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Plant Water Use in Owens Valley, CA:
Understanding the Influence of Climate and Depth to Groundwater

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Abstract

There is a long-standing controversy in Owens Valley, California about the potential impacts of water exports on the local ecosystem. It is currently extremely difficult to attribute changes in plant cover and community composition to hydrologic change, as the interactions between ecological and hydrologic processes are relatively poorly understood. Underlying predictions about losses of grasslands and expansion of shrublands in response to declining water tables in Owens Valley are assumptions about the differential access of grasses versus shrubs to groundwater and their physiological responses to water stress. We sought to test these assumptions with measurements of natural abundance isotope tracers in plants, soils, and groundwater, and with physiological measurements. We found that the grass species *Distichlis spicata* did use shallower water sources than co-occurring shrub species, particularly in late summer. However, at sites with watertable depths < 3 m we did not find evidence of water stress in the grass species. In fact, *Distichlis* was more resistant to water stress-induced cavitation than co-occurring shrub species, indicating greater tolerance of dry conditions. Instead, soil nutrient availability appeared to be strongly limiting grass photosynthesis and gas exchange at low nutrient sites. As has been found previously, our results showed that where water table depths exceeded 3 m, grass cover was extremely sparse across a depth to watertable gradient. We did find evidence of water stress at 6 m watertable depth in the phreatophytic shrub species *Ericameria nauseosa*. Vulnerability to cavitation, an important component of plant water stress response, increased with watertable depth in this species. Hence, plant hydraulic architecture showed intraspecific variation in response to water availability. Stem lignin content increased with vulnerability to cavitation, possibly because of the linkage between lignified xylem and the ability to withstand cavitation. We propose that this relationship is a potential mechanism linking ecosystem water and nutrient availability, which appear to be closely correlated in Owens Valley. Our results highlight the importance of nutrient limitation in these ecosystems, and suggest that models used to evaluate ecosystem responses to hydrologic change in this region will require explicit attention to the ecosystem nitrogen cycle and the spatial and temporal variability in nitrogen availability.

Introduction and Problem Statement

Owens Valley, California has been an important source of water for the city of Los Angeles for nearly one hundred years. Recent studies have suggested that lowering of the water table caused by groundwater pumping and diversion of water has led to decreases in live plant cover, primarily in groundwater dependent species such as grasses and phreatophytic shrubs (Griepentrog and Groeneveld 1981; Elmore et al. 2003; Elmore et al. 2006). Consequently, the interactions between ecology and hydrology have become central to decisions about management of water and natural resources in Owens Valley. Yet the mechanisms underlying these interactions remain highly uncertain.

Research focusing on altered and reduced streamflow has provided us with a fairly good understanding of the dependence of riparian trees on groundwater (see reviews by Friedman *et al.*, 1997, Stromberg, 1993a, b, 2001). Desert shrub and grassland communities may also use groundwater (Robinson, 1958), but the impacts of altered

water tables on these communities has been less studied. Semi-arid, shallow groundwater ecosystems are generally dominated by species that are not obligate phreatophytes. These species can occur in areas where they do not have access to groundwater and show great tolerance to water stress, as well as in shallow groundwater sites with abundant available water (Naumburg *et al.*, 2005). Several uncertainties limit our ability to predict responses of these ecosystems to hydrologic change, including a limited understanding of species differences in rooting depths and distribution, and of linkages between nutrient availability, groundwater uptake by vegetation, and community composition. A quantitative understanding of these interactions is critical for a variety of resource and land management issues in Owens Valley and in other arid and semi-arid ecosystems experiencing hydrologic change.

In addition to water availability, nitrogen (N) is known to be a highly limiting resource in arid ecosystems (Hadley and Szarek 1981) that is also an important determinant of ecosystem processes (McLendon and Redente 1992; Paschke *et al.* 2000; Billings *et al.* 2002; Billings *et al.* 2004; Drenovsky and Richards 2004; James *et al.* 2005; Drenovsky and Richards 2006; James and Richards 2007; Pataki *et al.* 2005; Pataki *et al.* 2008). In fact, water and nitrogen availability are often linked in arid ecosystems and may colimit plant productivity (Lajtha and Whitford 1989; Hooper and Johnson 1999; Carrera *et al.* 2003; James and Richards 2005; James *et al.* 2005), with potentially important differences among plant functional types. Woody shrubs tend to have deeper rooting structures with greater lateral spread, while herbaceous grasses tend to have more restricted rooting volumes (Lee and Lauenroth 1994; Canadell *et al.* 1996; Schenk and Jackson 2002). Therefore, grasses may be more sensitive to declining water table depths than shrubs, mainly due to dependence on summer precipitation and other shallow soil water sources (Ehleringer *et al.* 1991; Darrouzet-Nardi *et al.* 2006; Elmore *et al.* 2003; Elmore *et al.* 2006; Pataki *et al.* 2007). In contrast, semi-arid Great Basin shrubs may be more affected by N limitation (Drenovsky and Richards 2004; Drenovsky and Richards 2005; James and Richards 2005; James *et al.* 2005). In a manipulative experiment on playa communities near Mono Lake, the shrub species *Sarcobatus vermiculatus* and *Ericameria nauseosa* (formerly *Chrysothamnus nauseosus*) were nutrient limited, while the grass species *Distichlis spicata* increased nutrient uptake only with the addition of water (James and Richards 2005).

Due to the central importance of both water and N limitations in semi-arid ecosystems, the potential linkages between water and N are of great significance for evaluating ecosystem responses to hydrologic change. One mechanism that may link water stress and nutrient cycling is in the linkage between plant responses to water stress and plant chemical composition, which has not been previously explored. A major physiological response of plants to water stress is cavitation, or introduction of air embolisms, into xylem. Embolisms block the flow of water and prevent water uptake, potentially leading to catastrophic failure of the vascular system. Plants with greater resistance to cavitation have been shown to have greater xylem density (Hacke *et al.* 2001) and strength (Pratt *et al.* 2007), indicating that xylem of resistant species contains different proportions of material than xylem of less resistant species. Because litter chemical composition is closely related to rates of decomposition and ecosystem nutrient cycling (Melillo and Aber 1982, Taylor *et al.* 1989), there are important implications of variations in vulnerability to cavitation for biogeochemistry that have not yet been evaluated. Lignin is

a strengthening compound that is found predominantly in the secondary cell wall of vessel elements and fibers, and is likely to be closely associated with plant resistance to cavitation. Lignin is quite resistant to degradation, and plant material composed of a greater proportion of lignin may inhibit decomposition of plant litter and woody debris. If vulnerability to cavitation is correlated with stem and root lignification, changes in groundwater depth and ecosystem water availability may change the amount of lignin delivered to soils – either by increased lignification of xylem in existing plant populations, or by shifts in community composition toward more water stress resistant species.

Objectives

In this study, we wished to quantify differences in access to groundwater between grasses and shrubs in Owens Valley, and the impacts of differences in water availability on plant function. To account for potential differences in physiological processes caused by variations in nutrient uptake and availability, we also quantified ecosystem N pools and plant N content at our study sites. Finally, we evaluated potential linkages between hydrologic change, plant responses to water stress, and nutrient availability by evaluating the relationship between plant vulnerability to cavitation, chemical composition, and litter decomposition.

