

Report as of FY2006 for 2006CA170B: "Plant water use in Owens Valley, California:"

Publications

Project 2006CA170B has resulted in no reported publications as of FY2006.

Report Follows

**Plant water use in Owens Valley, California:
Understanding the influence of climate and depth to groundwater**

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Project Summary

Desert phreatophytic communities are increasingly experiencing hydrologic change due to redistribution of water resources. Water exports have been occurring in Owens Valley, California for almost a century, leading to questions about possible interactions between groundwater availability and community composition in phreatophytic ecosystems. While many studies of vegetation change in Owens Valley have focused on depth to groundwater as the primary factor influencing competitive interactions among grasses and shrubs, nutrient relations likely play an additional, important role in mediating changes in plant cover and composition. We evaluated differences in access to groundwater in grass and shrub species in Owens Valley via measurements of the isotopic composition of root, stem, soil, and groundwater. We also measured leaf nitrogen (N) and soil inorganic N availability in order to determine if differential access to water sources was associated with distinct patterns of N relations in grasses versus shrubs. Finally, we assessed the relative importance of water vs. nutrient relations in influencing plant transpiration and photosynthesis. We found that grasses accessed isotopically enriched water sources in the shallow surface soil in the late season while shrubs utilized groundwater throughout the growing season. Soil inorganic N concentrations declined from June to September at both grassland and shrubland study sites, likely due to gaseous loss of N from ammonia volatilization, nitrification, and denitrification. Correspondingly, leaf nitrogen declined throughout the season in both grass and shrub species at all sites. Grasses showed a large seasonal decline in transpiration; however, this pattern was more closely related to seasonal declines in leaf N than to plant water sources. These results suggest that seasonal N limitations are an important and somewhat overlooked control on temporal patterns of transpiration in the central Owens Valley, and that interactions between N availability, groundwater depth, and plant water relations are important governing features of plant community composition in shallow groundwater plant communities.

Problem and Research Objectives

Owens Valley, California is a closed hydrologic basin at the base of the Sierra Nevada Mountains. In 1913, the Los Angeles Department of Water and Power (LADWP) began diverting water from this semi-arid basin, which supports vegetation from both the Great Basin and the Mojave Deserts. Despite several decades of water management and monitoring in the valley, the current and potential impacts of water redistribution on local vegetation and ecosystem processes remain highly uncertain, in part due to a limited understanding of the interactions between vegetation dynamics and hydrology.

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; Stromberg 1993b; Stromberg 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 than in riparian ecosystems. 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.

Previous studies have attempted to quantify linkages between hydrologic change and shifts in the proportion of grass and shrub cover in Owens Valley. Groeneveld and Or (1994) attributed changes in the proportion of grasses and shrubs at an “ecotone” site to variations in groundwater depth, although local managers have suggested that land management played a more important role in community composition at this site than originally assumed. Elmore et al. (2006; 2003) attributed declines in herbaceous plant cover detected with remote sensing to lowered water tables caused both by groundwater pumping and drought. Several studies have suggested the importance of rainfall as a driver of plant productivity in the region, despite abundant groundwater resources that often are within reach of plant rooting zones. Sorensen et al. (1991) experimentally drew down the water table at four sites supporting a mixture of grasses and shrubs. Pumping did not achieve the planned drawdown goals, but leaf area index declined during the experiment relative to the pre-pumping year irrespective of the proximity to the pumping wells (Sorensen et al. 1991). Leaf area index also declined throughout the valley, at least in part due to above-average precipitation in the pre-pumping year followed by below-average precipitation (Sorensen et al. 1991). Over the study period, leaf area indices were impacted by variation in precipitation and not just the degree of water table decline (Groeneveld et al. 1994; Sorensen et al. 1991). Similar results were seen by Naumburg *et al.* (2005), who found that the two major grass species in the valley (*Distichlis spicata* and *Sporobolus airoides*) responded with declining aboveground biomass to a low rainfall year despite constant water tables. This was true even for locations where water tables were well within the rooting zone, indicating the importance of rainfall for plant productivity in these facultatively phreatophytic communities.

