletion was of greater magnitude in the top than in the bottom compartment, but this was particularly noticed in the Oregon ecotype.

Predawn water potential

Water potential became more negative through time for both ecotypes (Fig. 6), reflecting the lower water availability. The water distribution treatments produced more noticeable differences ($P < 0.05$) in water potential in the California ecotype than in the Oregon ecotype. However, in general for both ecotypes, plants under the TDBW treatment had the most negative water potential and plants under the TWBW treatment had the least negative water potential. Plants with the TWBW treatment experienced the least changes in water status through time.

Gas exchange

Photosynthesis rate declined through time for both ecotypes and the rate of decline was not affected by the water distribution treatments (Fig. 7). The general rate of photosynthesis decline was more pronounced in the Oregon ecotype than in the California ecotype. At the end of the measurement period the photosynthesis rate in the California ecotype was one third of the initial rate while for the Oregon ecotype it was only one sixth.

Transpiration rate tended to decline through the weeks of measurement but the decline was only significant ($P < 0.05$) in the California ecotype (Fig. 8). Even in the California ecotype the rate of decline was much lower than the decline observed in

photosynthesis. In general, the treatment with greater transpiration rate was TWBW and the treatment with lower transpiration rate was TDBW.

Distichlis spicata

Biomass

The water distribution treatments produced significant differences ($P < 0.05$) in aboveground mass in the California ecotype but not in the Oregon ecotype (Fig. 9). In the California ecotype plant production was 3 to 4 times greater for both treatments with irrigation in lower pot (TWBW and TDBW) than on the treatment with only top irrigation (TWBD). Similar to aboveground mass, the water distribution treatments affected ($P < 0.05$) the top root production in the California ecotype but not in the Oregon ecotype. The treatments with irrigation in the lower pot (TWBW and TDBW) produced greater top root mass than the treatment with only top irrigation (TWBD). Bottom root mass was not different among treatments for the California ecotype. For the Oregon ecotype, the treatment with the dry bottom pot (TWBD) had significantly greater ($P < 0.05$) bottom root mass than the other treatments. However, bottom root mass was in general very low (≤ 1 g) regardless of treatments or ecotypes.

Soil volumetric water content

Soil water content varied by treatments ($P < 0.05$) but not by ecotypes (Fig. 10).

Top soil water declined similarly through the weeks of measurement for both ecotypes in the treatments with top irrigation (TWBW and TWBD). For these two treatments there was a 40% decline in top soil water content at the end of the measurement period. In contrast, no changes in top soil water content were observed through time for both ecotypes in the treatment without top irrigation (TDBW). Bottom soil water declined in a similar fashion for treatments with water in the bottom pot (TDBW and TWBW) in both ecotypes. However, the decline was less pronounced (about 8-10%) than the decline observed in top soil water. No changes in bottom soil water were observed in TWBD, the treatment with no irrigation in the bottom pot.

Soil water depletion

Soil water depletion in both top and bottom compartments was similarly affected by the water distribution treatments for both ecotypes (Fig. 11). As expected, the two treatments with top irrigation (TWBD and TWBW) had greater (7 -9 times) top soil water depletion than the treatment without top irrigation (TDBW). Also, as expected, the two treatments with bottom irrigation (TDBW and TWBW) had greater bottom soil water depletion (7 to 10 times) than the treatment with no bottom irrigation (TWBD). In general, water depletion was of greater magnitude in the top than in the bottom compartment. Specifically, for the treatment with water in both

compartments (TWBW) water depletion was three times greater in the top than in the bottom compartment.

Predawn water potential

The water distribution treatments produced more noticeable differences ($P < 0.05$) in water potential in the California ecotype than in the Oregon ecotype (Fig. 12). However, in general for both ecotypes, water potential became more negative through time. In the California ecotype, the TDBW treatment had consistently more negative water potential than the other treatments while the TWBW treatment had the least negative water potential. Although in the Oregon ecotype the responses were not always different, both ecotypes had lower water potential on the treatment with water in both compartments (TWBW).

Gas Exchange

Photosynthesis was similarly affected by the water distribution treatments for both ecotypes (Fig. 13). For both ecotypes, there was a steep decline in photosynthesis rate through time regardless of treatments. The water distribution treatments affected transpiration in both ecotypes similarly (Fig. 14).

There was a similar decline through time in transpiration for both ecotypes. In the Oregon ecotype and for the third week, transpiration was 30% greater on the treatment with water in both compartments (TWBW) than on the treatment with only irrigation in top pot (TWBD) or the treatment with only irrigation in lower pot (TDBW).

Leymus triticoides

Biomass

The water distribution treatments produced significant differences ($P < 0.05$) in aboveground mass in both ecotypes (Fig. 15). In the California ecotype, plant production was more than three times greater on both treatments with irrigation in lower pot (TWBW and TDBW) than on the treatment with only top irrigation (TWBD). In the Oregon ecotype, mass production was 60% higher in the TDBW treatment than in the TWBW treatment. The water distribution treatments did not affect the top root mass production in the California ecotype. In the Oregon ecotype, both treatments with bottom watering (TWBW and TDBW) produced more top root mass than the treatment without bottom watering (TWBD). The water distribution treatments produced significant differences on bottom root mass in the California ecotype but not in the Oregon ecotype. In the California ecotype, plants with the TWBD treatment had the least bottom root mass.

Soil volumetric water content

Top soil water declined ($P < 0.05$) for both ecotypes and through the weeks of measurements for the treatments with top irrigation (TWBW and TWBD) (Fig. 16). For these two treatments there was a 40% decline in top soil water content at the end of the measurement period. In contrast, no changes in top soil water content were observed through time for both ecotypes in the treatment without top irrigation (TDBW). Bottom soil water declined for treatments with water in the bottom pot (TDBW and TWBW) in both ecotypes. However, the decline was less pronounced (about 8-12%) than the decline observed in top soil water. The treatment with only top water (TWBD) produced no changes through time in bottom soil water content for both ecotypes.

Soil water depletion

Soil water depletion in the top compartment was similarly affected by the water distribution treatments for both ecotypes (Fig. 17). As expected, the two treatments with top irrigation (TWBD and TWBW) had greater (more than 10 times) top soil water

depletion than the treatment without top irrigation (TDBW). Also, as expected, the two treatments with bottom irrigation (TDBW and TWBW) had greater bottom soil water depletion than the treatment with no bottom irrigation (TWBD). In general, water depletion was of higher magnitude in the top than in the bottom compartment.

Predawn water potential

The water potential patterns in *L. triticoides* were differently affected by treatments than the other two species. In both ecotypes, there was a trend of decline in the treatments with irrigation in lower pot (TWBW and TDBW), but the opposite was observed in the treatment with top irrigation (TWBD) (Fig. 18). Interestingly, for the most part, both ecotypes had lower water potential on the treatment with irrigation in lower pot (TDBW), which was different from the other species.

Gas Exchange

In the California ecotype and for the second and third weeks, photosynthesis was greater on the treatment with water in both compartments (TWBW) than on the other two treatments (Fig. 19). At the fourth week, photosynthesis further declined and was not different among treatments. In the Oregon ecotype for the second week, photosynthesis was greater on the treatments with irrigation in top pot (TWBW and

TWBD) than on the treatment with no irrigation in the top pot (TDBW). For the third week, photosynthesis declined and was greater on the treatment with irrigation on both compartments (TWBW) than on the other two treatments. As in the California ecotype, the water distribution treatments did not produce significant differences in photosynthesis among treatments during the fourth week.

In the California ecotype, transpiration was only greater on the treatment with water in both compartments (TWBW) than on the other treatments on the third week (Fig. 20). For the Oregon ecotype transpiration was greater on the treatments with irrigation in the top pot (TWBW and TWBD) than on the treatment with no irrigation in the top pot (TDBW) in the second week. In the Oregon ecotype also and for the third week, transpiration was greater on the treatment with irrigation on both compartments (TWBW) than on the other two treatments. The water distribution treatments did not produce significant differences in transpiration for both ecotypes at end of measurements.

DISCUSSION

I hypothesized, in general, that plants favor the use of surface soil water over groundwater. This can be analyzed from different perspectives. It can be expected that if plants favor surface-soil water over groundwater, plants with available surface water would grow more than plants with only groundwater. Results of this experiment did not

support this expectation, although there were variations by ecotype. Aboveground mass for the three species of study was lower when the plants had access to surface water than when the plants had access to groundwater, but only in the California ecotypes. In the Oregon ecotypes, the water distribution treatments produced little differences in aboveground mass for the three species. It appeared that, even across species, the California ecotypes responded more to the presence of groundwater than the Oregon ecotypes. This happened even though the root mass in the bottom compartment was mostly similar among ecotypes. This result suggests that the root systems of three species in the California site are better adapted to groundwater uptake than the same species in the Oregon sites. The water depletion data from the bottom compartment further supports that the California ecotypes are better at withdrawing groundwater than the Oregon ecotypes. This result can be related to the observation that the California ecotypes grow in areas with shallow water table (0.9 to 1.5 m) (Natural Resources Conservation Service 2002) underlying a dry soil layer at least some part of the year. Thus, presumably the California ecotypes are well adapted to acquire subsurface water (Mata-Gonzalez et al. 2012). In addition, the California ecotypes grow in areas with surface soils affected by salinity (Natural Resources Conservation Service 2002) which makes even more important for these plants to be able to acquire subsurface water. In contrast, the Oregon ecotypes do not grow in areas with shallow groundwater underlying dry or saline surfaces. Rather, the Oregon ecotypes seem adapted to occasional flooding (*J. arcticus* and *L. triticooides*) or only to surface moisture

(*D. spicata*). Although the results of this study require additional tests, it is suggested that the California ecotypes, growing in environments with shallow groundwater underlying dry or saline soil layers, have adapted to efficiently acquire water from subsurface layers utilizing deeper roots. The importance of intraspecific genetic variation for populations' success in variable environments is still poorly understood (Kubiske and Abrams 1992; Zhang et al. 2005) but clearly deserves further investigation.