We wished to address the following specific questions:

- Do grasses and shrubs differ in their access to groundwater in Owens Valley ecosystems?
- Is plant water availability correlated with access to ecosystem N pools?
- How does water and N availability influence photosynthesis and gas exchange of these species?
- How do these species differ in their vulnerability to cavitation?
- Is vulnerability to cavitation linked to plant chemical composition, and can this relationship be a link between plant responses to declining water availability and ecosystem nutrient cycling?

Procedure

In 2005 we selected three sites in Owens Valley which varied in the proportion of grass vs. shrub cover but had similar depth to groundwater (< 3 m). These sites consisted of: 1) an alkaline meadow near Chalk Bluffs north of the town of Bishop; 2) an intermediate, mixed grass-shrub community near the Owens River south of Bishop; and 3) a shrub dominated site with very sparse grass cover. The meadow site was dominated by *Distichlis spicata*, *Sporobolus airoides*, and *Leymus triticoides*; grass cover is nearly continuous at this site. Both the intermediate and shrub sites were dominated by the shrubs *Atriplex torreyi*, *Ericameria nauseosa*, and *Sarcobatus vermiculatus*, and the grasses *Distichlis spicata* and *Sporobolus airoides*. The depth to groundwater (DTW)

was < 3 m at all three sites throughout the study. At each site, leaves were collected for elemental and stable isotope analysis in July and stems were sampled for water extraction and stable isotope analysis in June, July, and August. In June 2005, soil cores were extracted for analysis of water and N isotopes from 0 – 200 cm depth. Soil collars for nitrous oxide (N₂O) and ammonia (NH₃) flux measurements were installed in June 2005 and sampled in July 2005. In June of 2005 and 2006, soil samples to 15 cm depth were extracted from the meadow site, and at the mixed grass-shrub and shrubland sites, both under shrubs and in intershrub spaces for laboratory assays of C and N fluxes and availability. Finally, in 2007 seven sites were chosen along a depth to groundwater gradient in order to explicitly evaluate the role of varying watertables on plant processes. A detailed description of each measurement is given below.

Stable isotope measurements – Sampled sun leaves at the top of the canopy were dried for at least 48 hours at 70°C and ground to a fine powder. Nitrogen isotope ratio ($\delta^{15}\text{N}$), leaf %N, and C:N ratio were measured with an elemental analyzer coupled to an Isotope Ratio Mass Spectrometer (Delta Plus IRMS, Thermofinnigan, San Jose, CA). Plants were sampled for stable isotope analysis of water by removing small sections of non-green woody stems for shrubs, and non-evaporating rhizomes extracted from the just below the soil surface for grasses. Samples were placed in vacutainers, sealed with parafilm, and stored in a cooler in the field. Soil samples at 10-20 cm increments from 0 – 200 cm depth were also stored in a cooler in sealed vacutainers. In the laboratory, stem, rhizome, and soil samples were stored at freezing temperatures until extraction by cryogenic vacuum distillation (West *et al.*, 2006). Water samples were analyzed for oxygen isotope ratio ($\delta^{18}\text{O}$) by pyrolysis after Gehre *et al.* (2004) using a TCEA interface coupled to an IRMS (Delta Plus XP, Thermofinnigan, San Jose, CA). Following the water extraction, roots were removed from the soil samples, and the remaining fraction was ground to a fine powder and analyzed for $\delta^{15}\text{N}$ as described above. Nitrogen isotope ratios were referenced to the atmospheric standard with a precision of 0.16 ‰. Oxygen isotope measurements were referenced to V-SMOW within a precision of 0.19 ‰. All isotope measurements were conducted at the University of California, Irvine IRMS facility.

Physiological Measurements - Gas exchange was measured on 3-5 individuals of *A. torreyi*, *E. nauseosa*, and *D. spicata* at the three sites in June and August of 2005, and in six week intervals throughout the summer growing season from mid June to mid September in 2006. Measurements were made with a portable gas exchange system (LI6400, Licor, Inc, Lincoln, NE) at saturating light conditions (1500 mmol·m⁻²·s⁻¹ photosynthetically active radiation) and ambient temperature (generally ~37°C). After each measurement, the measured shoot or leaf blades were harvested and the area of fresh leaves was measured (ImageJ software, NIH, Bethesda, MD) to express photosynthesis on a leaf area basis. Predawn water potential was measured during the same intervals in 2006 with a Scholander-type pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA).

Soil flux measurements and assays – Collars for gaseous N emissions in the field (625 cm²) were inserted ~5 cm into the soil profile at the meadow, mixed grass-shrub, and shrubland sites. At each site, we installed chambers in four plots. At the intermediate and shrubland sites, replicate chambers were installed under three different cover types

(intershrub, *Atriplex* and *Ericameria*) for a total of 12 collars. At the meadow site, all chambers were surrounded by grass species. On July 24, 2005, airtight lids were placed on the chambers and four sequential gas samples were taken (14 ml) over a period of approximately 45 minutes. Gas samples were injected into pre-evacuated, air-tight vials and transported to the University of Kansas, where they were analyzed for N₂O on a Varian CP3800 gas chromatograph equipped with an electron capture detector. Standards were also injected into vials in the field and analyzed in a similar manner to ensure that sample transport did not affect accuracy of the data. Rates of N₂O were calculated using chamber headspace and footprint and the rate of increase of N₂O concentration in the chamber over time (Billings *et al.*, 2003). On July 25, chambers were equipped with a small dish of 2% H₂SO₄ and sealed with Vaseline and aluminum foil for a 24 h period. H₂SO₄ samples were collected and transported to the University of Kansas, where they were analyzed for NH₄⁺ concentration. Rates of NH₃ volatilization were calculated as the amount of NH₄⁺ produced per unit time using the footprint of the chambers (Schlesinger & Peterjohn, 1991).

Soils collected in June 2005 were transported at 4°C to the University of Kansas, where they were maintained at this temperature until further processing. Within 1 week, all roots >2 mm were removed, and soils were sieved and homogenized. They subsequently were subjected to long-term soil incubations for determination of net N mineralization during decomposition of both labile and relatively recalcitrant soil organic matter. Fifty g of each soil (fresh weight) were weighed into a 5 cm diameter, 7.5 cm tall PVC core contained by glass fiber filter paper. Cores were leached with a N-free nutrient solution (Nadelhoffer, 1990) to remove inorganic N and placed in 1L incubation jars on a layer of marbles to maintain unsaturated conditions at the base of the cores. Jars were incubated at 25°C. On each sampling date, soil cores removed and leached with the N-free nutrient solution. Aerobic conditions were maintained in the incubation vessels between sampling dates. Leachate was stored at 4°C until analysis, and then analyzed colorimetrically for NH₄⁺ and NO₃⁻ on an autoanalyzer at the University of Kansas (Lachat Instruments, Loveland, Colorado, USA). Net N mineralization was calculated as the cumulative sum of inorganic N leached over time, using the equivalent dry weight of each soil sample (Billings, 2006). Leachate samples were obtained on days 3, 7, 15, 21, 31, 42, 56, and 72.