The strong correlation between productivity and precipitation in the valley, even at sites with shallow groundwater and unlimited water availability, highlights the potential importance of nutrient limitation and availability in this region. Mean annual precipitation at the valley floor is only 150 mm yr⁻¹, and rainfall occurs primarily in the

winter such that soil moisture becomes increasingly limited at shallow depths during the growing season (Steinwand et al. 2006). This likely inhibits decomposition and N mineralization at the end of the summer. While many studies of vegetation change in Owens Valley have focused on depth to groundwater as the primary factor influencing competitive interactions among grasses and shrubs, the responsiveness of these ecosystems to precipitation suggests that nutrient relations may also play an important role in mediating changes in plant cover and composition.

In this study, we evaluated species differences in plant water and nitrogen sources to explore potential drivers of the success of grass and shrub functional types within the central Owens Valley. Specifically, we posed the questions:

- ***How does groundwater withdrawal by vegetation vary with depth to the water table (DTW) for different species and plant functional groups in Owens Valley?*** There remains a paucity of data on plant rooting depths and distributions, particularly in semi-arid communities. Therefore, it is difficult to ascertain *a priori* the maximum DTW at which various species no longer have access to the saturated zone. This information is critical in order to quantify the temporal and spatial pattern of transpiration, as well as the sensitivity of the ecohydrologic system to change. The natural abundance of stable isotopes of water in ecosystems with seasonally varying water sources has been shown to be a useful tracer of shallow vs. groundwater or deep soil water uptake (Dawson and Ehleringer 1991; Ehleringer and Dawson 1992; Ehleringer et al. 1991). We hypothesized that if grasses are generally more shallowly rooted than shrubs, the isotopic composition of water in grass stems/rhizomes would be isotopically enriched relative to stem water of deeply rooted shrubs due to uptake of enriched water in the surface soil. To test this hypothesis, we measured the isotopic composition of plant stem water, soil water, and groundwater. We also collected other measurements of water stress such as predawn water potential.
- ***Are differences in water sources between grasses and shrubs coupled with differences in N relations?*** Because varying root distributions may lead to species differences in N availability and uptake, grasses may also take up N at a shallower depth than shrubs. This may result in isotopic enrichment of N in grasses, as shallow soil N is often isotopically enriched due to gaseous losses of N in the surface soil of semi-arid ecosystems (Amundson et al. 2003; Högberg 1997; van Groenigen and van Kessel 2002). By evaluating possible linkages between water and N relations, we hoped to elucidate the extent to which water and N sources may govern vegetation community composition in the region. To address this question, we sampled a variety of species and locations in the valley for the total leaf C:N ratio, the isotopic composition of leaf N, and the abundance of plant available nitrate and ammonium in the soil.
- ***How do spatial and temporal variations in access to water and nutrients affect plant gas exchange and transpiration?*** If plants have a continuous supply of groundwater, higher rates of transpiration are expected than if roots can only

access unsaturated soil with a limited water supply. In addition, N availability is a major constraint on photosynthesis and subsequently leaf transpiration that has seldom been measured in the central Owens Valley. Studies on the shores of Owens and Mono Lakes at the southern and northern borders of the valley have shown co-limitation of water and nutrients in playa plant communities (Donovan and Richards 2000; Drenovsky and Richards 2003; Drenovsky and Richards 2004; Drenovsky and Richards 2005; James and Richards 2005; James and Richards 2006; James et al. 2005). We evaluated the controls on leaf gas exchange at our study sites near Bishop to determine the relative importance of water and nutrient availability in influencing photosynthesis and transpiration in grass vs. shrub species.

