Ecosystem effects of groundwater depth in Owens Valley, California

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ABSTRACT

Owens Valley, California, USA, is an important source of water for the city of Los Angeles; however, recent studies have documented losses of grass cover coinciding with decreased watertable depths in many locations. These changes in community composition are assumed to be associated with shallower rooting depths and greater vulnerability to declining watertable depths in grasses compared to neighbouring shrubs. However, the hydraulic properties and water stress resistance of most species in Owens Valley have not been measured. In addition, the relationships between groundwater depth and other aspects of ecosystem function such as nutrient cycling are not well understood. In this study, we measured grass and shrub cover, vulnerability to cavitation, and plant and soil isotopic and chemical composition at 9 sites along a depth to watertable gradient of 0·3–5·7 m in Owens Valley. Contrary to expectations, the grass species was more resistant to water stress-induced cavitation than either shrub species. However, grass cover declined in sites with deeper watertables while shrub cover remained constant. Water isotopes indicated shallower rooting depths in grasses than in shrubs, although the phreatophytic shrub *Ericameria nauseosa* had enriched leaf water isotopes at deep groundwater sites, indicating water stress. Sites with lower grass cover contained less soil nitrogen (N) that was also more isotopically enriched, which is indicative of greater ecosystem N losses. These results show that groundwater depth is correlated with a number of ecosystem traits in these Great Basin Desert ecosystems and should be considered when evaluating future changes in groundwater depth. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS   depth to watertable; grass cover; nitrogen; nitrogen isotopes; Owens Valley; vulnerability to cavitation; water isotopes

INTRODUCTION

Population growth in many regions of the world has necessitated water imports and redistribution from natural ecosystems, often resulting in loss of vegetative cover and changes in community composition, particularly in areas where species are dependent on groundwater sources (Muñoz-Reinoso, 2001; Lamontagne *et al.*, 2005; Cooper *et al.*, 2006; Hao *et al.*, 2010). In California, Owens Valley has been an important source of water for the city of Los Angeles for nearly 100 years. Located between the Sierra Nevada and White Mountains in central California, this semi-arid area receives a majority of its water in the form of runoff from the adjacent mountains, resulting in relatively shallow watertables in many areas. Therefore, phreatophytic—or groundwater-dependent—plant communities are common in Owens Valley, and include both shrubs and grasses. Since the completion of the Los Angeles aqueduct in 1913, groundwater has been pumped, diverted, and transported to Los Angeles for the city's water supply. Within the last 30 years, studies have documented changes in vegetation, with trends of both decreased live plant cover and replacement of grasslands by shrubs in Owens

Valley (Griepentrog and Groeneveld, 1981; Elmore *et al.*, 2003, 2006). The extent to which changes in community composition are attributable to hydrologic change is widely debated; in addition, the consequences of changes in grass and shrub cover for ecosystem function are poorly understood.

The ability of plants to withstand water stress-induced cavitation is a major determinant of their ability to cope with changes in watertable depth. However, the cavitation resistance of many plants in Owens Valley has not yet been measured. Grasses in Owens Valley are assumed to have shallower rooting depths than neighbouring shrubs (Elmore *et al.*, 2003, 2006), which is thought to limit their distribution and to make them more vulnerable to declining watertable depths. Many shrub species in Owens Valley are phreatophytic, and species with greater groundwater dependence tend to be more vulnerable to cavitation (Hacke *et al.*, 2000b; Pockman and Sperry, 2000). Therefore, grass species with shallower root systems may be generally more vulnerable to cavitation than shrubs, although this assumption has seldom been tested. In addition, plants have been shown to experience changes in hydraulic function with greater water stress, with populations in drier environments exhibiting greater resistance to cavitation than populations of the same species in wetter environments. Increased resistance to cavitation in environments of greater water stress is

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likely due to phenotypic plasticity (Alder *et al.*, 1996; Hacke *et al.*, 2000a; Ladjal *et al.*, 2005; Holste *et al.*, 2006; Beikircher and Mayr, 2009); however, other studies have indicated that changes in hydraulic function are genetically controlled (Mencuccini and Comstock, 1997; Kavanagh *et al.*, 1999; Kolb and Sperry, 1999).

Changes in plant community composition linked to species differences or modifications of plant–water relations have many potential consequences for carbon and nutrient cycling. As plant species composition changes with reduced water availability, more drought-tolerant shrubs may have different wood and tissue chemical compositions, influencing carbon and nutrient cycling. Plants with greater resistance to cavitation tend to have greater xylem density (Hacke *et al.*, 2001) and mechanical strength (Jacobsen *et al.*, 2007; Pratt *et al.*, 2007), indicating that xylem of resistant species contains different proportions of material compared to less resistant species. Xylem is tissue that is composed not only of water-conducting vessels and tracheids but also of wood fibres (Hacke and Sperry, 2001). Jacobsen *et al.* (2005) found that the thickness of xylem fibre walls was positively correlated with increased resistance to cavitation in chaparral shrubs, suggesting that thicker, lignified fibres may provide the necessary vessel support to counter negative water potential. In addition, species adapted to xeric environments often contain vestured vessel pits, or protruding outgrowths in which lignin is concentrated (Jansen *et al.*, 2003, 2004). Therefore, water stress adaptations may have important implications for tissue chemistry that affects other aspects of ecosystem function. Species with greater litter lignin content and lignin:N ratio have been found to have lower decomposition rates (Melillo *et al.*, 1982, Taylor *et al.*, 1989).

Changes in the relative importance of grasses and shrubs may also play an important role in ecosystem nutrient relations. The amount of vegetative cover, and especially grass cover, influences soil nitrogen (N) content (Hook *et al.*, 1991; Schlesinger *et al.*, 1996; Schlesinger and Pilmanis, 1998; Burke *et al.*, 1999), and shifts in community composition resulting from woody encroachment may be associated with other important changes in ecosystem properties, such as rates of nitrogen cycling. Sites with less grass cover tend to have more bare ground area, which is subject to N losses through erosion and volatilization. Because the lighter isotope diffuses preferentially from the soil, soil N volatilization can result in reductions in soil N as well as more isotopically enriched soil N (Schlesinger and Pilmanis, 1998). In Owens Valley, soil nitrogen was less abundant and more isotopically enriched at sites with less grass cover (Pataki *et al.*, 2008; Goedhart *et al.*, 2010). Additionally, plant N relations differed between dominant shrub and grass species in Owens Valley (Pataki *et al.*, 2008). In particular, the halophytic shrub species *Atriplex torreyi* had higher concentrations of leaf N that were isotopically enriched relative to other neighbouring species. Because soil N becomes more enriched at the soil surface, *A. torreyi* was likely utilizing shallower pools of soil N and

consequently may have a competitive advantage in sites with less soil N (Pataki *et al.*, 2008). However, these previous studies were conducted at sites with similar watertable depths, so the role of depth of groundwater in plant water and N relations is still unclear.