Soil water depletion varied by species and ecotypes. In the California ecotype of *J. arcticus*, water depletion was similar in top and bottom containers for equivalent treatments (TWBD and TDBW). Therefore, this ecotype would be equally able to use water from precipitation or from the soil aquifer when available. This is remarkable because the root mass in the bottom container was only 1/30th of that in the top container. The Oregon ecotype of *J. arcticus*, the top roots were able to get three times more water than the bottom roots, which reinforces the theory that the California ecotype is better adapted to obtain groundwater than the Oregon ecotype.

In both ecotypes of *D. spicata* water depletion was about three times greater in top roots than in bottom roots for equivalent treatments (TWBD and TDBW). Although still remarkable given the small proportion of bottom root biomass, the water uptake of *D. spicata* seems more favored from the surface than from groundwater. In *L. triticoides*, a somewhat similar response to *J. arcticus* was observed. The California ecotype of *L. triticoides* had similar water uptake from top and bottom containers in equivalent treatments (TWBD and TDBW) but the Oregon ecotype was not as proficient

at obtaining groundwater as the California ecotype. Therefore, our general hypothesis that plants tend to favor the use of surface soil water over groundwater was supported in some species and ecotypes.

The treatment with water in both compartments (TWBW) provided another test of our hypothesis. In this case plants had equally available water for top and deeper roots. Under this condition, all species and ecotypes favored water uptake from the soil surface. In all species and ecotypes, water uptake from the top container was at least double that from the bottom container. Results from the TWBW treatment confirmed the observations that *D. spicata* tends to prefer surface water more than *J. arcticus* and *L. triticoides* and that the California ecotypes are better able to withdraw groundwater than the Oregon ecotypes. Previous studies (Goedhart et al. 2010; Kray et al. 2012) have shown that *D. spicata* tends to favor surface water use over groundwater and Kray et al. (2012) even stated that *D. spicata* does not function as a phreatophyte in some environments. In contrast, *D. spicata* was found to rely more on groundwater than some typical phreatophytes such as *Atriplex torreyi* in the Owens Valley, California (McLendon et al. 2008) and it is often mentioned that *D. spicata* is usually associated with shallow groundwater areas (Miller et al. 1982; Nichols 1994; Mata-Gonzalez et al. 2012). *D. spicata* is an environmentally versatile species (Kemp and Cunnigham 1981; Alpert 1990) that might be better adapted to surface water than to groundwater but can function well and successfully compete in shallow aquifer conditions.

An unexpected result was observed in water depletion of *J. arcticus* under the TWBD treatment. For both ecotypes, the dry bottom compartment became significantly wetter during the experiment. This was not observed in the other species and, therefore, the possibility of simple water movement by gravity was ruled out. Simple gravitational water leakage from the top to the bottom pots was also unlikely because initial irrigation was applied only to reach field capacity. I suggest that *J. arcticus* transferred water from the top to the bottom compartment through its roots and deposited it into the lower soil rooting matrix. This phenomenon is known as inverse hydraulic redistribution and tends to occur as downward root transfer of water when upper soil layers with low permeability become wet (Schulze et al. 1998; Burgess et al. 2001). Inverse hydraulic redistribution may serve as crucial mechanism to facilitate root growth and survival in very dry soil layers underlying surface soil where precipitation penetrates (Schulze et al. 1998). We speculate that this phenomenon occurred just in *J. arcticus* because of its greater root length per unit leaf area or its efficient water conducting system (Svejcar and Riegel 1998). Inverse hydraulic lift may serve *J. arcticus* to maintain root growth at deeper soil layers when groundwater is not present and to be better able to acquire water when groundwater becomes available.

There was a trend of increased water potential through time for both ecotypes of *J. arcticus* and *D. spicata*. However, in *L. triticoides* for both ecotypes, there was a trend of decline in the treatments with irrigation in the lower pot (TWBW and TDBW). However the opposite was observed in the treatment with top irrigation (TWBD). In

general, both ecotypes of *J.* and *D. spicata* had lower water potential under the treatment with water in both compartments (TWBW). But, this was not clear for *L. triticoides*. The TDBW treatment resulted in greater plant stress for both *J. arcticus* and *D. spicata* even though the same treatment resulted in greater aboveground production. It is possible that plants can rely on groundwater for growth, but perhaps in the long term it might become too stressful to only depend on groundwater. Adiku et al. (2000) indicated that if there is a homogeneous water distribution in the soil profile, plant water uptake will be greatest in the section where the root length density is also greatest. This might lead to less stress. However, as the soil profile dries out, water extraction patterns do not show any similarity to root distribution (Adiku et al. 2000).

In general, gas exchange was not affected by the treatments. That was indicated previously when Sala and Nowak (1997) discovered that there was no difference in leaf gas exchange for plants growing near a creek from those occurring distant from the creek. Leffler et al. (2004) also found that the gas exchange rate for *A. tridentata* was the same for all watering treatments indicating that this species was effective in utilizing water regardless of where it was applied. *D. spicata* in general had greater photosynthesis than the other two species. In Owens Valley, California, it was shown previously that *D. spicata* had generally greater photosynthesis in comparison to two other shrubs; *A. torreyi* and *Ericameria nauseosa* (Pataki et al. 2008). *J. arcticus* in general had greater transpiration than the other species. That finding was concurrent with another experiment where transpiration rate in general was greater in *J. arcticus*

than in *Carex lanuginosa* and *Carex nebrascensis* (Sala and Nowak 1997). The greater photosynthesis and relatively low transpiration rate of *D. spicata* results in greater water use efficiency because of its C₄ metabolism (Waller and Lewis 1979).

CONCLUSIONS

I had two general hypotheses for this study: 1) that the use of surface water is favored over groundwater and 2) that there are ecotypic differences in the response of the species to water availability. The first hypothesis was supported in some cases but variability existed among species. However when all species had equal access to both surface soil water and groundwater, plants tended to preferentially use surface water. The second hypothesis was clearly supported by our results. Although the mechanism is not clear, it is possible that an area with periodic and predictable fluctuations of groundwater, such as the California site, might favor higher proficiency in water acquisition by deeper roots than other areas.

Arid environments with groundwater within the reach of plants roots exist in many areas of North America and other parts of the world. Groundwater management in these environments should consider the competing need of fresh water for agriculture and urban uses with the need of water to maintain healthy vegetation communities. Knowledge of water use characteristics of vegetation is essential to provide management guidelines for areas where plants depend on both surface-soil

moisture and groundwater. This study contributed to provide some more pieces of that knowledge. Further studies on ecotypic variation and an expansion to different species that inhabit areas with shallow aquifers are recommended.

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FIGURES

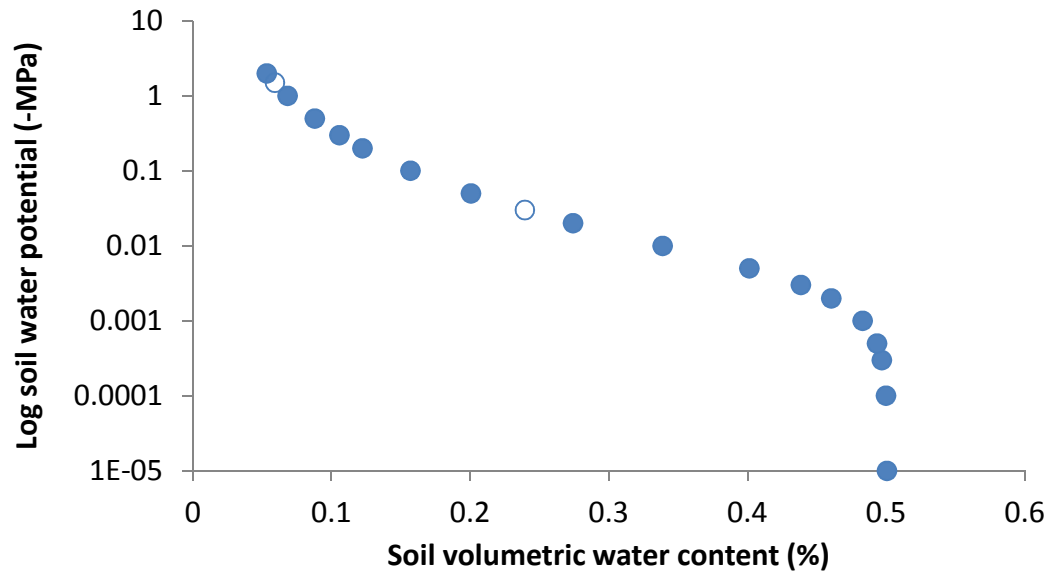


Figure 1. Characteristic soil water retention curve for the soil mix of the study. Values with empty symbols indicate the soil moisture at -0.03 MPa (field capacity) and -1.5 MPa (permanent wilting point).