Methodology

Owens Valley lies in the rainshadow of the Sierra Nevada and receives approximately 150 mm precipitation per year, of which ~75% falls from Nov-Mar. Precipitation increases with proximity to the Sierra Nevada. Depth to groundwater (DTW) ranges from the ground surface to well below maximal plant rooting depths of ~6 m (Groeneveld 1990). The majority of groundwater recharge comes from Sierra Nevada precipitation that infiltrates in the upper reaches of alluvial fans and through tributary stream channels (Hollett et al. 1989). Vegetation in the valley varies depending on groundwater depth and salinity, and has been classified into four major groups: 1. alkaline meadow on saline sites with 0-1.5 m DTW, 2. alkaline scrub on saline sites with 1-3 m DTW, 3. dryland alkaline scrub on saline sites with deeper groundwater, and 4. dryland scrub on coarse soils of low salinity and deep water tables (Griepentrog and Groeneveld 1981). Dominant species in the valley are the shrub species *Artemisia tridentata*, *Sarcobatus vermiculatus*, *Ericameria nauseosa*, and *Atriplex* spp., and the grass species *Distichlis spicata*, *Leymus triticoides*, and *Sporobolus airoides*.

Study sites – In 2005 we selected three sites which varied in the proportion of grass vs. shrub cover for intensive plant and soil sampling. These sites consisted of: 1) an alkaline meadow near Chalk Bluffs north of the town of Bishop (“grassland” site); 2) an intermediate, mixed grass-shrub community near the Owens River south of Bishop (“intermediate” site); and 3) a shrub dominated site with very sparse grass cover (“shrubland” site). The grassland 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. In 2006, we measured leaf gas exchange, predawn leaf water potential, and the isotopic composition of stem and soil water during 3-4 sampling periods from May to September. We also collected leaf material for analysis of chemical and isotopic composition, as well as soil samples for analysis of inorganic N availability. A detailed description of each measurement is given below.

Stable isotope measurements – Sampled leaves 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). All isotope measurements were conducted at the University of California, Irvine IRMS facility. Nitrogen isotopes were referenced to atmospheric N_2 and oxygen isotopes were referenced to Vienna Standard Mean Ocean Water (V-SMOW).

Leaf-level gas exchange and water potential – Photosynthesis, transpiration and stomatal conductance were measured at the three sites at midday in June and August of 2005 and June, July, and August of 2006 with a LI6400 leaf gas exchange system (Licor, Lincoln, NE). Three replicate individuals of *Distichlis spicata*, *Ericameria nauseosa*, and *Atriplex torreyi* were measured at saturating light ($1500 \mu\text{mol m}^{-2}\text{s}^{-1}$) and ambient temperature and relative humidity. Measured shoots were harvested after each sampling period to correct each gas exchange estimate for true shoot leaf area. Predawn and midday water potential were measured during the same periods with a Scholander-type pressure chamber (PWSC 3000, Soil Moisture Equipment Corp, Goleta, CA). Three to five individual shoots of *Distichlis spicata*, *Ericameria nauseosa*, *Atriplex torreyi*, and *Sarcobatus vermiculatus* were measured at each site during each sampling period.

Soil assays – Twelve soil samples were collected at each site from 0-10 cm depth in June and September of 2006. At the two shrub sites, sampling was stratified to collect three replicates under each of three shrub species as well as in intershrub (grass-dominated) spaces. Samples were transported at 4°C to the University of Kansas, where they were extracted in 2M KCl. Soil extracts were analyzed colorimetrically for NH_4^+ and NO_3^- on a Lachat autoanalyzer.