Soil Inorganic N Measurements - In June and September 2006, soil samples were collected at each site by combining a composite of three subsamples from 0-15 cm depth underneath each shrub species and in grass dominated intershrub spaces. Soil samples were immediately chilled at 4°C until extracted with 2M KCl and analyzed for ammonium and nitrate colorimetrically. In addition, *in situ* soil inorganic N availability was determined using 3-5 2.5 x 5 cm cation and anion resin strips under each species and in open areas (GE Infrastructure Water & Process Technologies, Watertown, MA) placed in the top 5 cm of the soil profile for 5 days. Resin strips were extracted with 2M KCl and analyzed colorimetrically for ammonium and nitrate concentration.

Plant vulnerability to cavitation and chemical composition – In addition to the three sites where we made intensive measurements of water and nutrient relationships, we established 7 sites that span a 0.3 to 6 m groundwater depth gradient. We selected these sites using groundwater depth records provided by the Los Angeles Dept. of Water and

Power and confirmed that watertable depths were relatively constant at each monitoring well for at least a 10 year period prior to sampling. We quantified grass and shrub cover across this gradient, which varied with water table depth. We also sampled stems and roots of the shrubs *Atriplex torreyi* and *Ericameria nauseosa*, and roots of the grass *Distichlis spicata* for measurements of vulnerability to cavitation. Water stress resistance of each species was determined at each site by measuring vulnerability to cavitation of stems and roots using a hydraulic conductivity system coupled with a tension-inducing centrifuge (Sperry 1988; Alder 1997). Total lignin was then determined for these samples by acetone drying and weighing samples following extraction in 72% H₂SO₄.

Results

The oxygen isotope composition of groundwater in Owens Valley ranged from -14.1 to -17.0‰, or -16.2‰ on average (Figure 1). The isotopic composition of soil water was similar to groundwater at depths of approximately 35, 65, and 200 cm in the grassland, intermediate, and shrubland sites, respectively, with large enrichments at the soil surface (Figure 1). The isotopic composition of soil water at all depths did not change throughout the season in the grassland site. Soil water from 50 – 200 cm in the intermediate site was more isotopically enriched midway through the season than early in the season, and soil water at 50 – 100 cm in the shrubland site was more isotopically enriched early in the season than late in the season (Figure 1, $p < 0.05$). Stem water collected from the two shrub species throughout the 2006 season was more depleted than the grasses (Figure 3, $p < 0.0001$). Grass rhizome water in both the grassland and shrubland sites was more enriched in August after a rain event in late July and in the intermediate site after a rain event in mid May. However, the isotopic composition of shrub stem water did not vary significantly with time (Figure 2, $p > 0.1$).

Nitrogen isotopes also varied with depth, with the most enriched values at the soil surface and the most depleted values at depth (Figure 3). In the top 15 cm of the soil profile, there was a strong gradient of soil organic C and N concentration across the three sites, with much greater soil % C and N at the meadow sites than at the two shrub sites. Soil N isotopes showed a gradient of greater enrichment at both sites supporting shrubs compared to the meadow (Figure 4). Laboratory assays of cumulative net N mineralization exhibited the greatest net mineralization at the meadow site ($p=0.019$, Figure 5). We observed similar, non-significant trends in gaseous losses of N measured in the field, with meadow soils exhibiting generally higher, but more variable, rates of N₂O fluxes ($p=0.084$) and NH₃ volatilization ($p=0.13$) than the intermediate and shrub sites (Figure 5).

A trend of decreasing soil KCl extractable inorganic N from June to September 2006 was evident under all species at all sites, with significant declines in inorganic N under *D. spicata* in the grassland and shrubland sites, and under *E. nauseosa* in the intermediate site (Figure 6a, $p < 0.05$). Inorganic N concentrations were generally greater in soils from grassland and intermediate sites than the shrubland site ($p < 0.0001$). In addition, the percentage of inorganic soil N in the form of ammonium was greatest in the grassland and lowest in the intermediate site (Figure 6a, $p < 0.0001$). Percent ammonium did not change during the season under any species or at any site with the exception of *A. torreyi*

in the shrubland, where percent ammonium increased during the season ($p < 0.05$). There were no overall species differences in either ammonium or nitrate availability as measured with resin strips ($p > 0.1$). Nitrate availability did not vary by site ($p < 0.05$), but ammonium availability was greater under *D. spicata* in the shrubland versus the intermediate site ($p < 0.05$).

Declines in soil inorganic N from June to September were consistent with an overall decrease in leaf percent N over the 2006 season for all species and sites except *A. torreyi* in the intermediate site (Figure 6b, $p < 0.05$). Differences in leaf percent N among sites were apparent in June for both *D. spicata* and *E. nauseosa*. Leaf N in *D. spicata* was greater in both the grassland and intermediate sites than in the shrubland site (Figure 6b, $p < 0.001$). Likewise, percent leaf N in *E. nauseosa* was greater in the intermediate site than the shrubland site (Figure 6b, $p < 0.05$).

Overall, *Atriplex torreyi* showed the most negative predawn water potentials, particularly at the intermediate site (Figure 7, $p < 0.05$). For all other species and sites, values remained more positive than -2 MPa. Water potential did not vary significantly among sites or sampling periods for either shrub species or grasses, with the exception of *A. torreyi* in August, when predawn water potentials were lower in the intermediate site (Figure 7, $p < 0.01$).

Leaf level photosynthesis was generally higher in the grass species *Distichlis spicata* in comparison to the two shrub species (Figure 8, $p < 0.0001$). Photosynthesis of *A. torreyi* was relatively low and constant throughout the season and did not differ between sites in either 2005 or 2006 ($p > 0.1$). Photosynthesis of *E. nauseosa* was also relatively low and constant in 2006; however, photosynthesis of *E. nauseosa* in 2005 was greater at the intermediate than the shrubland site early in the season (Figure 8, $p < 0.05$), but similar at both sites in August (Figure 8, $p > 0.1$). There was a marginally significant trend of greater grass photosynthesis at the grassland site than the shrubland site early in the season in both 2005 and 2006 (Figure 8, $p < 0.1$). After the June measurement period, photosynthesis in the grassland site dropped significantly ($p < 0.05$), while at the intermediate and shrubland sites grass photosynthesis remained low and relatively constant throughout the season (Figure 8).

Leaf N of all species, including the halophytic shrub *Sarcobatus vermiculatus*, was correlated with leaf $\delta^{15}\text{N}$ during each sampling period; this relationship was strongest when leaf N was expressed as C:N ratio rather than leaf percent N (Figure 9, $p < 0.05$). The slope of this relationship was greater in September than in May and June (ANCOVA, $p < 0.01$ and $p < 0.05$, respectively), with the non-halophytic shrub species and the halophytic grass species showing larger declines in leaf N late in the growing season than the two halophytic shrub species (Figure 9).