In this study, we investigated the linkages between groundwater depth, community composition, and plant properties along a depth to watertable (DTW) gradient in Owens Valley. We addressed the following questions: How does community composition vary along the DTW gradient? Do plant traits associated with water stress-induced cavitation resistance vary with DTW? Does increased cavitation resistance influence tissue lignin and N content? How do plant and soil N relations vary with DTW? We hypothesized that grasses would have shallower rooting depth and would be more vulnerable to cavitation induced by water stress than neighbouring shrubs. Additionally, in all species, we expected plant resistance to cavitation to increase in sites with increasing DTW, with corresponding increases in xylem lignin content. As we expected grasses to be more vulnerable to water stress, we also hypothesized that grass cover would be negatively related to site DTW. We previously found that given constant DTW, sites with less grass cover had less soil N and more isotopically enriched soil N (Pataki *et al.*, 2008; Goedhart *et al.*, 2010), and we expected that we would see this same trend in this study across the DTW gradient. Quantifying these linkages should help improve our understanding of how plant and soil attributes may change as groundwater depth decreases.

MATERIALS AND METHODS

Study sites

Using groundwater depth data obtained from the Los Angeles Department of Water and Power, nine sites were chosen along a DTW gradient of 0·3–5·7 m. Only sites near wells with relatively stable watertable depths over the last ten years were chosen, and sampling sites were located within 30 m of each well. Soil texture in 5 sites was classified as loam, 3 sites had loamy sand, and 1 site had soil texture of silt loam (USDA Soil Survey of Benton-Owens Valley area, California, Parts of Inyo, and Mono Counties). Circa 1931, 2 sites were used for alfalfa farming, 4 sites were classified as grasslands, and 3 sites were classified as rabbitbrush (*Ericameria nauseosa*) meadow (Ritch Books, courtesy of the Los Angeles Department of Water and Power).

Measurements in this study focused on the shrub species *Atriplex torreyi* (S. Wats.) and *Ericameria nauseosa* (Pall. ex Pursh), and the grass species *Distichlis spicata* (L.) Greene. The two shrub species were not found in sites with DTW less than 1·2 m, with the exception of *E. nauseosa* seedlings in the site with 0·3 m DTW, and the grass species *D. spicata* was only found in sites with DTW up to 3·2 m. The shrub *A. torreyi* is a C$_4$, winter deciduous, halophytic shrub known to be a successful competitor in both water-stressed and non-water-stressed

environments (Naumburg et al., 2005). This is likely due to the ability of this species to utilize N sources within the saline surface soil (Pataki et al., 2008; Goedhart et al., 2010). E. nauseosa, formerly known as Chrysothamnus nauseosus, is a winter deciduous, C_3 shrub. At least two varieties of E. nauseosa are located within Owens Valley. E. nauseosa var. hololeucus is normally found in well-drained soils and in areas where watertable depths exceed plant rooting depth. E. nauseosa var. consimilis is found in phreatophytic communities in more alkaline soils. E. nauseosa var. consimilis was the only variety located at all sites, with the exception of the site with the deepest watertable, where both varieties were present. Because these two varieties vary in chemical composition (unpublished data), we were careful to exclusively sample from E. nauseosa var. consimilis individuals. This variety depends predominantly on groundwater (Pataki et al., 2008; Goedhart et al., 2010), and when the watertable drops below the rooting zone, E. nauseosa var. consimilis is susceptible to significant dieback and mortality (Toft, 1995). Finally, D. spicata is a C_4 perennial halophytic grass commonly found in salt marshes and areas with relatively shallow watertables (Dahlgren et al., 1997; Elmore et al., 2006). Seasonal photosynthesis in this species has been shown to be correlated with soil N availability, which may influence distribution (Goedhart et al., 2010).

Plant/soil water isotopic measurements

In late September 2007, three non-green shrub stems and grass rhizomes from each species and site were collected within five days following a rain event to determine whether plants were utilizing shallow rain water. Collected samples were stored in vacutainers sealed with parafilm, and immediately chilled in coolers in the field until frozen in the lab. Samples remained frozen until water was extracted with cryogenic vacuum distillation (West et al., 2006). Extracted water was frozen until analysed for oxygen isotope ratio ($\delta^{18}O$) using a thermal conversion elemental analyser (TC EA, Thermofinnigan, San Jose, CA, USA) coupled to an Isotope Ratio Mass Spectrometer (Delta Plus XP, Thermofinnigan, San Jose, CA, USA) after Gehre et al. (2004). Oxygen isotope measurements were expressed in common δ notation and referenced to V-SMOW within a precision of 0·08‰.

Soil water samples were collected at the same time as stems. Augers were used to extract soil from two cores at approximately 10–50 cm depth intervals from 5 to 200 cm below the soil surface. Groundwater samples were collected using a hand pump from the well nearest each site, with the exception of the sites with DTW of 1·8 and 3·2 m. Typically, 3–5 well volumes must be purged before sampling for groundwater isotopes, as evaporation may cause artifacts in the measured isotope ratio of stagnant well water. Although we were unable to completely purge the wells, we did purge approximately 4 l of water from each well before sampling. The measured well water isotope ratios were similar to

previously reported groundwater values in Owens Valley (Pataki et al., 2008). Additionally, well water isotopic composition was very similar to values obtained from auguring to the saturated zone at the same location. Soil water and groundwater samples were collected in vacutainers, frozen until water extraction, and analysed for $\delta^{18}O$. Oxygen isotope measurements were expressed in common δ notation and referenced to V-SMOW within a precision of 0·09‰. Because water isotopes in soil at depths shallower than the watertable were similar to groundwater isotopes in all sites, plant water source was defined as either deep or shallow rather than groundwater versus soil water, using well water and surface soil water isotope values as end members. When well water was not available at a given site, the average well water value across sites was used, as the isotopic composition of well water only varied by 0·33‰. Isotope measurements were used to calculate the percent of deep soil water used by the plant according to the equation: (surface soil water $\delta^{18}O$ − plant water $\delta^{18}O$)/(surface soil water $\delta^{18}O$ − groundwater $\delta^{18}O$) × 100. This equation describes the difference between water isotopes in the plant versus surface soil as compared to the difference between water isotopes in surface soil versus groundwater.