Principle findings and significance

Repeated sampling of stem water isotopes during the summer showed that there was temporal variability in water sources in *Distichlis*, but not in the shrub species, which remained isotopically depleted throughout the season (Figure 1). In May and August, *Distichlis* appeared to be transpiring isotopically enriched local precipitation in the shallow surface soil rather than groundwater (Figure 1). In contrast, the shrubs appeared to be accessing groundwater at both shrub sites and all time periods. Soil water profiles for the two shrub sites in June showed the typical evaporative enrichment in the surface

soil, where the isotopic composition of water was as enriched as -3 ‰ (Figure 2). In contrast, estimates of the isotopic composition of local groundwater as measured in tap water samples were approximately -17 ‰. At the grassland and intermediate sites, which were characterized by a very fine textured soil, soil water isotopes became indistinguishable from groundwater at about 50 - 60 cm depth (Figure 2). At the shrubland site, the isotopic composition of soil water approached groundwater at about 150 cm (Figure 2). Soils at this site are much sandier and therefore less likely to be influenced by capillary action from the saturated zone.

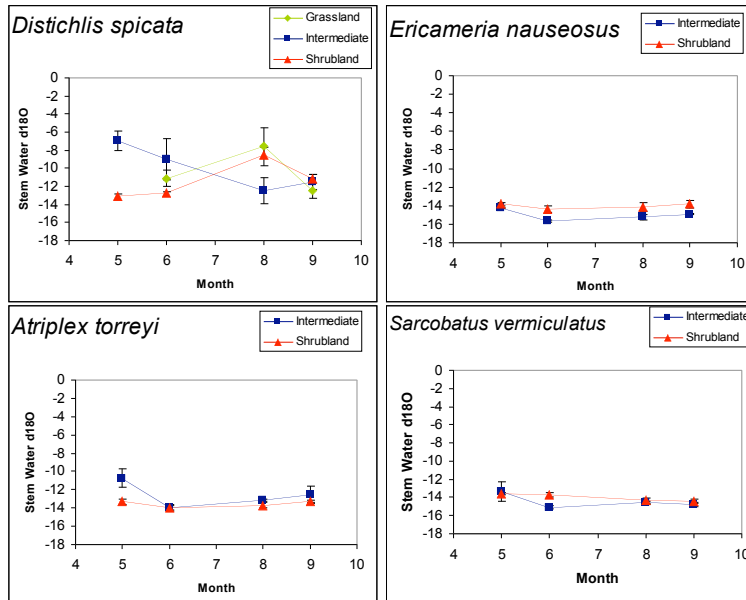


Figure 1 - The oxygen isotope composition of plant stem water at each site.

The water potential of plants measured before dawn (ψ_{PD}) provides an estimate of the average soil water potential in the rooting zone, assuming that there is negligible transpiration at night such that plants and soils are in equilibrium. ψ_{PD} remained relatively constant throughout the growing season for all species except *Sarcobatus vermiculatus* (Figure 3). Hence, there was little evidence of progressive seasonal water stress in most species. Even in *Sarcobatus*, it is unlikely that declining seasonal water potentials reflected increasing water stress during the growing season. Donovan et al. (1996) suggested ψ_{PD} may not accurately reflect xylem water potential in halophytic *Sarcobatus* due to high solute concentrations and the subsequent effect on osmotic potentials. In addition, *Sarcobatus* has been found to have relatively high rates of nighttime transpiration, resulting in disequilibrium between plants and soils predawn (Donovan et al. 2001).

Leaf C:N ratio increased throughout the growing season at all species and sites, indicative of a decline in total leaf N content (Figure 4). This corresponded to a decline in inorganic N availability at all three sites from June to September, although the total amount of soil inorganic N varied among sites (Figure 5). Total inorganic N was lowest at the shrubland