Total leaf N was positively correlated with inorganic N availability across species and sites ($r^2 = 0.34$, $p < 0.05$). However, when species were analyzed individually, only *D. spicata* showed a significant relationship (Figure 10, $p < 0.05$). Leaf percent N was also positively correlated with photosynthesis in *D. spicata* when data from 2005 and 2006 were combined (Figure 10, $r^2 = 0.51$, $p < 0.01$). No relationship between leaf N and photosynthesis was observed for the other species ($p > 0.1$). Photosynthesis was not

correlated with stem water isotopes or predawn water potential for any species or site ($p > 0.1$).

Across the seven sites that spanned the 0.3 – 6m depth to watertable gradient, grass cover consistently declined and shrub cover increased (Figure 11). For *Ericameria nauseosa*, $\delta^{13}\text{C}$ of leaves became more enriched across the gradient, indicating greater water stress at deeper water table depths (Figure 12). This metric of water stress was correlated with stem vulnerability to cavitation, which also declined across the gradient (Figure 13). Hence, shrubs of this species located at sites of greater watertable depth showed altered vascular anatomy that resulted in greater vulnerability to cavitation. As hypothesized, vulnerability to cavitation was in fact correlated with stem lignin content in this species (Figure 14). When the three co-occurring species were compared at the same site, the grass species *Distichlis spicata* was the most resistant to cavitation, while *Ericameria nauseosa* was the least resistant (Figure 15).

Conclusions

Our results support some previous assumptions of interactions between ecology and hydrology in Owens Valley, but refute others. Our measurements of the isotopic composition of groundwater, plant water, and soil water confirmed that grasses have a shallower root distribution than shrubs, and may use shallow water sources for transpiration, particularly at the end of the growing season (Figures 1 and 2). However, we did not find strong evidence of water stress in grasses at sites where the depth to watertable did not exceed 3 m (Figure 7). In fact, we found that the grass species *Distichlis spicata* showed more ~~or~~ somewhat more resistance to cavitation than the shrub species (Figure 15), which is the opposite of what was expected given previous assumptions about the vulnerability of grassland species to drought. However, given that *Distichlis* roots are restricted to a drier, shallower rooter zone than the shrub species, a high degree of resistance to cavitation is a logical adaptation to prolonged drought.

Rather than water stress, we did find strong evidence of nutrient limitation in grasses at nutrient poor sites. Unlike shrub species, *Distichlis spicata* showed a strong correlation between soil inorganic N pools, leaf N, and photosynthetic rates (Figures 6, 8 and 10). Hence, the temporal and spatial distribution of N as well as water is likely to play an important role in the distribution and stability of grassland ecosystems. We also found that shrub species, particularly the salt tolerant species *Atriplex torreyi*, is particularly well adapted to thrive on low nutrient sites where N is isotopically enriched due to large gaseous losses (Figures 3-5 and 9). Hence, ecosystem and soil N losses that follow a disturbance or loss of grass cover may promote woody encroachment and invasions of grasslands by shrubs.

We did see evidence of plant water stress across a depth to groundwater gradient where water tables were as deep as 6 m. In particular, the phreatophytic shrub species *Ericameria nauseosa* showed enrichment of leaf carbon isotopes, a measure of water stress, with watertable depth (Figure 12). Vulnerability to cavitation also increased across this gradient (Figure 13), and was correlated with an increase in stem lignin content (Figure 14). These relationships have led to the development of our conceptual

model for the linkages between soil and groundwater availability, plant water stress adaptations, the chemical content of plant material, and ecosystem nutrient cycling (Figure 16). Plant material with a high proportion of lignin has been shown to be relatively resistant to decomposition, which may inhibit nutrient cycling. This may constitute an important linkage between changes in hydrology and water availability, which may affect plant vulnerability to cavitation and ecosystem nutrient availability. Such a feedback has important management implications as such changes in nutrient status are particularly difficult to reverse, even if plant water availability and groundwater levels have been restored.

We have a proposal pending to further test the conceptual model developed under the current grant. Important next steps are to test the generality of linkages between plant vulnerability to cavitation and chemical content, and to further explore the role of litter chemical composition in rates of nutrient cycling at these sites. The current grant has allowed us to develop a potentially new area in ecohydrology that can help us better quantify how hydrologic and ecological processes are explicitly linked.

List of publications

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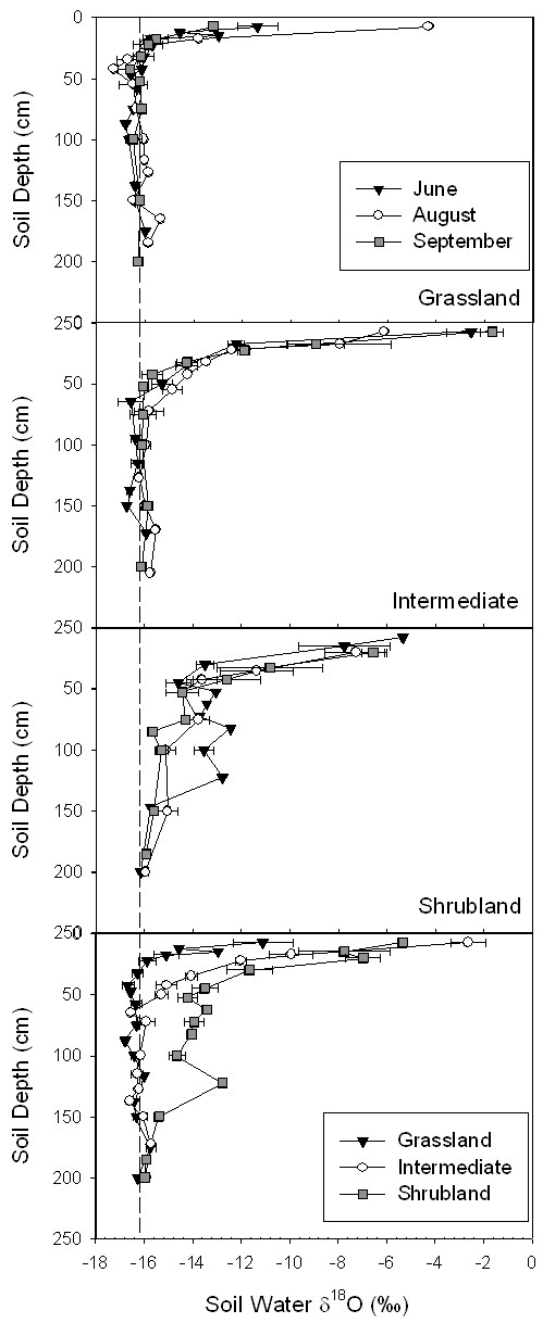


Figure 1 - The oxygen isotopic composition ($\delta^{18}\text{O}$) of soil water with depth in the grassland, intermediate, and shrubland sites separated by month in 2006 (top three panels) and average seasonal values for all three sites in 2006 (lower panel). The dotted line shows the isotopic composition of groundwater. Error bars show the standard error (n varies from 1 to 5 replicates in the first 3 panels and from 1 to 10 replicates in the last panel).