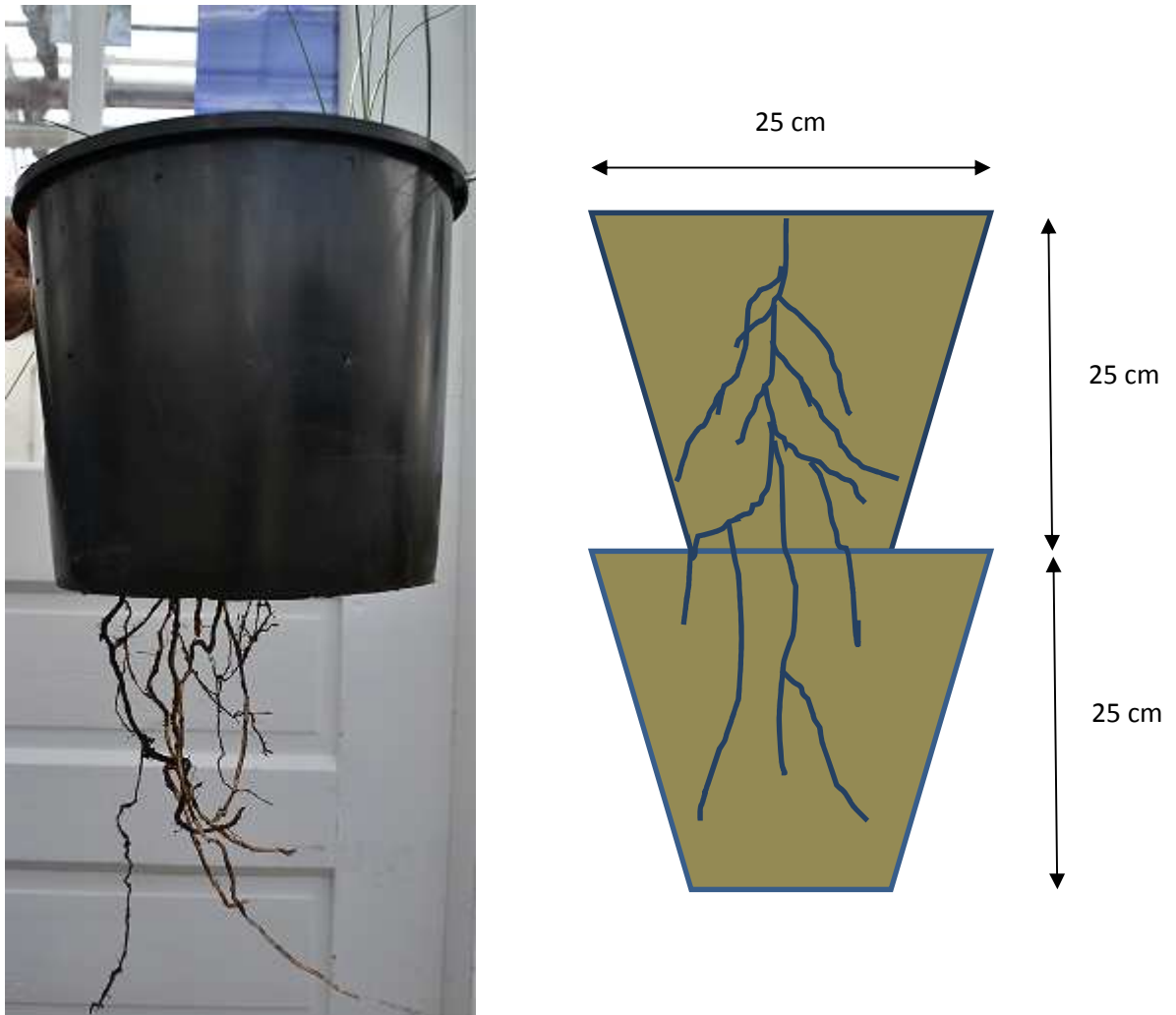


Figure 2. Split-root apparatus showing the intended root distribution of a single plant into two containers that were individually managed to control water availability. Roots were manually passed through the bottom of the top container to the lower container to ensure that roots were actually growing in the lower container.

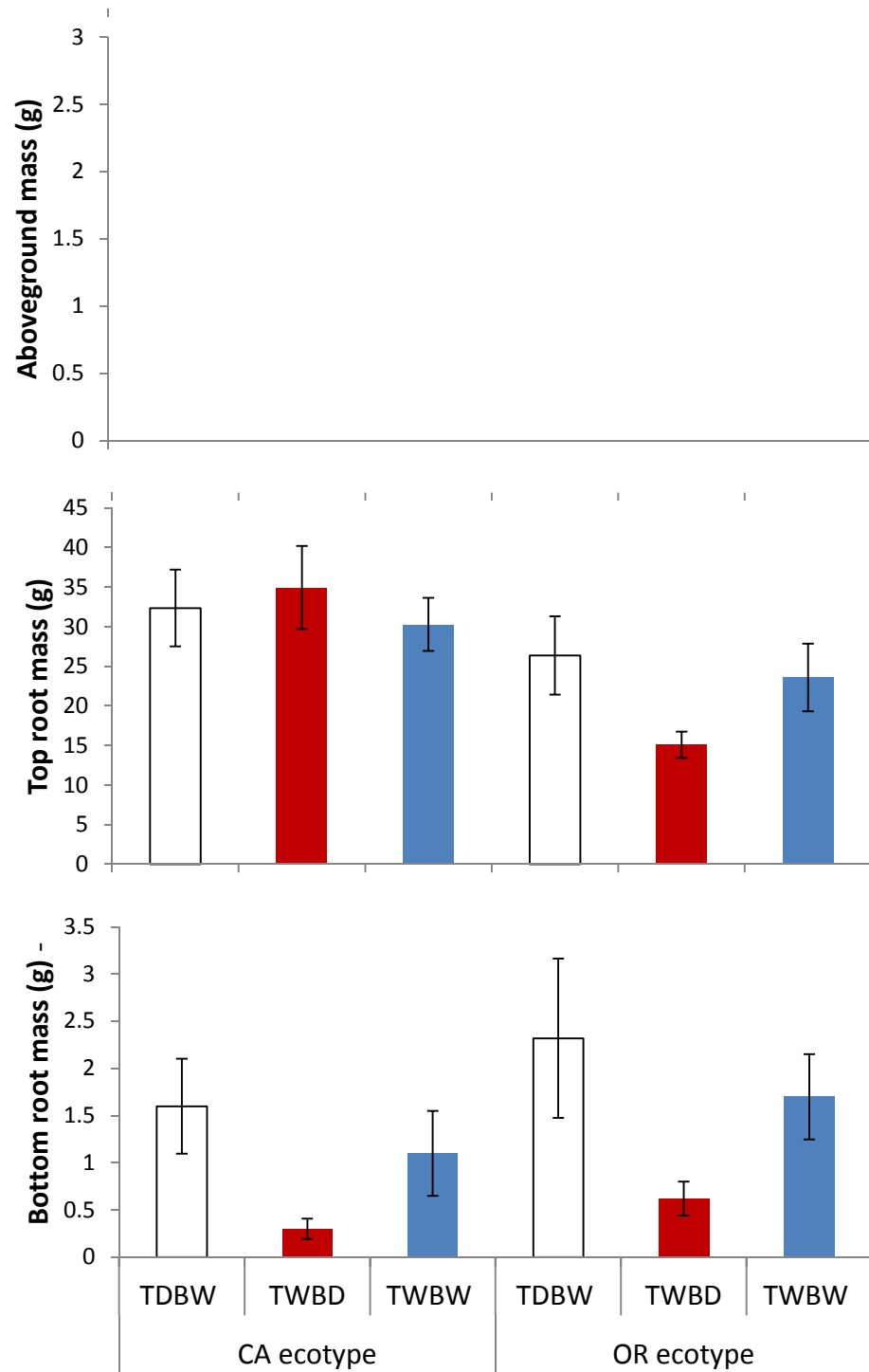


Figure 3. Biomass components of two *Juncus arcticus* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error

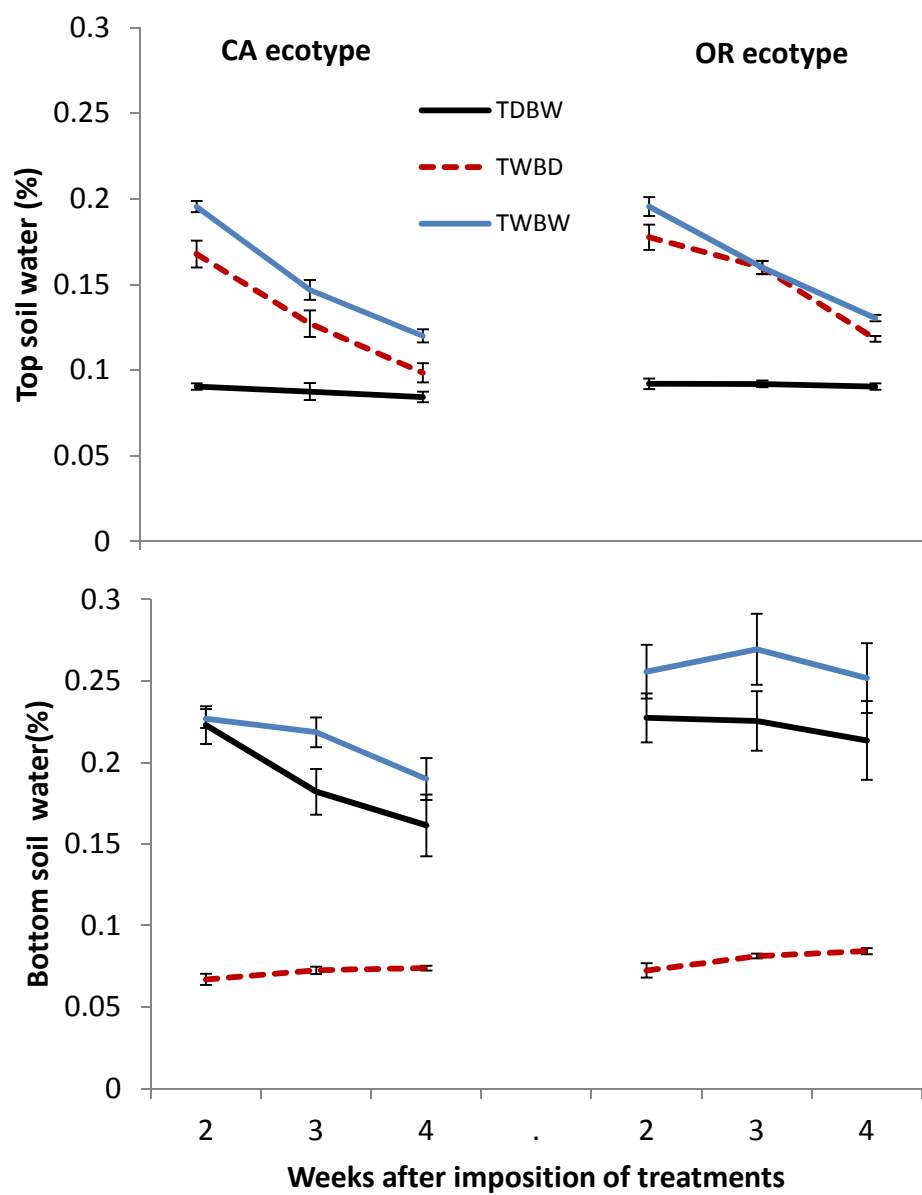


Figure 4. Volumetric soil water content through time for two *Juncus arcticus* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