Plant water stress resistance measurements

Plant water stress resistance was determined by measuring vulnerability to cavitation of roots and branches for shrubs and grass rhizomes in each site. Root and rhizome samples were collected from 0 to 50 cm soil depth. Root and branch samples at least 20 cm in length and 2–6 (shrubs) or 1–2 (grass rhizomes) mm in diameter were collected, stored in a sealed plastic bag surrounded by wet paper towels, and immediately chilled in coolers until refrigerated at 4 °C in the lab. Analysis for vulnerability to cavitation was carried out in the lab within five days of collection. E. nauseosa root samples from all sites were collected in May and June 2008, and branch samples from all sites were collected in September 2008. A. torreyi and D. spicata root, rhizome, and branch samples from all sites were collected in November and December 2008. Vulnerability to cavitation was measured using the centrifuge method (Alder et al., 1997) in a manner similar to Hacke et al. (2000b). Briefly, roots, rhizomes, and stems were cut underwater to a final segment length of 14·2 cm in the lab. They were then connected to a tubing apparatus and flushed with ultrapure water (water resistivity = 18 ohms) at a constant pressure of 1 bar for 1 h. Immediately following flushing, segments were secured into a specially made rotor (Alder et al., 1997) and spun in a centrifuge (Sorvall RC-5C PLUS Superspeed Floor Model, Thermo Scientific, Waltham, MA) at the speed corresponding to −0·25 MPa. The segments were initially spun at this low pressure to prevent water from flowing through xylem elements that would not normally function in the natural environment (Pratt and Black, 2006). After the initial spin, segments were attached to a tubing apparatus where hydraulic conductance was measured in a manner similar to that of Sperry

et al. (1988). Water was allowed to flow gravimetrically through the segment and into a reservoir located on an analytical balance (Accu-124, readability 0·1 mg, Fisher Scientific, Pittsburgh, PA, USA). The rate of water movement through the segment was used to calculate hydraulic conductivity. Following each hydraulic conductivity measurement, the segment was reinserted into the centrifuge and spun at a faster speed. Hydraulic conductivity was then remeasured and the process repeated until there was no longer any water flow through the segment. Percent loss of conductivity was determined for each hydraulic conductivity measurement based on the initial hydraulic conductivity measurement. The pressure at which 50 and 75% of conductivity was lost was obtained by fitting the data with a three-parameter sigmoidal curve.

Plant chemical and isotopic measurements

Fully expanded sun leaves in the upper canopy from 3 to 6 individuals of each species were collected in July 2007 and dried at approximately 65 °C for at least 48 h. Immediately following vulnerability to cavitation measurements, root, rhizome and branch samples were dried at approximately 65 °C for at least 72 h. Dried roots, rhizomes, branches, and leaves were ground to a fine homogenous powder and analysed for carbon (C), nitrogen (N), carbon stable isotope composition ($\delta^{13}C$), and nitrogen stable isotope composition ($\delta^{15}N$) using an elemental analyser coupled to an Isotope Ratio Mass Spectrometer (Delta Plus IRMS, Thermofinnigan, San Jose, CA) at the University of California, Irvine. Because the primary carbon-fixing enzyme in C_3 species discriminates against ^{13}C, leaf carbon isotopes can be used as a measure of internal versus external CO_2 concentration (C_i/C_a), which is controlled by stomatal regulation and photosynthesis (Farquhar *et al.*, 1989). Soil N isotopes can be used to indicate N losses via ammonia volatilization, nitrification, and denitrification (Högberg, 1990). Carbon and nitrogen isotope ratios were expressed in common δ notation and referenced to the V-PDB and atmospheric standards, respectively, with a precision of 0·07 and 0·09‰, respectively. Acid detergent lignin content of roots, rhizomes, branches, and leaves for each species at all sites was also determined by extraction in 72% H_2SO_4, followed by acetone drying and ashing at 550 °C.

Site canopy cover measurements

In August 2008, total shrub and grass canopy cover was measured at each site using a technique similar to that of Daubenmire (1959). Five 30 m transects were established at each site. For each transect, a 1 m^2 quadrat was placed in 3 m increments and at a distance of 0–5 m, which was randomly chosen from the transect line for a total of 10 quadrats per each transect line. In each quadrat, species cover was visually estimated and fit into one of seven percent cover categories. Visual estimations were used to determine percent canopy cover for all shrub and grass species at each site.

Soil N measurements

In July 2007, soil samples were collected at each site by combining a composite of three sub-samples from 0 to 5 cm depth under three individuals of each shrub, and in three grass dominated or intershrub spaces. Soil samples were dried in an oven at 60 °C for at least 72 h. After drying, soil was sieved to exclude material larger than 2 mm. All plant material was removed before grinding the soil with a mortar and pestle. Soil samples were analysed for N content and $\delta^{15}N$ using an elemental analyser coupled to an Isotope Ratio Mass Spectrometer (Delta Plus IRMS, Thermofinnigan, San Jose, CA, USA) at the University of California, Irvine. Nitrogen isotope ratios were expressed in common δ notation and referenced to the atmospheric standard with a precision of 0·10‰. Soil from the site with 0·3 m DTW was excluded from soil N analyses due to recent human disturbance associated with restoration efforts of the Lower Owens Valley River region.

Data analysis

All data were analysed using SAS 9·1·3 software (SAS Institute Inc., Cary, NC, USA). Comparisons of measurements among sites were analysed using the General Linear Model for Analysis of Variance. *Post hoc* tests were conducted using the Tukey standardized range test, and homogeneity of variance was tested using Levene's test. Relationships between measurements were analysed using simple regressions. Relationships with $p < 0.05$ were considered significant, and $p < 0.1$ were considered marginally significant.