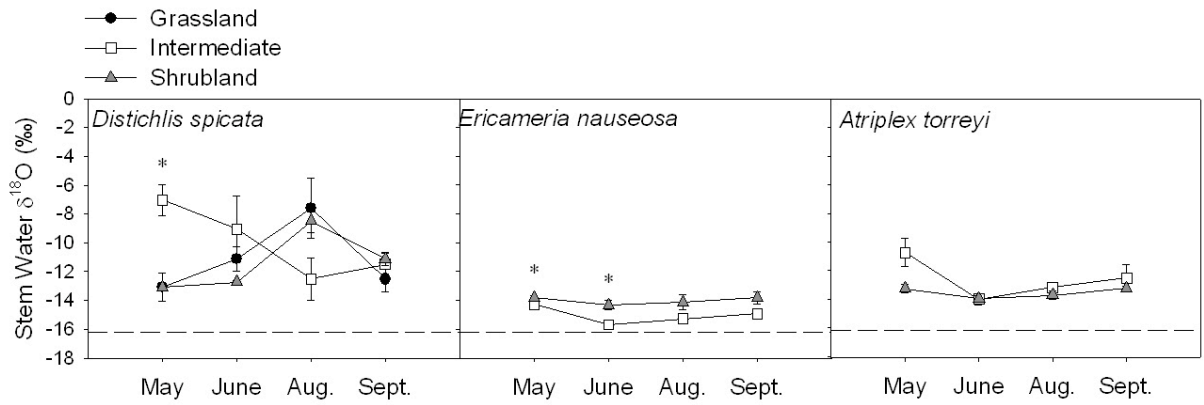


Figure 2 - The oxygen isotopic composition ($\delta^{18}\text{O}$) of grass and shrub species in the grassland, intermediate, and shrubland sites in 2006. The dotted line shows the isotopic composition of soil water. Error bars show the standard error (n varies from 3 to 5 replicates). Asterisks show significant differences among sites at $\alpha = 0.05$.

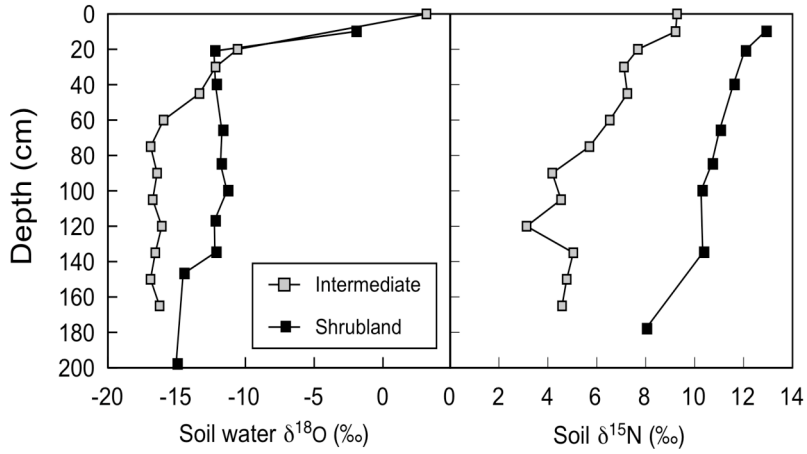


Figure 3 – The oxygen isotope ratio ($\delta^{18}\text{O}$) of soil water and the nitrogen isotope ratio ($\delta^{15}\text{N}$) of root free soil as a function of depth at the two shrub sites sampled in 2005.

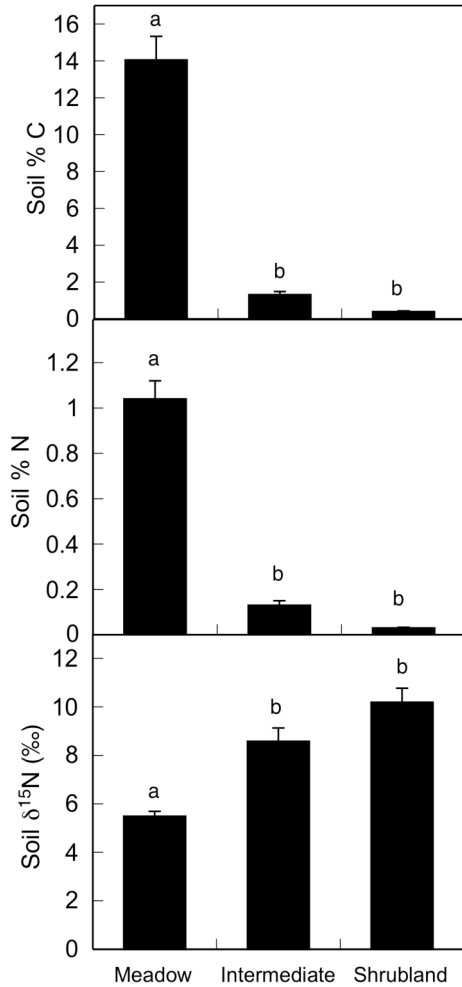


Figure 4 – The total % C and N and the nitrogen isotope ratio ($\delta^{15}\text{N}$) of soil sampled from 0 – 15 depth. Error bars show the standard error (n=9). Letters show significance at $\alpha = 0.05$ (ANOVA and Tukey-Kramer post-hoc test).

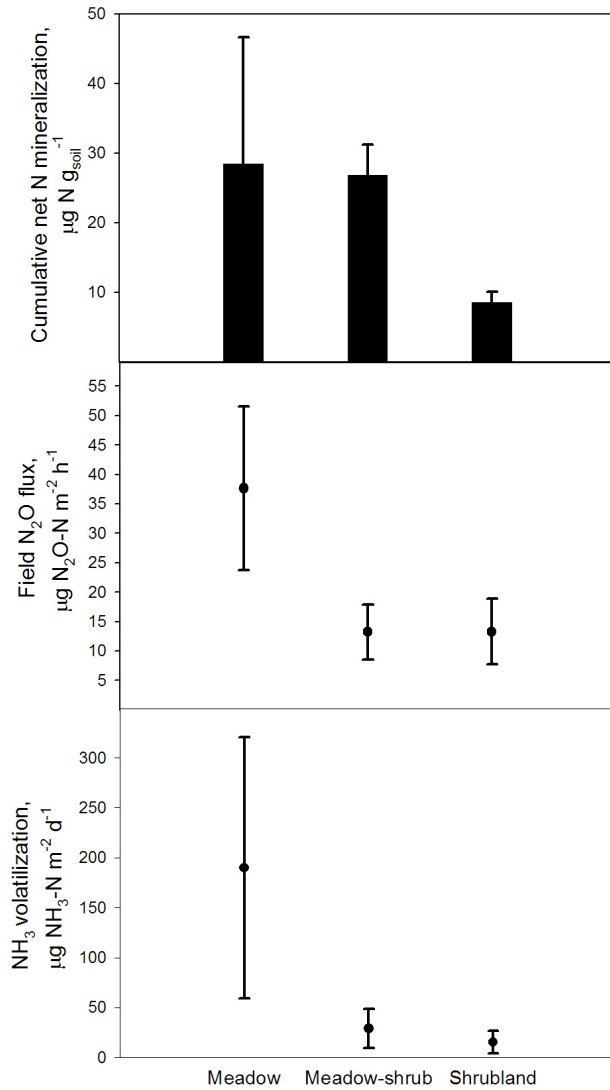


Figure 5 – Cumulative net N mineralized in laboratory soil incubations (top panel), field measurements of nitrous oxide (N_2O) fluxes, and field measurements of ammonia (NH_3) fluxes at each site sampled in 2005. Cumulative N mineralization was significantly different among sites (ANOVA, $p=0.019$), while N_2O fluxes were marginally significant ($p=0.084$) and NH_3 fluxes were not significant ($p=0.13$). Error bars show the standard error ($n=12$).