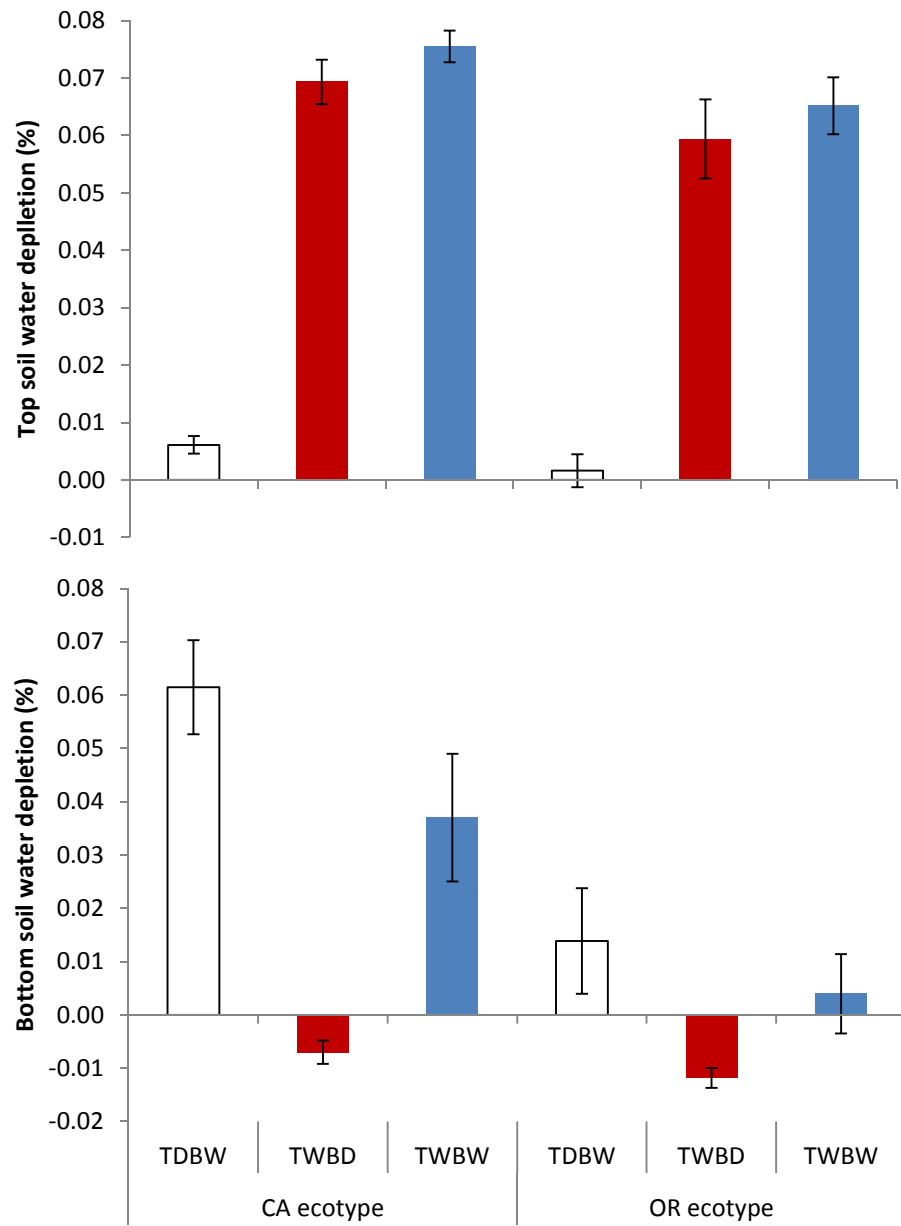


Figure 5. Soil water depletion for two *Juncus arcticus* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

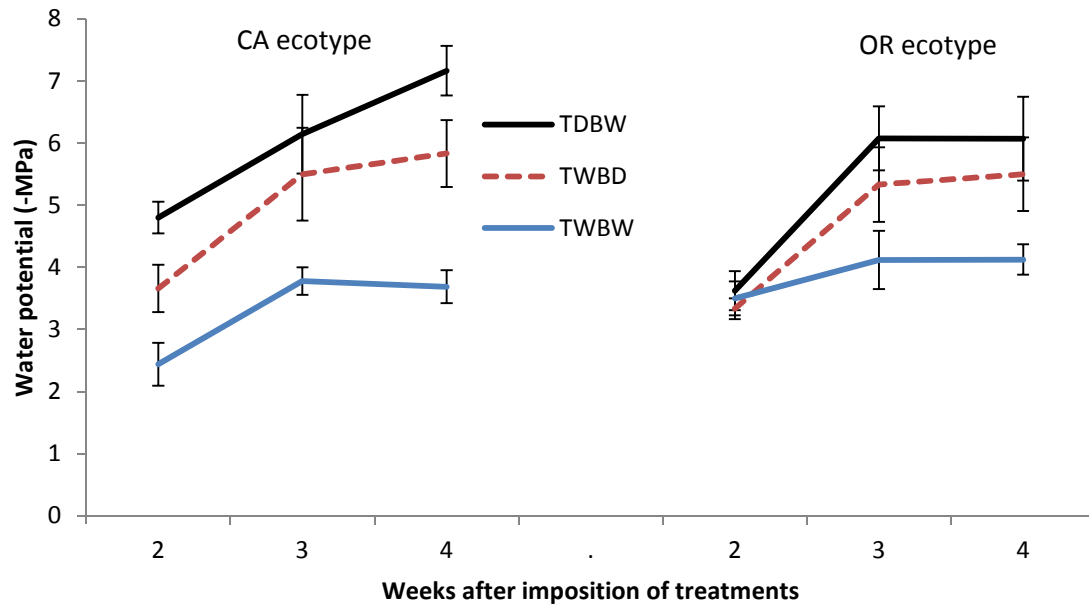


Figure 6. Water potential through time for two *Juncus arcticus* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

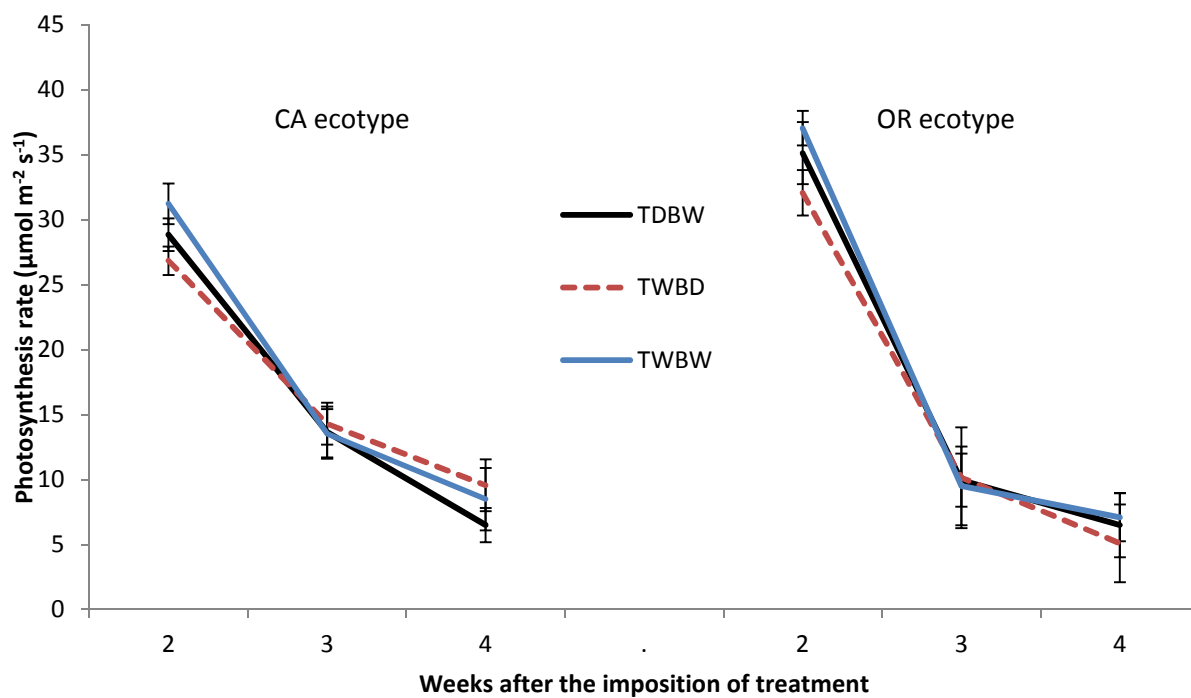


Figure 7. Photosynthesis through time for two *Juncus arcticus* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