RESULTS

Both grass and shrub species predominantly utilized deep soil water, despite a rain even prior to stem water collection (Figure 1). Because *D. spicata* plant water isotopes were more enriched than water isotopes measured at the surface soil for the site with 0·3 m DTW, we reported percent deep soil water utilization to be 0% for this species and site. There was no correlation between deep water utilization and DTW for any of the species; however, *D. spicata* utilized more shallow soil water in the site with the deepest DTW (3·2 m, $p < 0.01$). Percent deep soil water utilization was generally greater for shrubs than for grasses ($p < 0.01$), and did not vary among sites (Figure 1, $p > 0.05$). *E. nauseosa* was the only species to consistently utilize deep soil water at all sites, and percent deep soil water usage did not vary among sites ($p > 0.05$) (Figure 1). Despite uniform water source among sites, *E. nauseosa* bulk leaf $\delta^{13}C$ was more enriched in sites with deeper DTW (Figure 2, $R^2 = 0.87$, $p < 0.01$). Xylem pressure at 50 and 75% loss of conductivity, which are measures of resistance to water stress, was not significantly different among sites for either roots or branches in any of the species; hence, with the exception of a marginally significant positive correlation in *E. nauseosa* branches, there was no
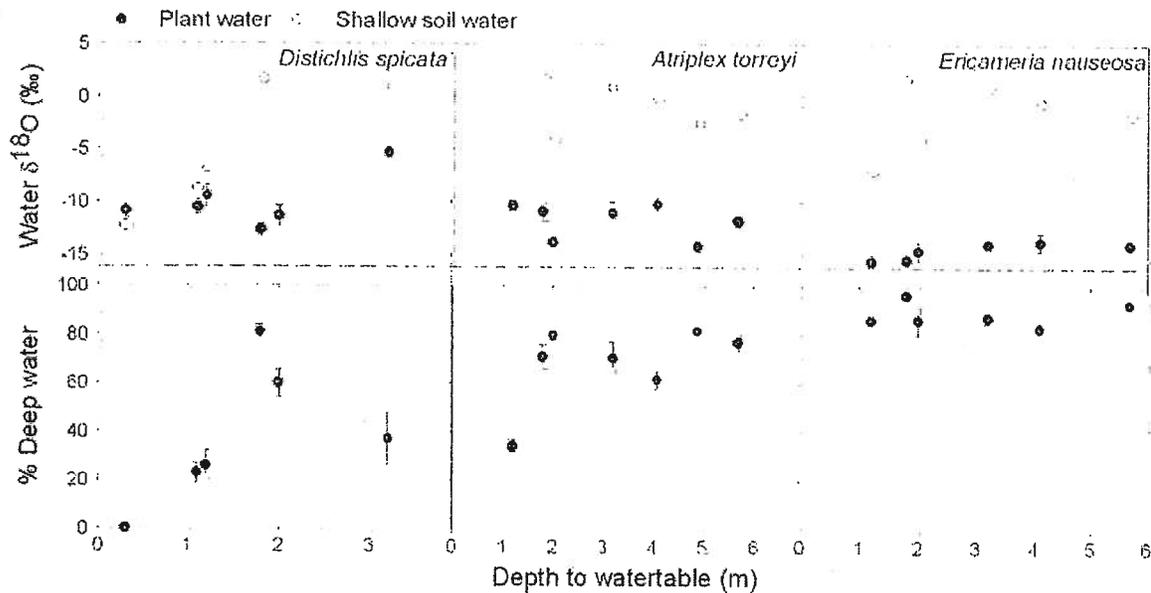
Figure 1. Upper panels: The oxygen isotope composition ($\delta^{18}O$) of plant water, shallow soil water at 5–10 cm depth, and groundwater for the grass species *D. spicata* and shrub species *A. torreyi* and *E. nauseosa* in sites along a DTW gradient (m). The dotted line shows the average isotopic composition of groundwater, which did not vary among sites. Lower panels: Calculated percent utilization of deep soil water from the data in the upper panel. Soil water and groundwater were not distinguishable below 50 cm at the shallow groundwater sites and 200 cm at the deep groundwater sites. Error bars show one standard error (*n* varies from 3 to 4 replicates).
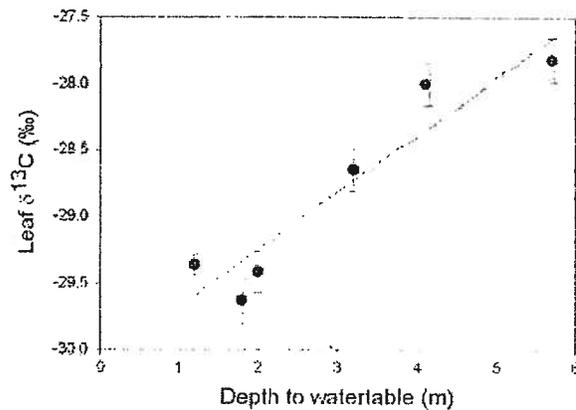

Figure 2. Leaf carbon isotope composition ($\delta^{13}C$) for *E. nauseosa* leaves in sites along a DTW gradient ($R^2 = 0.87$, $p < 0.01$). Error bars show one standard error ($n = 3$).

relationship between resistance to water stress and DTW for roots, rhizomes, or branches of any species (Table I). Xylem pressure at both 50 and 75% loss of conductivity was greater for the grass species *D. spicata* than either shrub species (Figure 3, $p < 0.05$). The pressure at which 50% loss of conductivity occurred in branches was not significantly different between the two shrub species, but *A. torreyi* branches reached 75% loss of conductivity at a significantly lower pressure than *E. nauseosa* branches (Figure 3, $p < 0.05$), and roots were more vulnerable to water stress than branches in both shrub species (Figure 3).

Lignin content varied among sites, but was not correlated with DTW for *D. spicata* or *E. nauseosa* (Table I,

$p > 0.1$). In the shrub species *A. torreyi*, lignin content was negatively correlated with DTW in branches (Table I, $R^2 = 0.75$, $p < 0.05$) and marginally correlated with DTW in roots (Table I, $R^2 = 0.43$, $p < 0.1$), but there was no correlation between lignin content and DTW in leaves (Table I, $p > 0.1$). There was a positive correlation between leaf N isotopes and DTW in *D. spicata* (Table I, $R^2 = 0.76$, $p < 0.05$); however, this was not seen in either shrub species (Table I). Although %N in roots, rhizomes, and branches did not vary with DTW in either the grass species *D. spicata* or the shrub species *E. nauseosa*, percent N increased with DTW in *A. torreyi* branches (Table I, $R^2 = 0.91$, $p < 0.01$), and marginally increased with DTW in *A. torreyi* roots (Table I, $R^2 = 0.57$, $p < 0.1$). Lignin : N ratios of both branches and roots decreased with DTW in *A. torreyi* (Figure 4, Table I, branches: $R^2 = 0.98$, $p < 0.0001$; roots: $R^2 = 0.88$, $p < 0.01$); however, there was no correlation between lignin : N and DTW in *D. spicata*, *E. nauseosa*, or *A. torreyi* leaves (Table I).

Site DTW was not correlated with soil texture (data not shown); however, both grass and shrub percent cover was related to site DTW (Figure 5). Grass percent cover declined sigmoidally with DTW (Figure 5, $R^2 = 0.96$, $p < 0.0001$), with the greatest decline in grass cover between 1 and 2 m DTW. Conversely, shrub percent cover increased sigmoidally with DTW (Figure 5, $R^2 = 0.75$, $p < 0.05$), and this increase was at approximately 1 m DTW. Maximum rooting depth for grasses has been estimated to be 2.5 m (Elmore *et al.*, 2003, 2006), and soil water $\delta^{18}O$ in sites with DTW <2.5 m were more depleted at shallower depths than soil water $\delta^{18}O$ in sites with DTW >2.5 m (Figure 6). Groundwater samples

Table I. The results of regression analyses of depth to groundwater as the independent variable, and tissue lignin content, nitrogen content, lignin : nitrogen, nitrogen isotope ratio ($\delta^{15}N$), and water potential at 50 and 75% loss of conductivity (ψ_{50} and ψ_{75}, respectively) as the dependent variables.

	Lignin (%)	Nitrogen (%)	Lignin : nitrogen	$\delta^{15}N$ (‰)	Ψ_{50} (MPa)	ψ_{75} (MPa)
D. spicata						
Rhizomes	ns	ns	ns	ns	ns	ns
Leaves	ns	ns	ns	0.7599*	—	—
A. torreyi						
Roots	0.4276#	0.5654#	0.8807**	ns	ns	ns
Branches	0.7507*	0.9061**	0.9810***	ns	ns	ns
Leaves	ns	ns	ns	ns	—	—
E. nauseosa						
Roots	ns	ns	ns	ns	ns	ns
Branches	ns	ns	ns	ns	ns	0.4904#
Leaves	ns	ns	0.4582#	ns	—	—