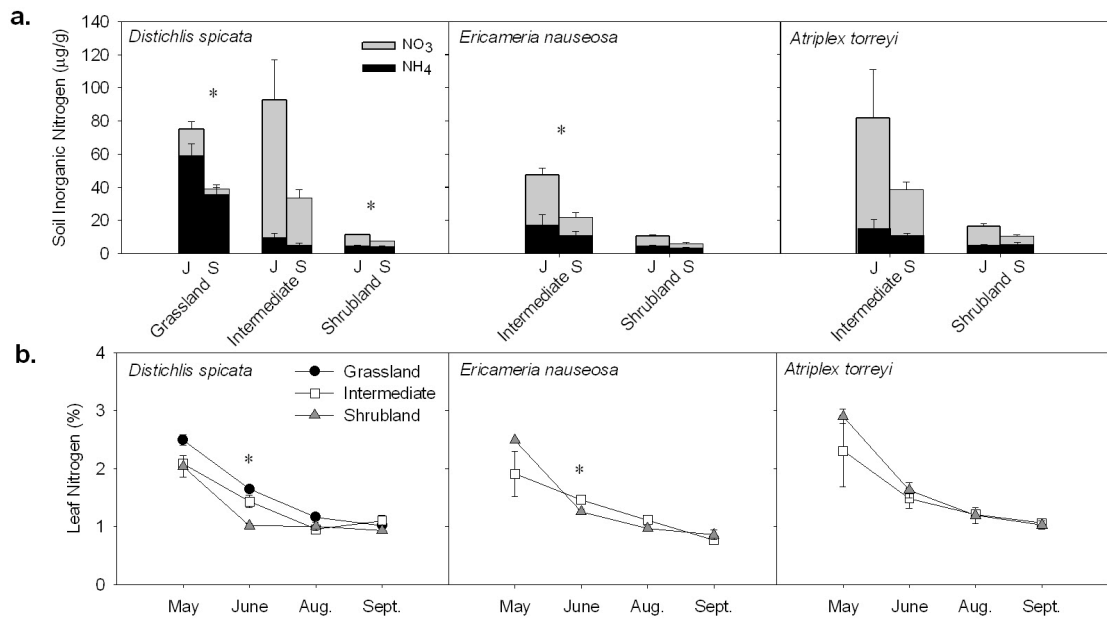


Figure 6 - a) Soil inorganic N in the form of nitrate and ammonium under each species at each site in July (J) and September (S) 2006. b) Leaf percent N in each species and site in 2006. Error bars show the standard error (n varies from 3 to 5 replicates). Asterisks show significant differences among sites at $\alpha = 0.05$.

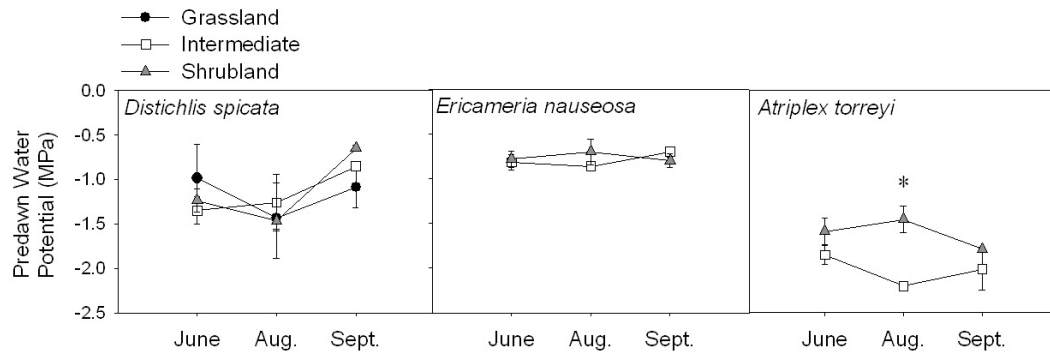


Figure 7 - Predawn water potential (MPa) of grass and shrub species in the grassland, intermediate, and shrubland sites in 2006. Error bars show the standard error (n varies from 3 to 8 replicates). Asterisks show significant differences among sites at $\alpha = 0.05$.

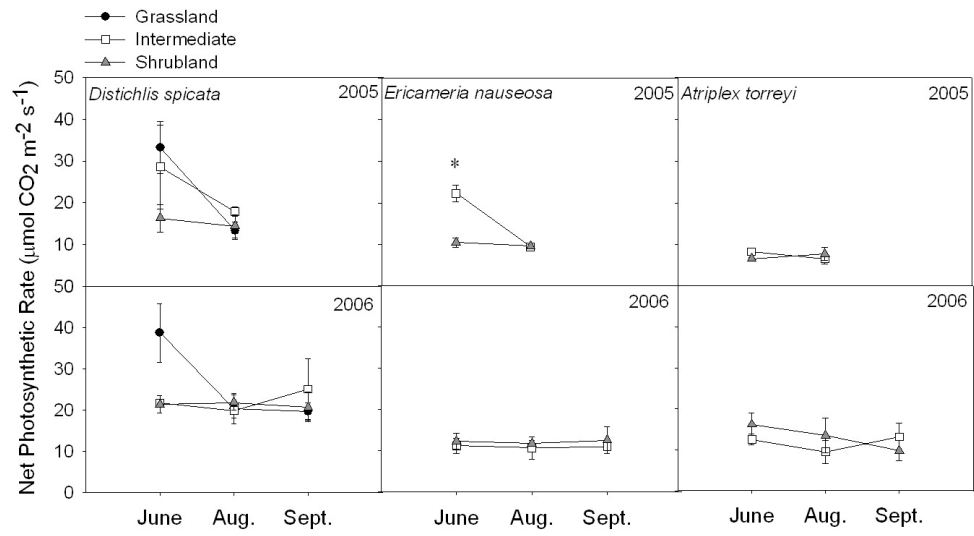


Figure 8 - Leaf level photosynthesis during the 2005 and 2006 growing seasons. Error bars show the standard error (n varies from 3 to 5 replicates). Asterisks show significant differences among sites at $\alpha = 0.05$.