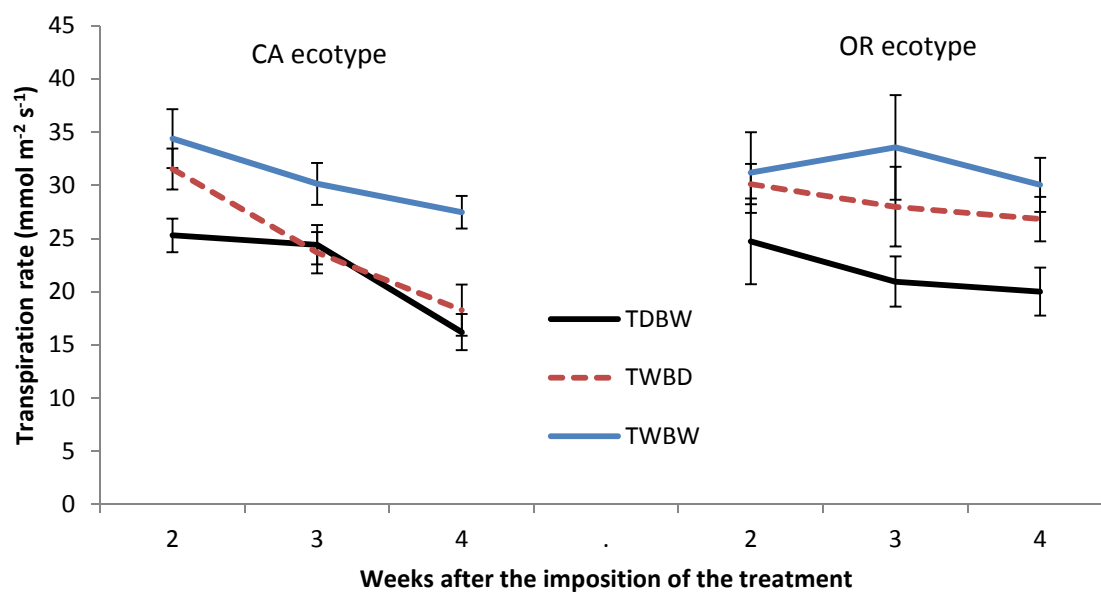


Figure 8. Transpiration through time for two *Juncus arcticus* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

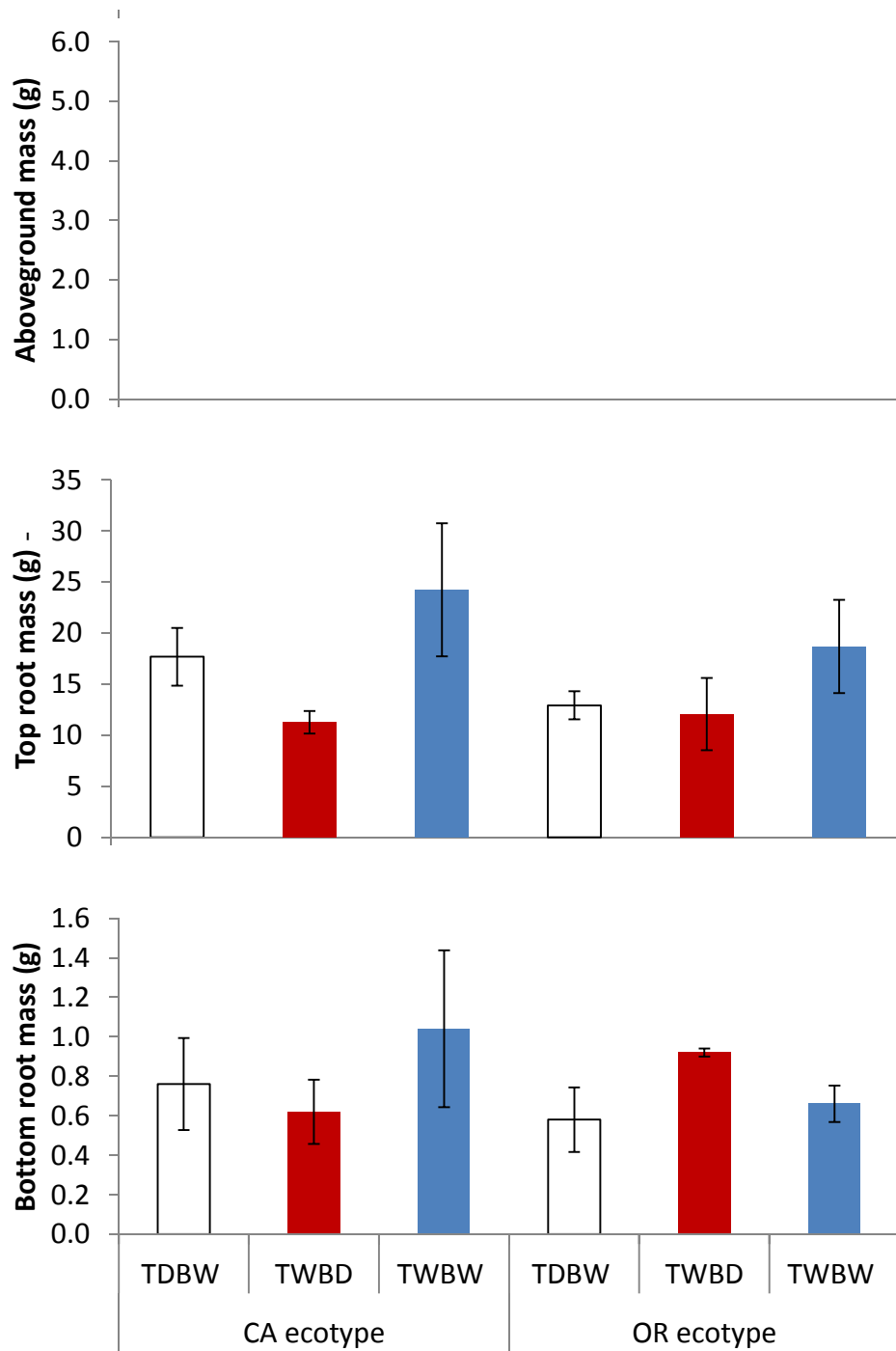


Figure 9. Biomass components of two *Distichlis spicata* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

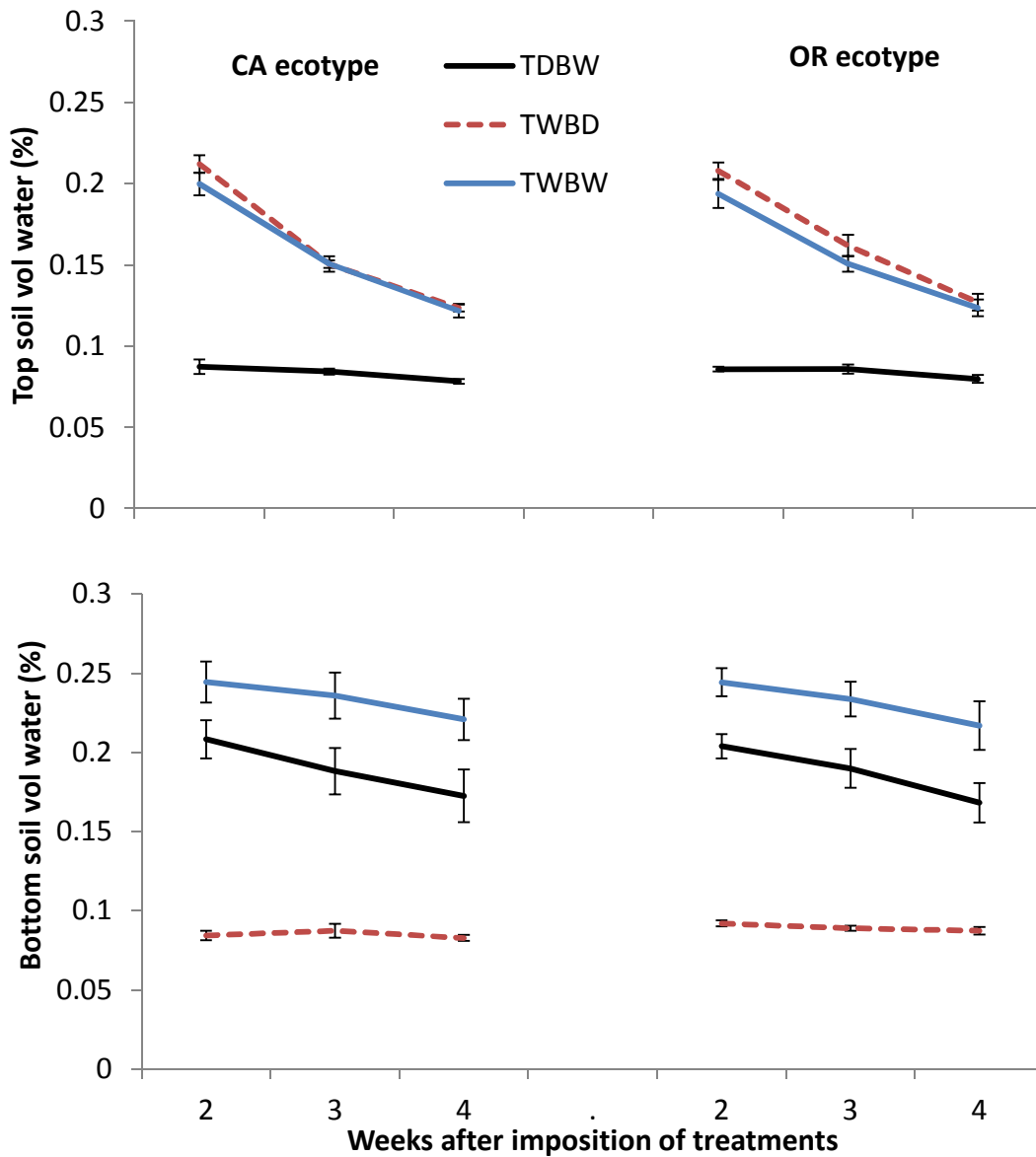


Figure 10. Volumetric soil water content through time for two *Distichlis spicata* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