The R^2 value of the regression is shown when the model was significant at # $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; or *** $p < 0.0001$.
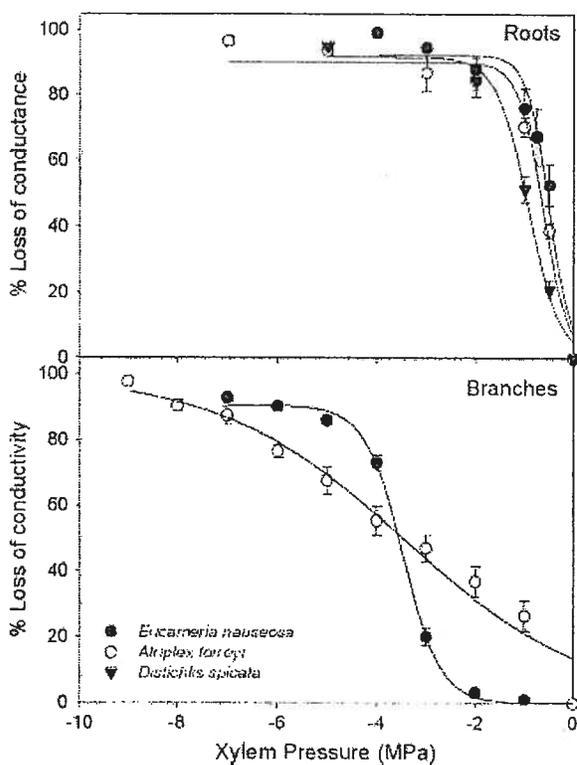

Figure 3. Average percent loss of conductivity as a function of xylem pressure (MPa) for root samples of the grass species *D. spicata* and the shrub species *A. torreyi* and *E. nauseosa*, and branch samples for the shrub species *A. torreyi* and *E. nauseosa* in all sites. Error bars show one standard error ($n = 4$–6). Data were fitted with three-parameter sigmoidal curves.

Figure 4. Lignin : nitrogen in roots and branches of *A. torreyi* (roots: $R^2 = 0.88$, $p < 0.01$; branches: $R^2 = 0.98$, $p < 0.0001$). Error bars show one standard error ($n = 3$).

collected from wells had an average $\delta^{18}O$ of -16.2‰. At sites with DTW <2.5 m, soil water $\delta^{18}O$ was similar to groundwater $\delta^{18}O$ at approximately 50 cm in depth, while at sites with DTW >2.5 m, soil water $\delta^{18}O$ was similar to groundwater $\delta^{18}O$ at approximately 150–200 cm in depth (Figure 6).

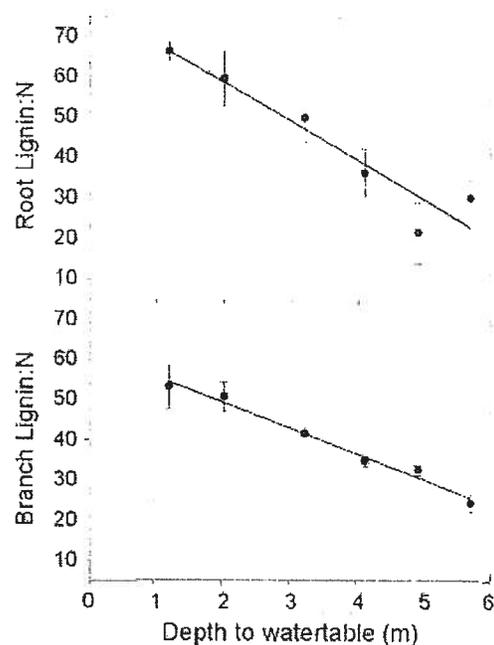Percent soil organic N increased in sites with increasing grass cover (Figure 7, $R^2 = 0.75$, $p < 0.01$); however, there was no relationship between percent soil organic N and percent leaf N for any of the species. Additionally, percent leaf N was not correlated with grass cover (Table I, $p > 0.05$). Soil N isotopes were more depleted in sites with greater grass cover (Figure 7, $R^2 = 0.50$, $p < 0.05$), and there was a positive relationship between soil N isotopes and leaf N isotopes for all species (Figure 8, $p < 0.05$). There was no correlation between leaf N isotopes and grass cover for any of the species.

DISCUSSION

In this study, we investigated how community composition and plant and soil characteristics varied along a DTW gradient. As we hypothesized, grasses generally
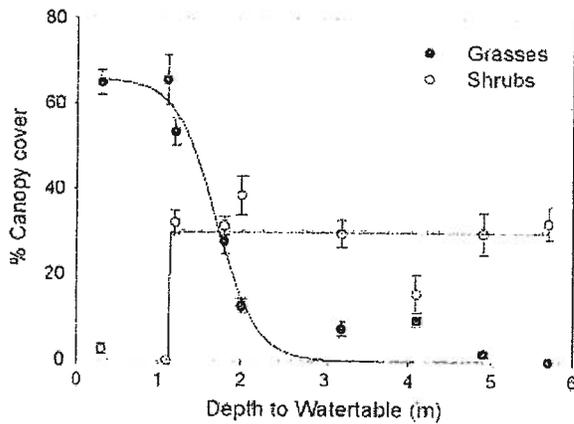
Figure 5. Shrub and grass canopy cover (%) in sites varying with DTW (metres). Data were fit with a three-parameter sigmoidal curve (grasses: $R^2 = 0.96$, $p < 0.0001$; shrubs: $R^2 = 0.75$, $p < 0.01$). Error bars show one standard error ($n = 5$).
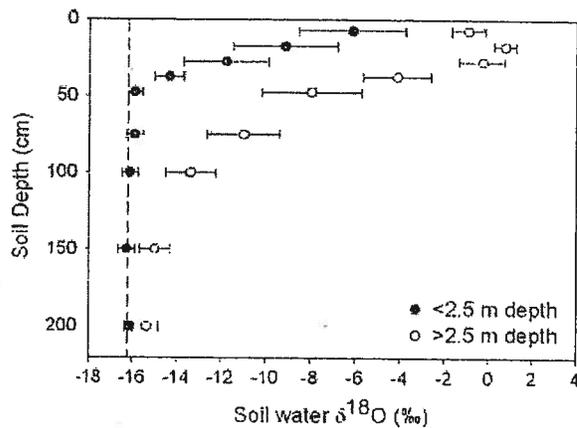

Figure 6. The average oxygen isotopic composition ($\delta^{18}O$) of soil water with depth for sites with DTW <2.5 m (closed circles) and >2.5 m (open circles). The dotted line shows the isotopic average composition of groundwater. Error bars show one standard error (n varies from 3 to 5).

utilized shallower soil water than shrubs as indicated by water isotope measurements (Figure 1), and grass cover declined sharply with declining DTW (Figure 5). In addition, soil N declined with decreasing grass cover (Figure 7) as expected. However, contrary to our initial hypotheses, grasses were more resistant to cavitation than shrubs (Figure 3). Unexpectedly, vulnerability to cavitation was not correlated with lignin content (Table I); instead, lignin : N ratios declined with increasing DTW in *A. torreyi* (Figure 4). Our results show that many community, ecosystem, and plant traits vary with DTW, but there is still some uncertainty in the mechanisms linking groundwater depth with plant and ecosystem function.