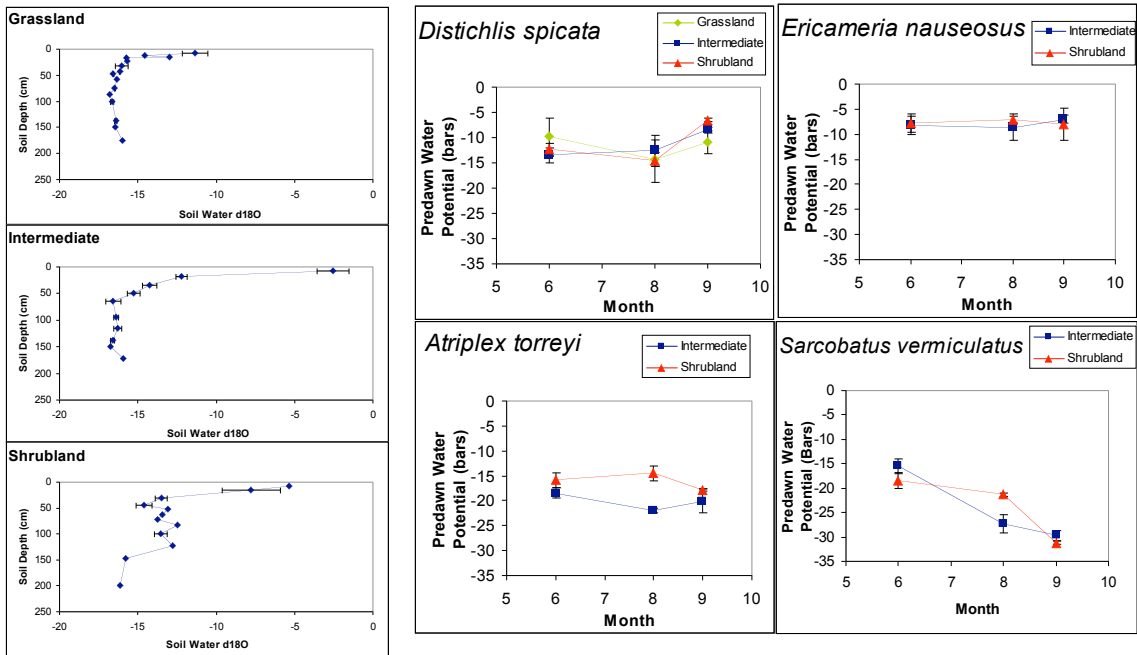


Figure 2 - The isotopic composition of soil water with depth at each site.

Figure 3 - Predawn shoot water potential at each site.

site and similar at the two high grass cover sites. Ammonium dominated inorganic N availability at the grassland site, while nitrate dominated inorganic N under shrubs (Figure 5). Despite differences in N availability among sites and microsites, the nitrogen isotope ratio ($\delta^{15}N$) of leaves was not correlated with site fertility, soil organic matter, or soil isotopic composition, but instead was most strongly correlated with leaf C:N (Figure 6). This likely indicates that species with greater leaf N concentrations accessed

isotopically enriched soil N pools.

Enriched N pools may be in the surface soils, which are isotopically enriched due to gaseous loss, and/or associated with mycorrhizal uptake or varying N sources, such as preferences for nitrate vs. ammonium uptake. In the 2004 and 2005 growing seasons, we found that the halophytic (salt-adapted) shrubs, particularly *Atriplex torreyi*, contained the most isotopically enriched leaf N across all sites (Pataki et al. 2007), which was confirmed by the 2006 data. These species are well adapted to nutrient uptake in the saline surface soil, where N is most available but