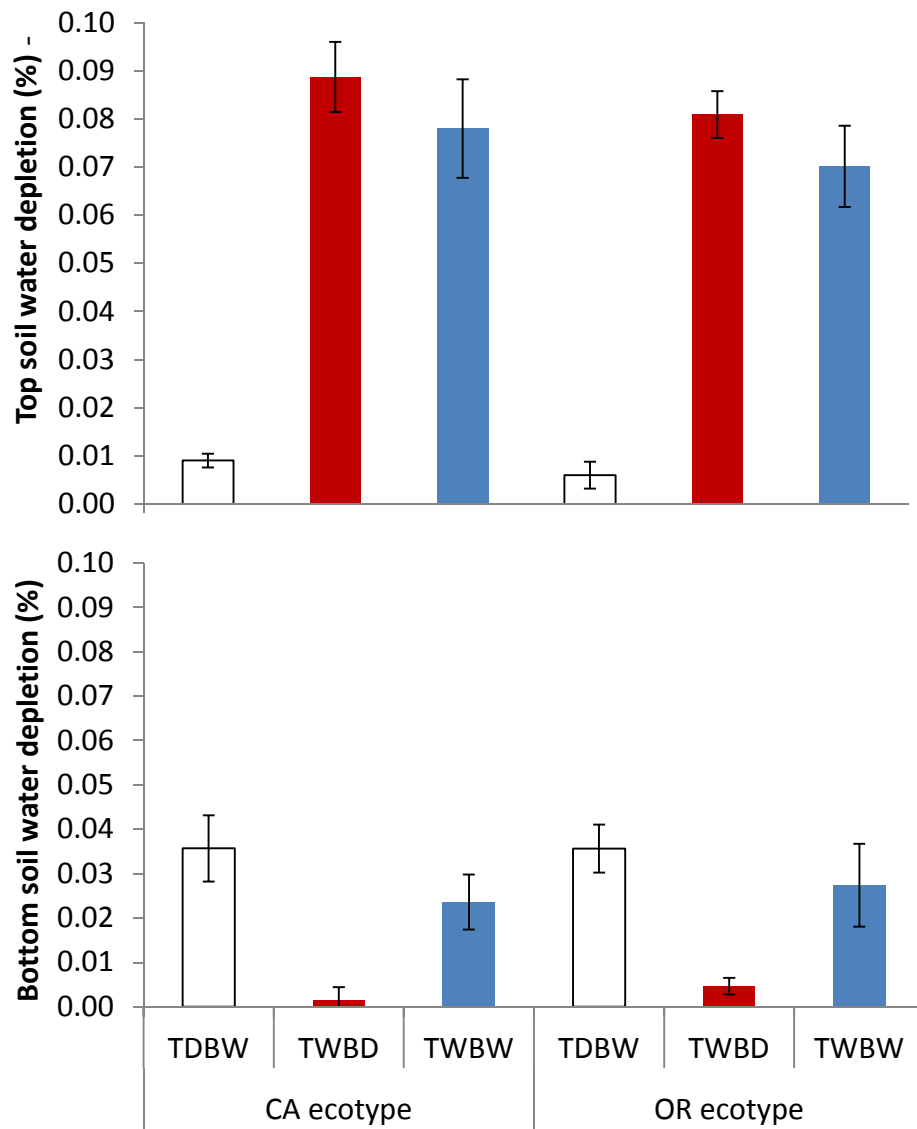


Figure 11. Soil water depletion at the end of the experiment for two *Distichlis spicata* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

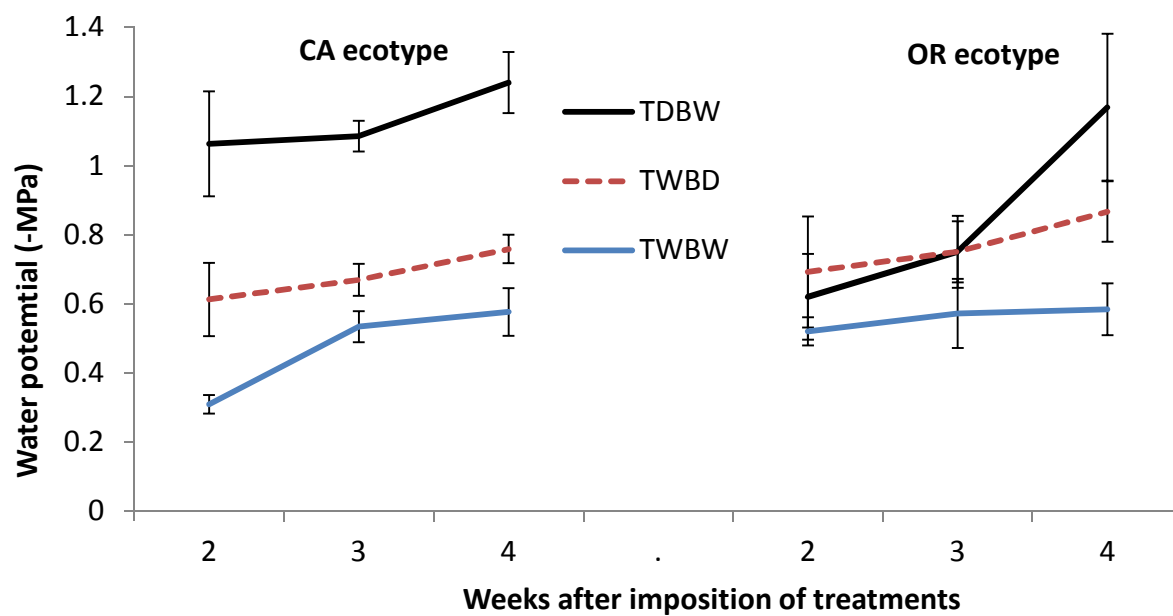


Figure 12. Water potential through time for two *Distichlis spicata* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

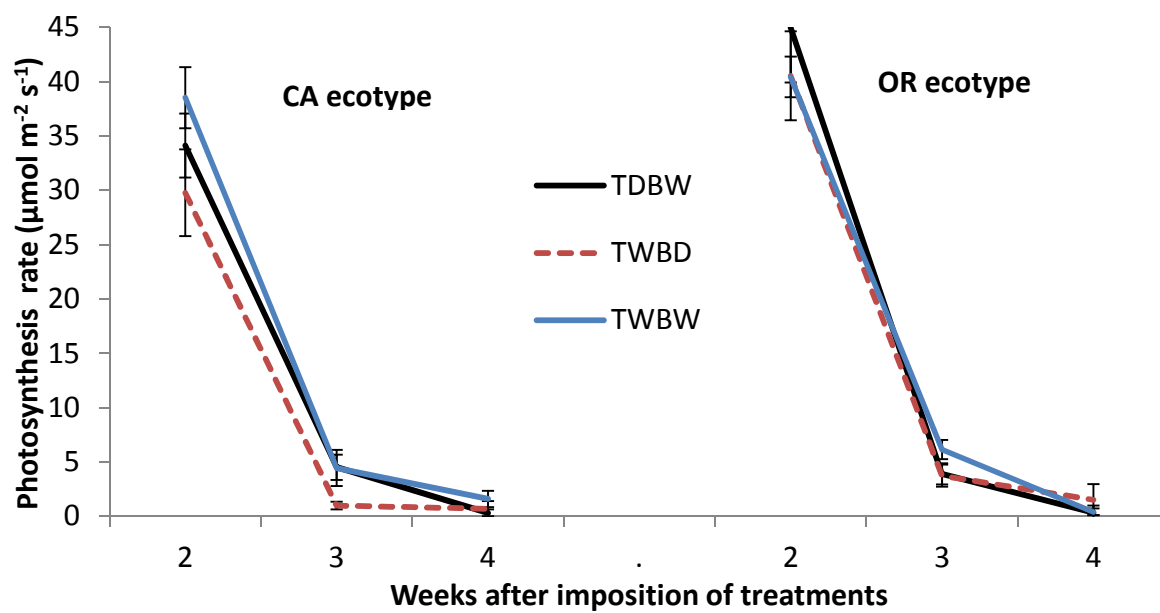


Figure 13. Photosynthesis through time for two *Distichlis spicata* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