Plant water sources

Plant species in the Great Basin Desert are known to utilize a variety of soil water sources (Ehleringer *et al.*, 1991; Donovan and Ehleringer, 1994; Pataki *et al.*, 2008; Goedhart *et al.*, 2010). In general, herbaceous species tend to utilize shallower sources of soil water, while
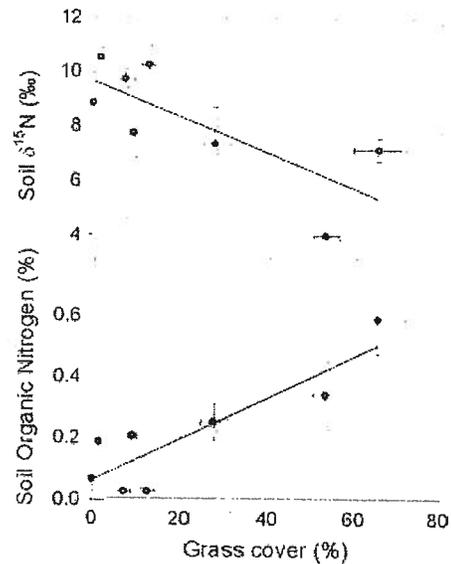

Figure 7. Soil nitrogen isotope ratio ($\delta^{15}N$) (‰, $R^2 = 0.50$, $p < 0.05$) and soil organic nitrogen (%, $R^2 = 0.75$, $p < 0.01$) in sites varying in grass cover (percent). Error bars show one standard error (n varies between 3 and 5 samples for soil N characteristics and $n = 5$ for grass cover).

woody perennial species tend to utilize deeper soil water (Ehleringer *et al.*, 1991). We found this same trend in this study, as well as in our previous work in Owens Valley, where the grass species *D. spicata* had rhizome water isotopes that were more similar to shallow soil water isotopes, and the shrub species *A. torreyi* and *E. nauseosa* had stem water isotopes that were more similar to groundwater isotopes at sites with DTW of 1.5–2 m (Pataki *et al.*, 2008; Goedhart *et al.*, 2010). Great Basin species are also known to have varying responses to summer rain events (Ehleringer *et al.*, 1991; Flanagan *et al.*, 1992; Donovan and Ehleringer, 1994; Pataki *et al.*, 2008; Goedhart *et al.*, 2010), where grasses and shallowly rooted drought deciduous species tend to utilize summer precipitation to a greater degree than deeply rooted woody species. Additionally, DTW has been shown to play a role in the extent to which plants utilize precipitation, with greater use of precipitation in sites with greater DTW (McLendon *et al.*, 2008). In this study, we sampled plant water of all species in all sites following a rain event in September. *A. torreyi* and *D. spicata* showed variation in the amount of deep soil water utilization among sites. This variation was not correlated with DTW in *A. torreyi*, but the large decreases in deep water utilization in *D. spicata* at the deepest DTW site indicates that this species was either utilizing a shallower source of soil water or water from recent precipitation (Figure 1). *E. nauseosa*, a known phreatophyte, has consistently been found to utilize deep sources of water, even following precipitation events (Ehleringer *et al.*, 1991; Donovan and Ehleringer 1994; Pataki *et al.*, 2008; Goedhart *et al.*, 2010). In this study, *E. nauseosa* utilized deep soil water at all sites (Figure 1). However, bulk leaf $\delta^{13}C$, which is an
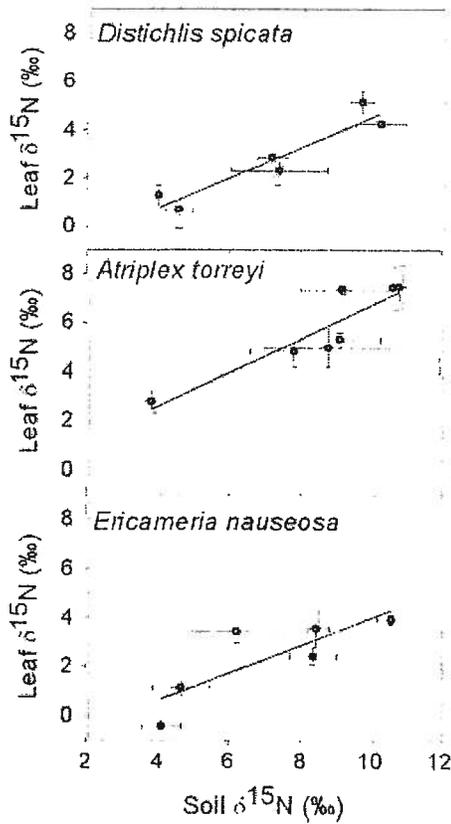
Figure 8. Leaf nitrogen isotope ratio ($\delta^{15}N$) versus soil $\delta^{15}N$ (‰) for the grass species *D. spicata* (DISP) and the shrub species *A. torreyi* (ATTO) and *E. nauseosa* (ERNA). (DISP: $R^2 = 0.86$, $p < 0.01$; ATTO: $R^2 = 0.80$, $p < 0.01$; ERNA: $R^2 = 0.61$, $p < 0.05$.) Error bars show one standard error (n varies between 3 and 5 for soil $\delta^{15}N$ and $n = 3$ for leaf $\delta^{15}N$).

integrated measure of the ratio of photosynthesis and stomatal conductance, increased with increasing DTW, indicating that *E. nauseosa* was utilizing greater stomatal regulation, likely due to greater water stress experienced in sites with greater DTW (Figure 2). Phreatophytic species are common in other arid and semi-arid regions of the world (Pavón and Briones, 2001; Arndt *et al.*, 2004; Cooper *et al.*, 2006; O'Grady *et al.*, 2009; Hao *et al.*, 2010), and experience dieback with decreased watertable depths (Cooper *et al.*, 2006; Hao *et al.*, 2010). As the other two study species are C$_4$ plants, carbon isotopes could not be used as a measure of plant water stress in *D. spicata* and *A. torreyi*.

Plant water stress resistance

In addition to variations in water sources, Great Basin species have also been shown to have varying resistance to water stress, which has been correlated with water availability (Hacke *et al.*, 2000b). Generally, species that are exposed to greater water stress tend to have adaptations that allow for greater water stress resistance (Hacke *et al.*, 2000b, Sperry and Hacke, 2002). In this study, rhizomes from the grass species *D. spicata* were more resistant to water stress-induced cavitation than

in either shrub species (Figure 3). Because grasses are restricted to shallow rooting zones, they likely experience greater water stress than deeply rooted shrubs, even though *D. spicata* appears to be limited in its distribution to sites with shallow DTW. All of the shrub roots and grass rhizomes in this study were collected near the soil surface and were at least 1 mm in diameter, so we do not know if cavitation vulnerability varies with root size or depth. For shrubs, we measured cavitation vulnerability of both stems and roots, and found that stems were much more resistant to water stress than roots (Figure 3), consistent with previous studies (Hacke *et al.*, 2000b; Sperry and Hacke, 2002). Vulnerability curves of roots were similar for all species; however, branch vulnerability curves for *A. torreyi* had a shallower slope than *E. nauseosa*. Consequently, although the pressure at which 50% loss of conductivity occurred was not different between species, 75% loss of conductivity occurred at higher pressures for *E. nauseosa* than for *A. torreyi*, suggesting that *A. torreyi* may be better adapted for conditions of extreme water stress (Figure 3).