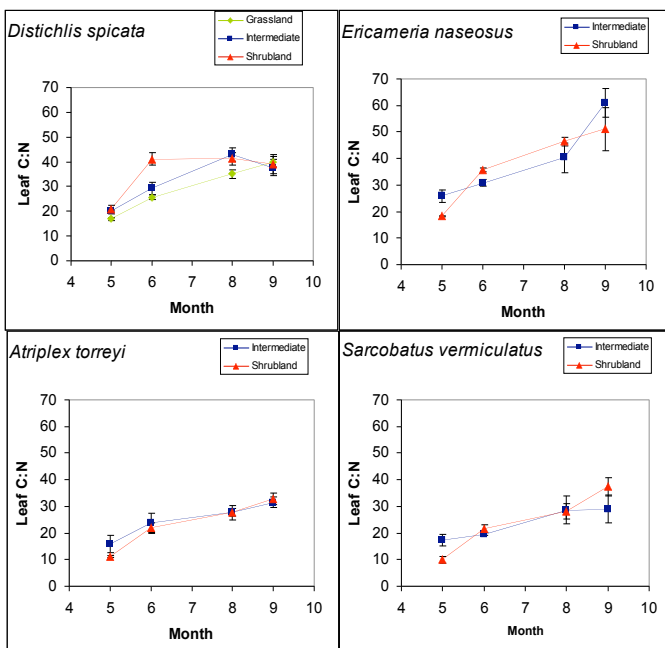


Figure 4 - The C:N ratio of live leaves.

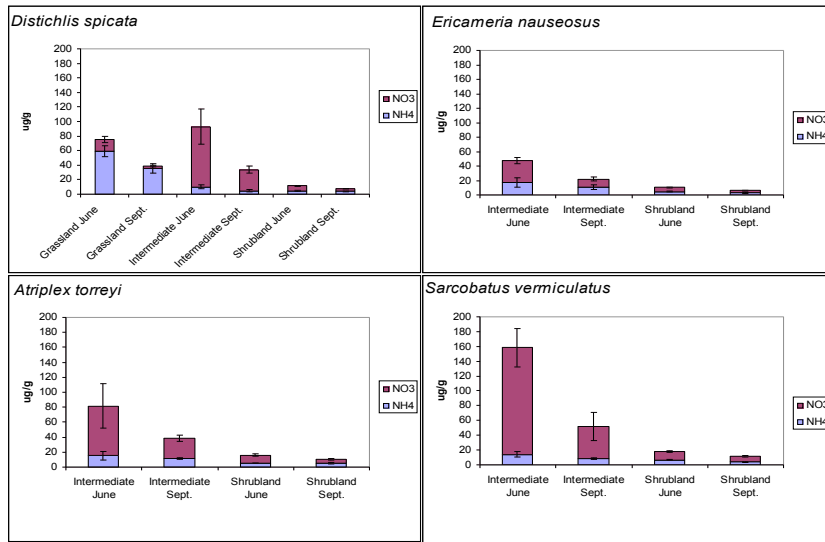


Figure 5 - Soil inorganic nitrate (NO₃) and ammonium (NH₄) concentrations from 0-10cm.

also highly isotopically enriched. Notably, the relationship between leaf $\delta^{15}\text{N}$ and C:N showed a seasonal trend (Figure 6) that reflected the decline in soil inorganic N pools (Figure 5) and subsequently leaf C:N (Figure 4) from May to September.

Our measurements of leaf-level gas exchange showed a large reduction in transpiration of grasses at the grassland site from June to September (Figure 7). While stem water isotopes indicated that grasses were more shallowly rooted than shrubs (Figure 1), our measurements of predawn leaf water potential did not reveal significant seasonal water stress of grasses at any site (Figure 3). Instead, leaf level gas exchange of the grass species *Distichlis* was correlated with leaf N content (Figure 8). Our results suggest that the seasonal pattern of transpiration at the grassland shown in Figure 7 is largely a consequence of N limitations to photosynthesis caused by progressive gaseous N losses and declining inorganic N availability throughout the season (Figure 5). In particular, losses of nitrate appear to be high at the grassland site, possibly due to high rates of denitrification associated with high soil moisture and high soil organic matter. Our 2005 measurements showed that soils at the grassland site contained 14 % carbon vs. 1.3 % at the intermediate site and 0.4 % at the shrubland site (Pataki et al. 2007). In addition, N₂O fluxes at the grassland site were three times higher than the two shrubland sites in 2005 (Pataki et al. 2007), also indicative of large losses of N from denitrification.