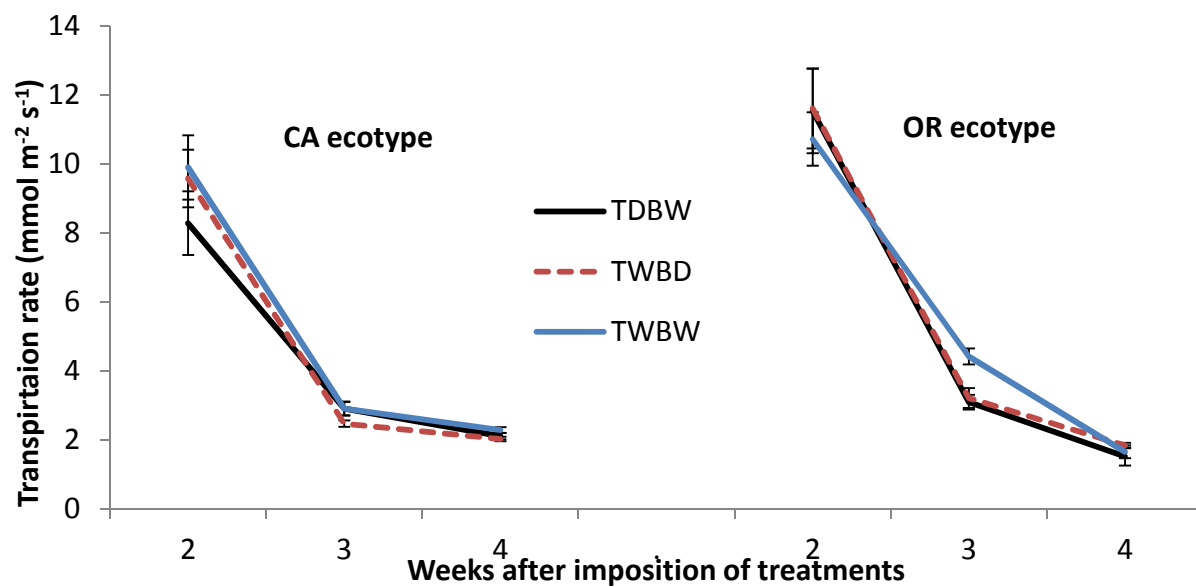


Figure 14. Transpiration through time for two *Distichlis spicata* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

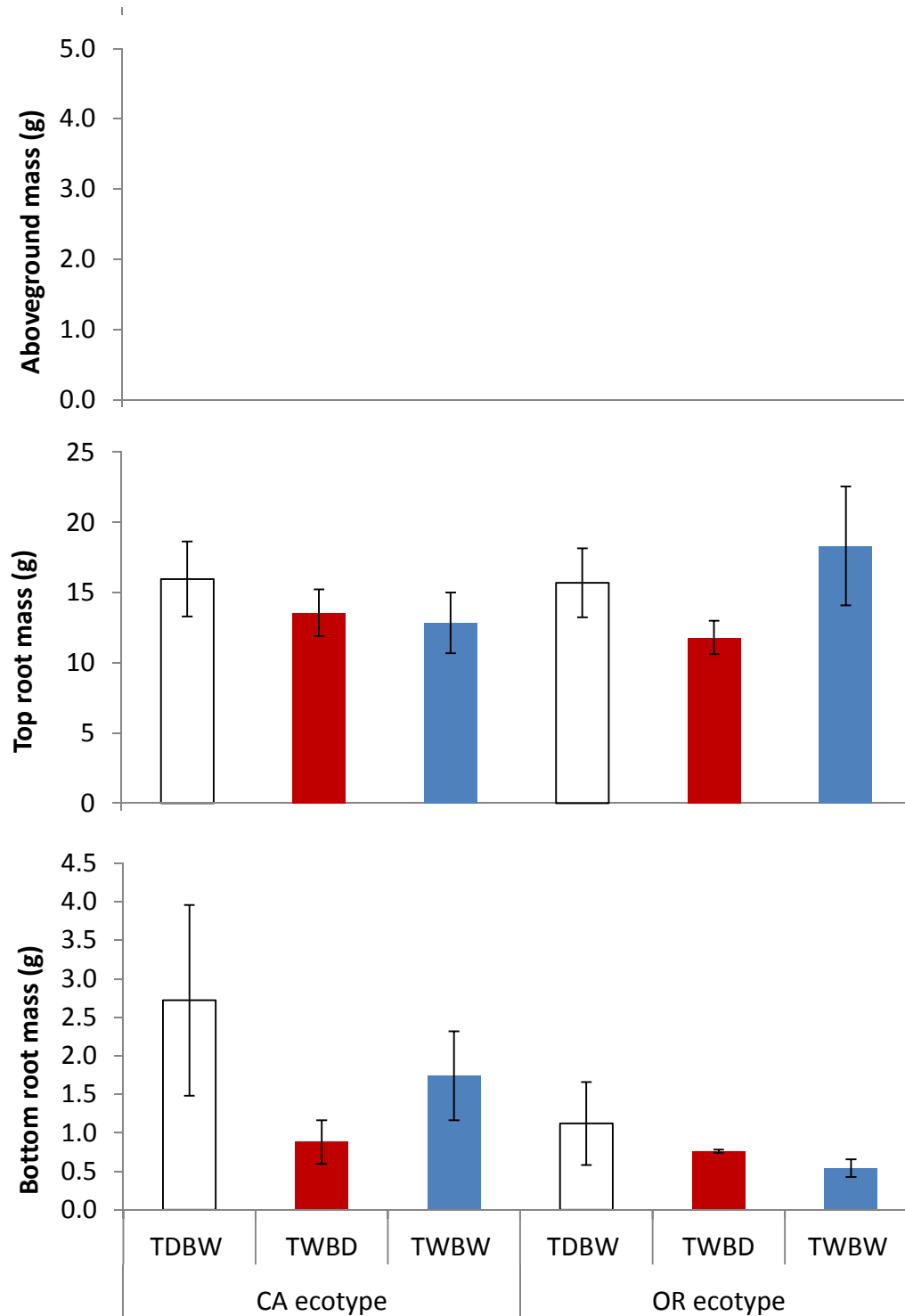


Figure 15. Biomass components of two *Leymus triticoides* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

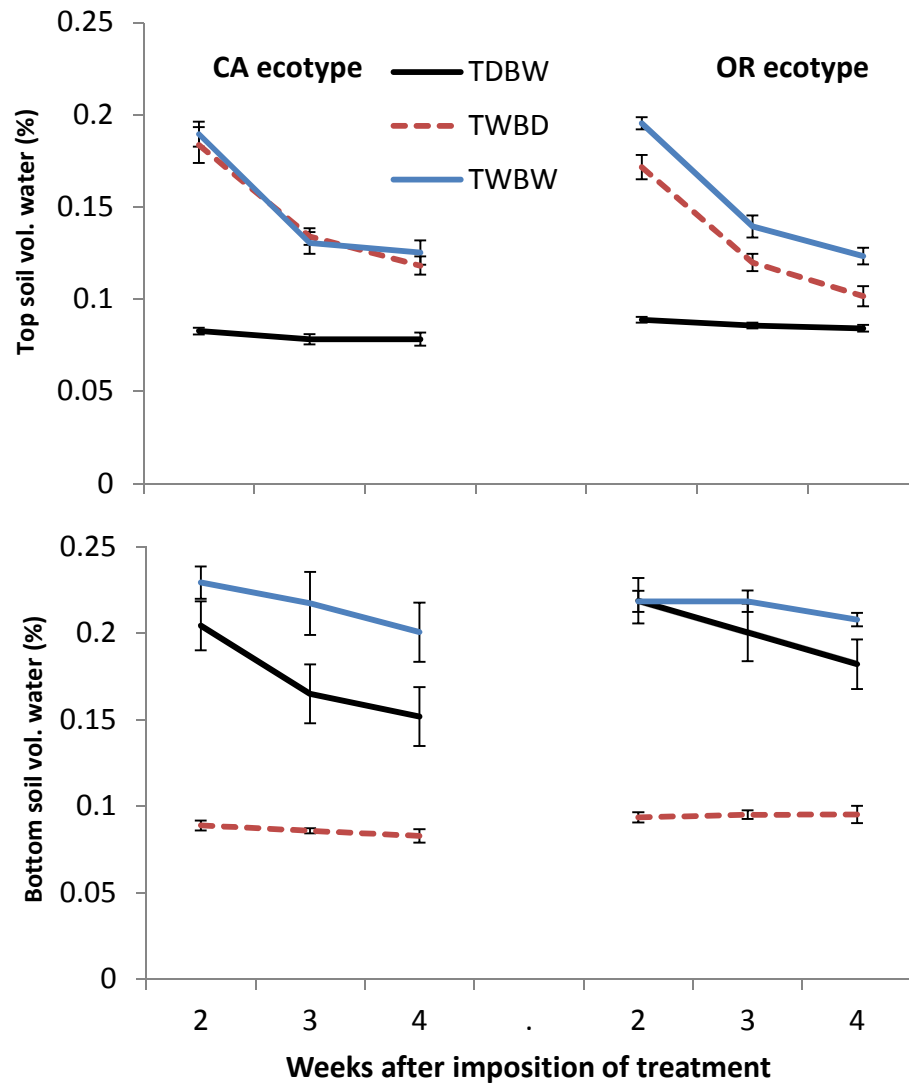


Figure 16. Volumetric soil water content through time for two *Leymus triticoides* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