We hypothesized that vulnerability to cavitation would vary intraspecifically with DTW; however, this was not the case for any of the three species (Table I). Although there was variation in vulnerability to cavitation among sites for each species, this variation was not correlated with DTW, nor was it correlated with soil type, which has been shown to influence both water availability and resistance to water stress (Sperry and Hacke, 2002). While *E. nauseosa* branches from sites with deeper DTW were marginally more resistant to water stress than branches from sites with shallower DTW, the overall lack of correlation between resistance to water stress and DTW was slightly surprising, given that $\delta^{13}C$ indicated that populations in sites with greater DTW experienced greater water stress. However, differences in DTW at these sites may not have been consistent enough over time to allow for distinct populations with varying adaptations to water stress.

Plant and soil chemical composition

Resistance to cavitation has been associated with xylem chemical and anatomical composition. In particular, species and populations with greater resistance to cavitation tend to have stronger, denser xylem and greater fibre wall area (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005; Pratt *et al.*, 2007). Because lignin is a main strengthening component in plant xylem cells, we hypothesized that populations with greater resistance to cavitation would also have greater xylem lignin content. Although lignin content varied among populations in all three species, there was no correlation between lignin content and resistance to cavitation. Additionally, the species with the greatest resistance to cavitation, *D. spicata*, had the least root xylem tissue lignin content. Grass lignin may be underestimated due to a greater probability that part of the lignin portion of the sample may be dissolved in the acid solution (Hatfield and Fukushima, 2005).

Interestingly, *A. torreyi* had greater lignin content in branches and marginally greater lignin content in roots in sites with less DTW; however, this was not true for the other species (Table I). Increased lignin content of wood and bark is a method of plant defense against herbivory and parasitism (Wainhouse *et al.*, 1990), and degree of lignin production has shown to be controlled by environmental and climatic conditions (Wainhouse and Ashburner, 1996). The correlation between lignin content and site DTW in *A. torreyi* could be due to other factors associated with decreased DTW, such as increases in plant productivity, which would provide more substrate for lignin production, or increases in occurrence of herbivores. Insect larvae were common in the wood samples analysed in this study. In addition to correlations between lignin content and DTW, *A. torreyi* also had greater nitrogen content of branches and marginally greater nitrogen content of roots in sites with greater DTW (Table I). Our previous work in Owens Valley indicated that *A. torreyi* may be better able to utilize soil N than neighbouring species, especially in sites with less soil N (Pataki *et al.*, 2008; Goedhart *et al.*, 2010). In this study, sites with greater DTW generally had less soil N, and *A. torreyi* may be a better competitor for soil N in sites with greater DTW than in sites with shallow DTW. Lignin : N in roots and branches, but not leaves, of *A. torreyi* was greatest in sites with shallow DTW (Figure 4). Lignin : N has been shown to be correlated with decomposition rates in some ecosystems (Melillo *et al.*, 1982, Taylor *et al.*, 1989), suggesting that the prevalence of *A. torreyi* and associated rhizodeposition of root and stem material may influence nutrient cycling.

Soil N characteristics were correlated with site grass cover, as sites with greater grass cover had both greater soil organic N and more isotopically depleted soil N (Figure 7). Previous studies have also found that vegetation cover, and especially grass cover, is often correlated with soil N (Hook *et al.*, 1991; Schlesinger *et al.*, 1996; Schlesinger and Pilmanis, 1998; Burke *et al.*, 1999). Sites with continuous grass cover tend to have a more homogeneous distribution of soil N, while sites with large areas of bareground between shrubs tend to have lower soil N due to erosion and N volatilization (Schlesinger and Pilmanis, 1998). Lighter isotopes volatilize at a greater rate, leaving a greater proportion of heavy isotopes in the soil (Högberg, 1990). We observed isotopic enrichment at the deep DTW sites (Figures 7 and 8) in both soil and leaf N, which is consistent with greater N losses.

Site characteristics and canopy cover

It has been estimated that maximum rooting depth of grasses in Owens Valley is approximately 2·5 m, based on grass distribution and well data throughout the valley (Elmore *et al.*, 2003). In this study, we found that total shrub cover was sigmoidally related to DTW, and total grass cover was inversely related. Canopy cover of grasses was greatest in sites with shallow DTW, sharply decreased in sites with DTW between approximately 1 and 2 m, and remained low in sites with DTW greater than 2 m (Figure 5). Conversely, shrub cover was low at sites with shallow DTW, drastically increased at the site with 1·1 m DTW, and was high in sites with greater DTW (Figure 5). Soil water isotope profiles differed significantly between sites with DTW less than 2·5 m versus sites with DTW greater than 2·5 m (Figure 6). In sites with shallow DTW, soil water was isotopically similar to groundwater at shallower depths than in sites with greater DTW, suggesting that there was transport from groundwater to shallower soil depths at sites with shallow DTW. The shallow rooting depth of grasses may limit them to sites with shallower DTW than shrubs, even though they are more resistant to water stress. Hence, the isotopic composition of stem and root water is influenced by differences in the isotopic composition of the soil water profile in addition to rooting depth. In general, results from this study support the assumption that grass cover is predominantly limited to sites with less than 2·5 m DTW.

CONCLUSIONS

Despite the assumption of strong controls of DTW on ecosystem function in Owens Valley, the relationships between DTW, community composition, and ecosystem processes such as water and nutrient cycles have seldom been empirically tested. In this study, we found that the grass species *D. spicata* generally utilized shallower sources of soil water and was more resistant to water stress-induced cavitation than either shrub species *A. torreyi* or *E. nauseosa*. However, despite greater resistance to water stress, grass distribution was limited to sites with shallower DTW than shrubs likely due to restrictions in rooting depth. Soil percent N and N isotopic composition were correlated with grass cover, indicating that DTW and soil N characteristics are linked through controls on grass cover. While this groundwater depth gradient is not necessarily a proxy for changes in groundwater depth over time, the results of this study highlight the important role of groundwater in influencing a variety of ecosystem properties. DTW is linked not only with community composition but also with plant water stress as indicated by carbon isotopes and ecosystem N losses as indicated by N isotopes. These aspects of ecohydrology should be considered in evaluating potential future changes in phreatophytic plant communities.

REFERENCES

Alder NN, Sperry JS, Pockman WT. 1996. Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* 105: 293–301.

Alder NN, Pockman WT, Sperry JS, Nuismer SM. 1997. Use of centrifugal force in the study of xylem cavitation. *Journal of Experimental Botany* 48: 665–674.

Arndt SK, Arampatsis C, Foetzki A, Li X, Zeng F, Zhang X. 2004. Contrasting patterns of leaf solute accumulation and salt adaptation in four phreatophytic desert plants in a hyperarid desert with saline groundwater. *Journal of Arid Environments* 59: 259–270.