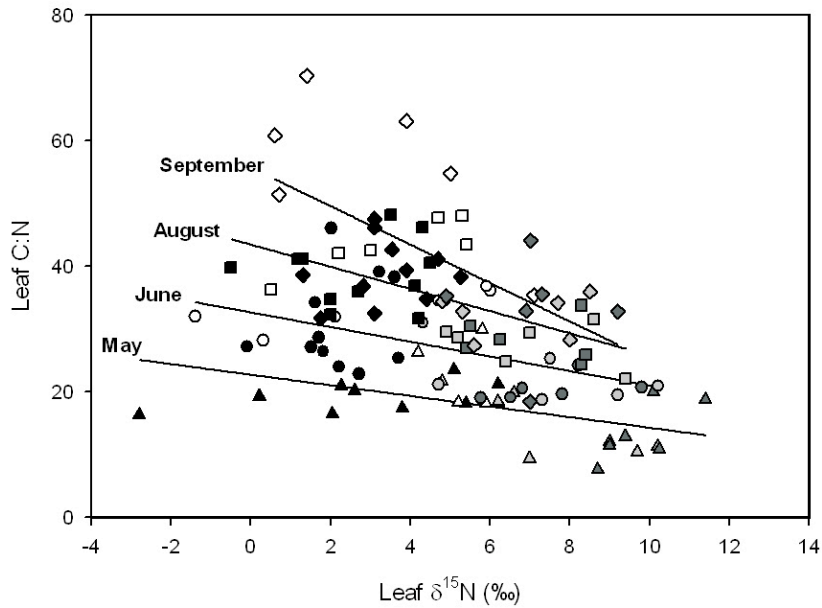


Figure 9 - Leaf C:N versus leaf nitrogen isotope ratio ($\delta^{15}\text{N}$) for dominant glycophytic shrub (*Ericameria nauseosa* – white symbols), halophytic grass (*Distichlis spicata* – black symbols) and halophytic shrub (*Atriplex torreyi* (light gray symbols), and *Sarcobatus vermiculatus* (dark gray symbols) species in all sites in 2006 (May (triangles), $r^2 = 0.18$, $p < 0.05$; June (circles), $r^2 = 0.24$, $p < 0.01$; August (squares), $r^2 = 0.30$, $p < 0.01$; September (diamonds), $r^2 = 0.31$, $p < 0.01$). Regression lines are shown for each month. The slopes for May and June are significantly different than for September ($p < 0.01$, $p < 0.05$, respectively).

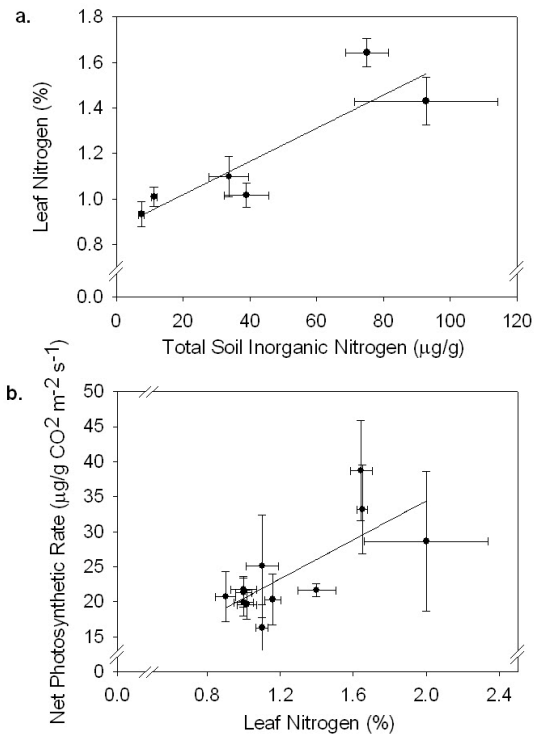


Figure 10 - a) Percent leaf nitrogen versus total soil inorganic nitrogen for *D. spicata* in 2006 ($R^2=0.71$, $p<0.05$). b) Leaf level photosynthesis versus percent leaf nitrogen for the grass species *Distichlis spicata* in both 2005 and 2006 ($R^2=0.50$, $p<0.01$). Error bars show the standard error (n varies from 3-5 replicates).

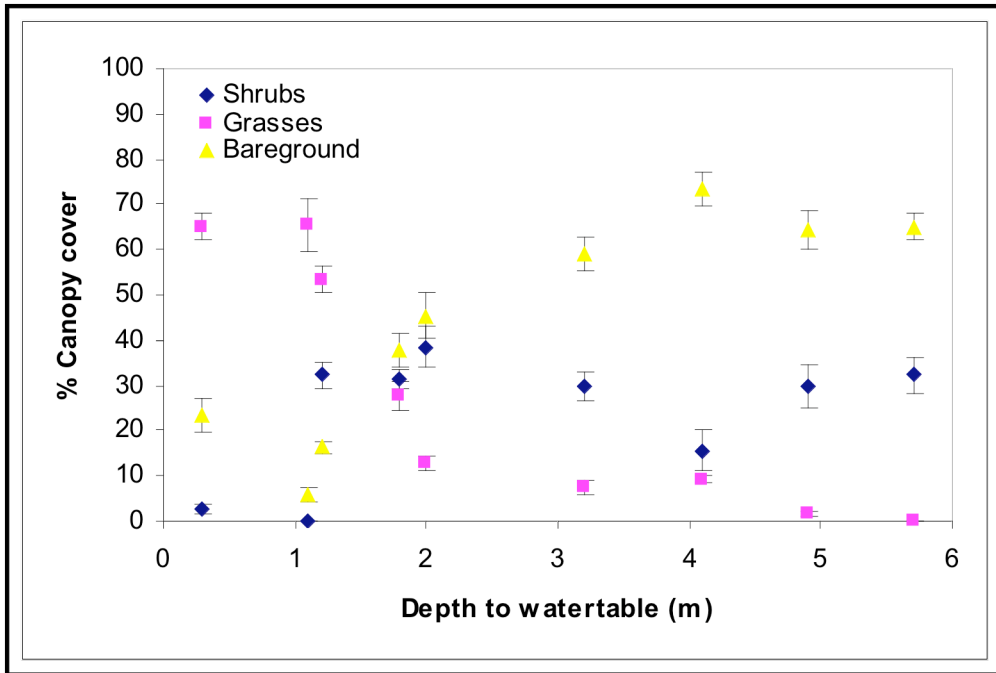


Figure 11 – Percent cover by shrubs, grasses, and bareground at seven sites spanning a gradient in depth to watertable.