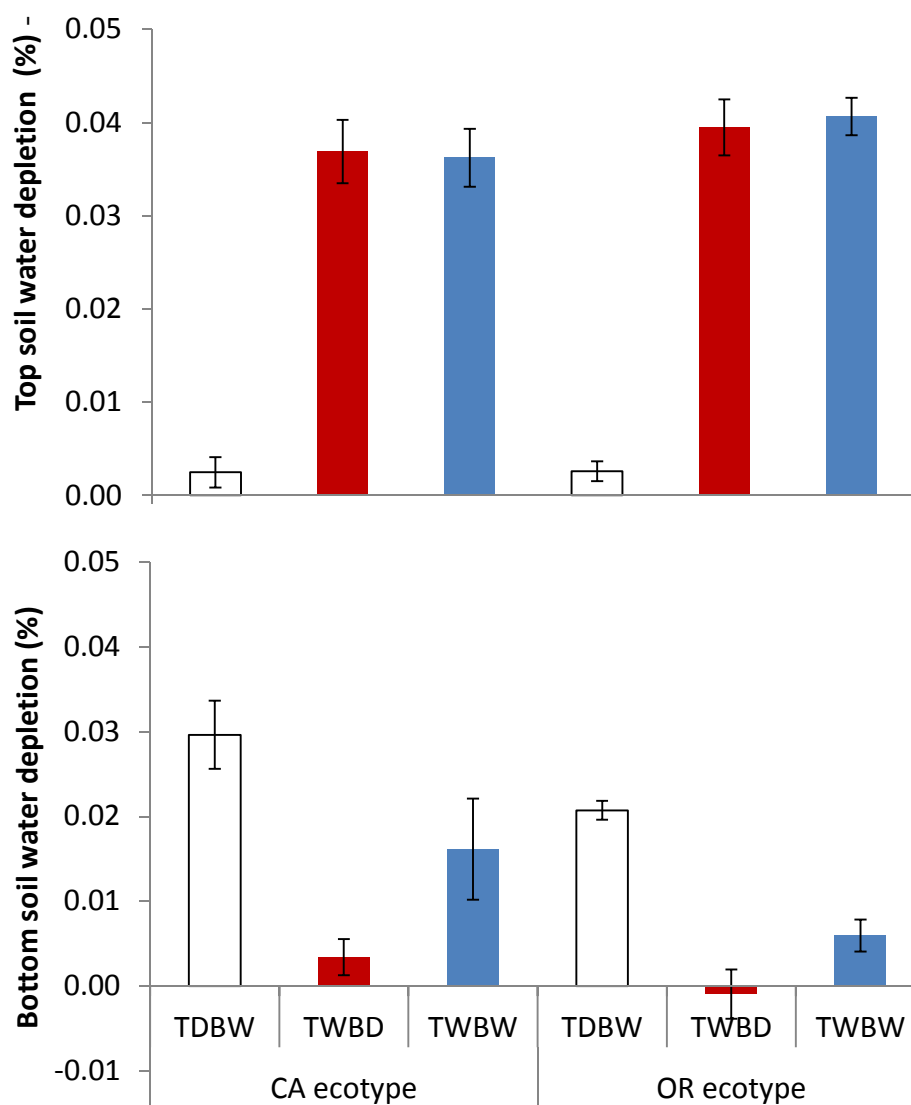


Figure 17. Soil water depletion at the end of the experiment for two *Leymus triticoides* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

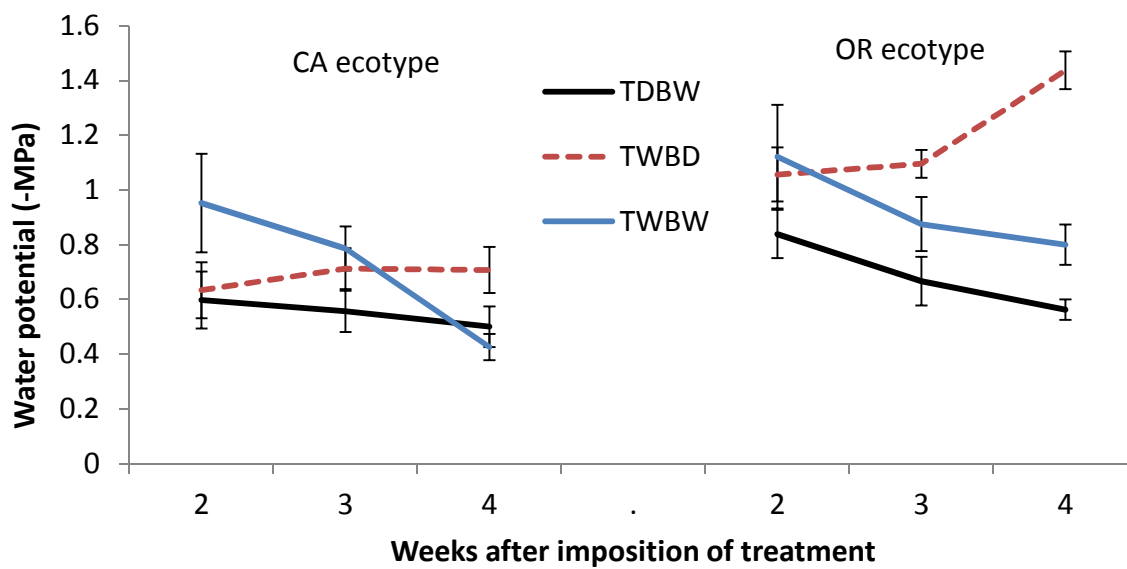


Figure 18. Water potential through time for two *Leymus triticoides* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

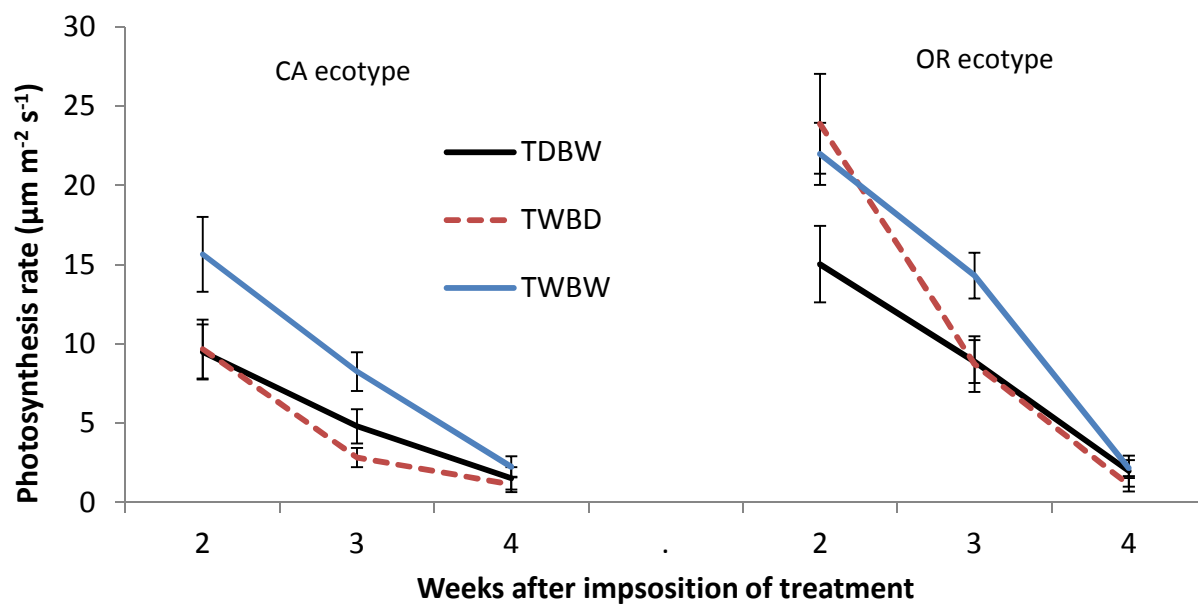


Figure 19. Photosynthesis through time for two *Leymus triticoides* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

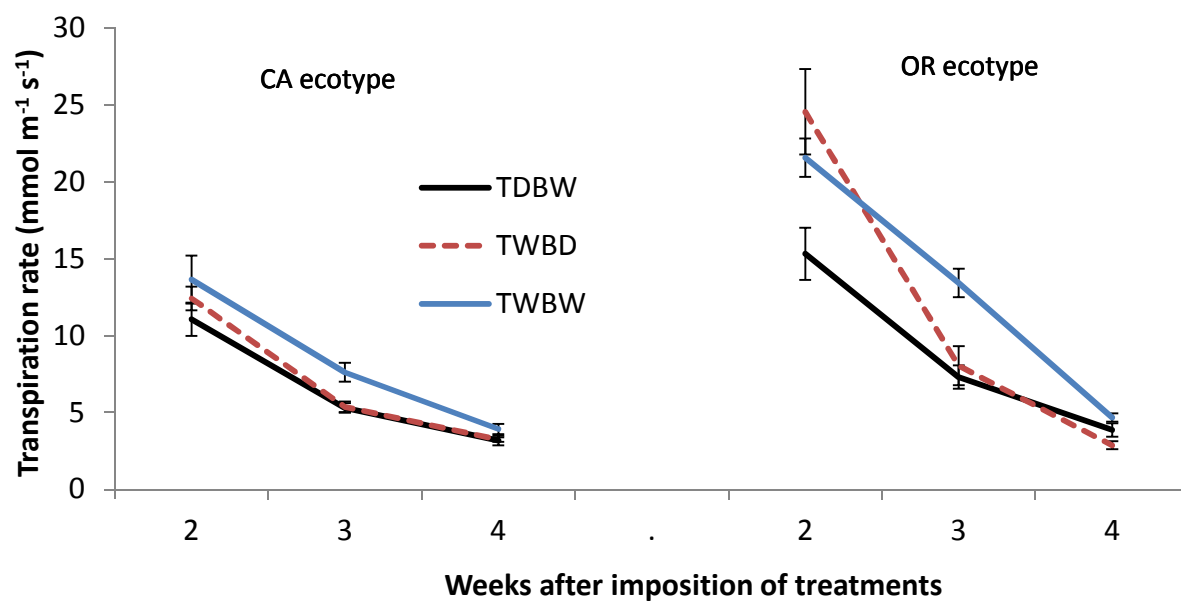


Figure 20. Transpiration through time for two *Leymus triticoides* ecotypes as affected by water distribution treatments. TDBW = top dry, bottom wet; TWBD = top wet, bottom dry; TWBW = top wet, bottom wet. Values are means \pm standard error.

APPENDIX



Figure A1. Split-root apparatus used in this study.