Beikircher B, Mayr S. 2009. Intraspecific differences in drought tolerance and acclimation in hydraulics of *Ligustrum vulgare* and *Viburnum lantana*. *Tree Physiology*. 29: 765–775.

Burke IC, Lauenroth WK, Riggle R, Brannen P, Madigan B, Beard S. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. *Ecosystems* 2: 422–438.

Cooper DJ, Sanderson JS, Stannard DI, Groeneveld DP. 2006. Effects of long-term water table drawdown on evapotranspiration and vegetation in an arid region phreatophyte community. *Journal of Hydrology* 325: 21–34.

Dahlgren RA, Richards JH, Yu Z. 1997. Soil and groundwater chemistry and vegetation distribution in a desert playa, Owens Lake, California. *Arid Soil Research and Rehabilitation* 11: 221–244.

Daubenmire R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33: 43–64.

Donovan LA, Ehleringer JR. 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology* 8: 289–297.

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR. 1991. Differential utilization of summer rains by desert plants. *Oecologia* 88: 430–434.

Elmore AJ, Mustard JF, Manning SJ. 2003. Regional patterns of plant community response to changes in water: Owens Valley, California. *Ecological Applications* 13: 443–460.

Elmore AJ, Manning SJ, Mustard JF, Craine JM. 2006. Decline in alkali meadow vegetation cover in California: the effects of groundwater extraction and drought. *Journal of Applied Ecology* 43: 770–779.

Farquhar GD, Ehleringer JR, Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40: 503–537.

Flanagan LB, Ehleringer JR, Marshall JD. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant, Cell and Environment* 15: 831–836.

Gehre M, Geilmann H, Richter J, Werner RA, Brand WA. 2004. Continuous flow $^2H/^1H$ and $^{18}O/^{16}O$ analysis of water samples with dual inlet precision. *Rapid Communications in Mass Spectrometry* 18: 2650–2660.

Goedhart CM, Pataki DE, Billings SA. 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 DOI: 10.1007/s11104-009-0048-4.

Griepentrog TE, Groeneveld DP. 1981. *The Owens Valley Management Report*. Prepared for the County of Inyo, California.

Hacke UG, Sperry JS. 2001. Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics*. 4/2: 97–115.

Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schäfer R, Oren R. 2000a. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124: 495–505.

Hacke UG, Sperry JS, Pitterman J. 2000b. Drought experience and cavitation resistance in six desert shrubs of the Great Basin, Utah. *Basic Applied Ecology* 1: 31–41.

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.

Hao X, Li W, Huang X, Zhu C, Ma J. 2010. Assessment of the groundwater threshold of desert riparian forest vegetation along the middle and lower reaches of the Tarim River, China. *Hydrological Processes* 24: 178–186.

Hatfield R, Fukushima RS. 2005. Can lignin be accurately measured? *Crop Science* 45: 832–839.

Högberg P. 1990. Forests losing large quantities of nitrogen have elevated $^{15}N:^{14}N$ ratios. *Oecologia* 84: 229–231.

Holste EK, Jerke MJ, Matzner SL. 2006. Long-term acclimatization of hydraulic properties, xylem conduit size, wall strength and cavitation resistance in *Phaseolus vulgaris* in response to different environmental effects. *Plant, Cell and Environment* 29: 836–843.

Hook PB, Burke IC, Lauenroth WK. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. *Plant and Soil* 138: 247–256.

Jacobsen AL, Ewers FW, Pratt RB, Paddock WA, Davis SD. 2005. Do xylem fibers affect vessel cavitation resistance? *Plant Physiology* 139: 546–556.

Jacobsen AL, Pratt RB, Ewers FW, Davis SD. 2007. Cavitation resistance among 26 chaparral species of Southern California. *Ecological Monographs* 77: 99–115.

Jansen S, Baas P, Gasson P, Smets E. 2003. Vestured pits: do they promote safer water transport? *International Journal of Plant Sciences* 164: 405–413.

Jansen S, Baas P, Gasson P, Lens F, Smets E. 2004. Variation in xylem structure from tropics to tundra: evidence from vestured pits. *Proceedings of the National Academy of Sciences* 101: 8833–8837.

Kavanagh KL, Bond BJ, Aitken SN, Gartner BL, Knowe S. 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. *Tree Physiology* 19: 31–37.

Kolb KJ, Sperry JS. 1999. Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology* 80: 2373–2384.

Ladjal M, Huc R, Ducrey M. 2005. Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. *Tree Physiology* 25: 1109–1117.

Lamontagne S, Cook PG, O'Grady A, Eamus D. 2005. Groundwater use by vegetation in a tropical savanna riparian zone (Daly River, Australia). *Journal of Hydrology* 310: 280–293.

McLendon T, Hubbard PJ, Martin DW. 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.

Melillo JM, Aber JD, Muratore JF. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621–626.

Mencuccini M, Comstock J. 1997. Vulnerability to cavitation in populations of two desert species, *Hymenoclea salsola* and *Ambrosia dumosa*, from different climatic regions. *Journal of Experimental Botany* 48: 1323–1334.

Muñoz-Reinoso JC. 2001. Vegetation changes and groundwater abstraction in SW Doñana, Spain. *Journal of Hydrology* 242: 197–209.

Naumburg E, Mata-Gonzalez R, Hunter RG, McLendon T, Martin DW. 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.

O'Grady AP, Cook PG, Eamus D, Duguid A, Wischusen JDH, Fass T, Worldege D. 2009. Convergence of tree water use within an arid-zone woodland. *Oecologia* 160: 643–655.

Pataki DE, Billings SA, Naumburg E, Goedhart CM. 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.

Pavón NP, Briones O. 2001. Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. *Journal of Arid Environments* 49: 265–277.

Pockman WT, Sperry JS. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* 87: 1287–1299.

Pratt RB, Black RA. 2006. Do invasive trees have a hydraulic advantage over native trees? *Biological Invasions* 29: 261–299.

Pratt RB, Jacobsen AL, Ewers FW, Davis SD. 2007. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist* 174: 787–798.

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

Schlesinger WH, Raikes JA, Hartley AE, Cross AF. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77: 364–374.

Sperry JS, Hacke UG. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* 16: 367–378.

Sperry JS, Donnelly JR, Tyree MT. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* 11: 35–40.

Taylor BR, Parkinson D, Parsons WFJ. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70: 97–104.

Toft CA. 1995. A 10-year demographic study of rabbitbrush (*Chysothamnus nauseosus*): growth, survival and water limitation. *Oecologia* 101: 1–12.

Wainhouse D, Ashburner R. 1996. The influence of genetic and environmental factors on a quantitative defensive trait in spruce. *Functional Ecology* 10: 137–143.

Wainhouse D, Cross DJ, Howell RS. 1990. The roles of lignin as a defence against the spruce bark beetle *Dendroctonus micans*: effect on larvae and adults. *Oecologia* 85: 257–265.

West AG, Patrickson SJ, Ehleringer JR. 2006. Water extraction times for plant and soil materials used in stable isotope analysis. *Rapid Communications in Mass Spectrometry* 20: 1317–1321.