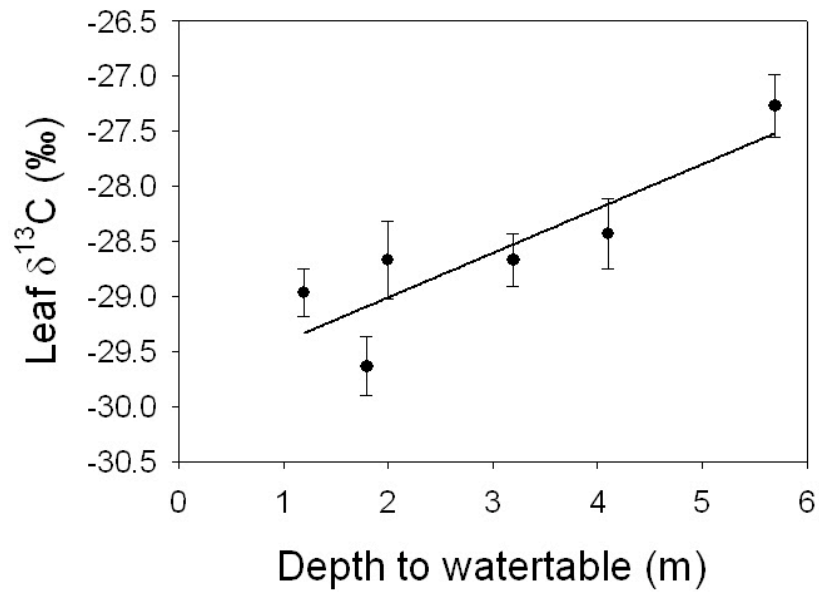


Figure 12 – Leaf carbon isotope ratio ($\delta^{13}\text{C}$), a measure of plant water stress, in the shrub species *Ericameria nauseosa* across a depth to watertable gradient.

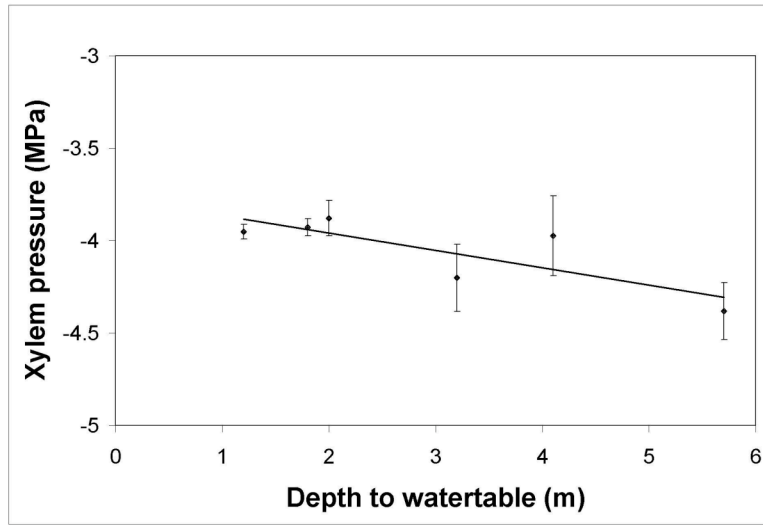


Figure 13 – The xylem pressure at a 50% loss of conductivity in the shrub species *Ericameria nauseosa* across a depth to watertable gradient.

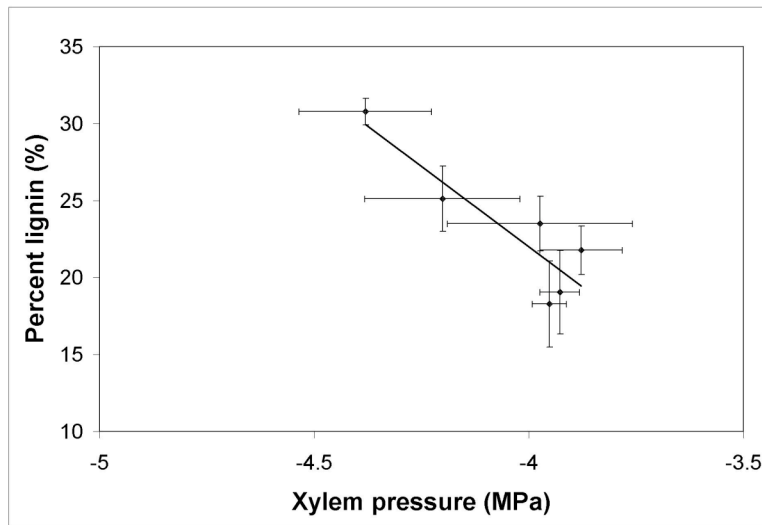


Figure 14 - Stem percent lignin vs. leaf carbon isotope ratio ($\delta^{13}\text{C}$) in *Ericameria nauseosa* ($R^2 = 0.79$, $p < 0.05$) across a depth to watertable gradient.

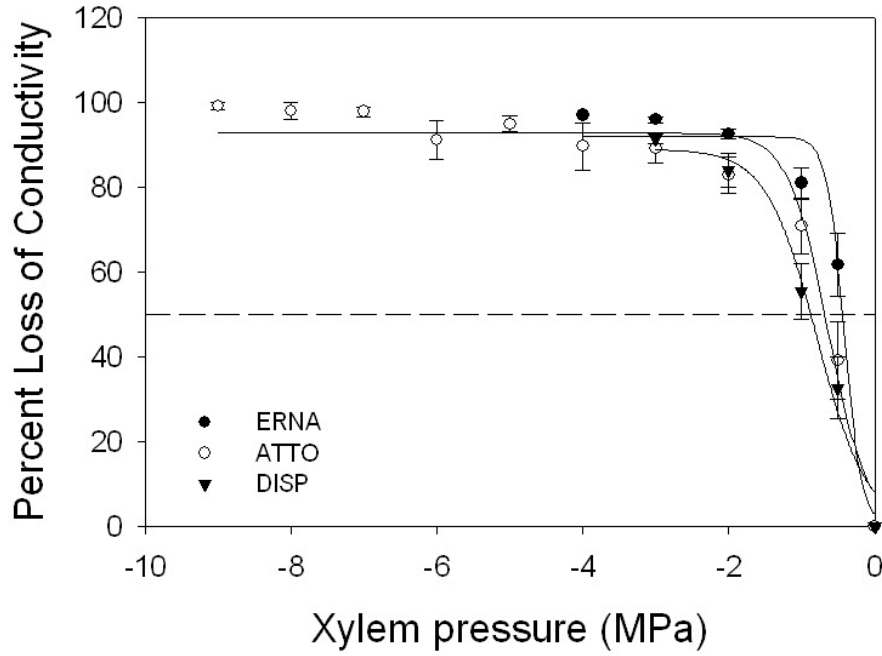


Figure 15 - Root vulnerability to cavitation for shrubs – *Ericameria nauseosa* (ERNA) and *Atriplex torreyi* (ATTO) – and grasses *Distichlis spicata* (DISP). The dotted line represents 50% loss of conductivity. The grass species DISP is more resistant to cavitation than the phreatophytic shrub species ERNA ($p < 0.05$).

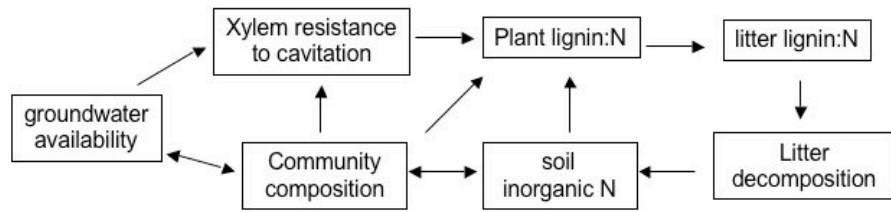


Figure 16 – Conceptual model of the linkages between groundwater availability, plant responses to water stress, plant chemical composition, and ecosystem nutrient availability.