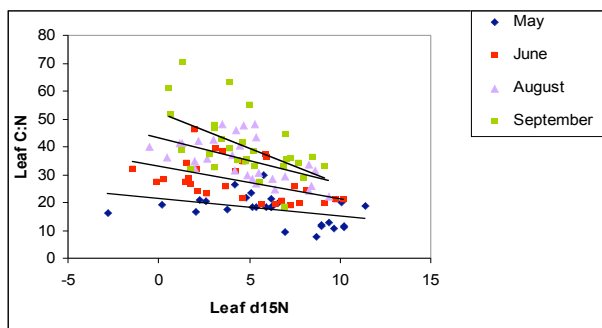


Figure 6 – Live leaf C:N ratio versus nitrogen isotope ratio ($\delta^{15}\text{N}$) from May to September in all species and sites combined.

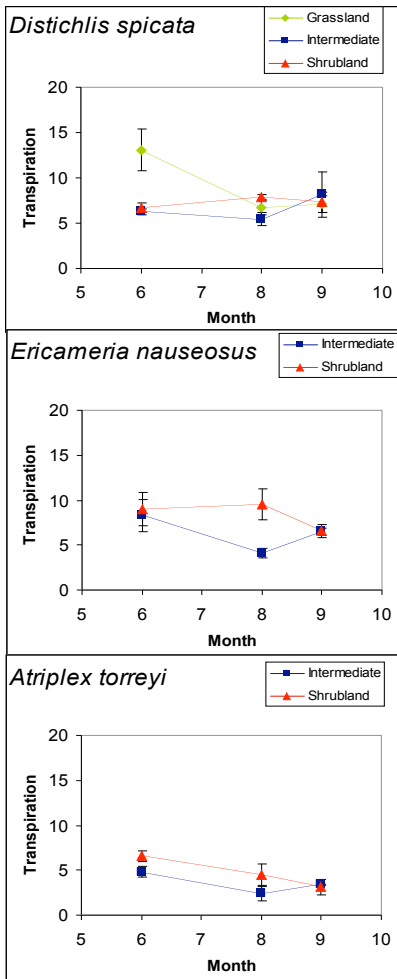


Figure 7 - Leaf level transpiration at each site.

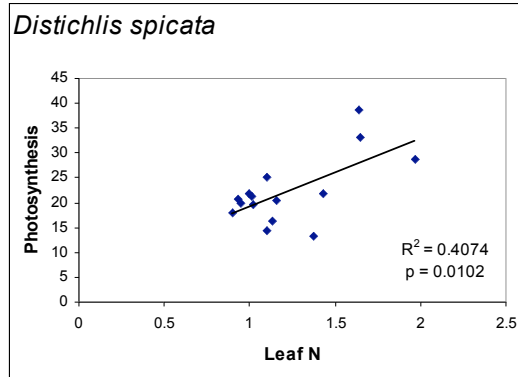


Figure 8 – Leaf level photosynthesis vs. leaf % N.

These results are highly significant given that previous studies have focused almost exclusively on depth to groundwater as the primary factor that influences plant cover, physiology, and composition at phreatophytic sites in the central Owens Valley (Elmore et al. 2006; Elmore et al. 2003; Groeneveld 1990; Groeneveld and Or 1994; Groeneveld et al. 1994; Sorenson et al. 1991). Additionally we have shown that large seasonal N limitations strongly influence temporal patterns of photosynthesis and transpiration, particularly at the grassland site. Hence, previous observations of increases in leaf area and productivity in high rainfall years, even at sites with shallow water tables, are likely due to increased N availability associated with higher rates of N mineralization in water limited surface soils. More significantly, our results point to ecosystem N

cycling as an important mechanism mediating the balance between grasses and shrubs in these ecosystems. Halophytic shrubs appear to be particularly well adapted to accessing limited N pools in these saline soils, while grasses appear to be particularly sensitive to seasonal cycles of nitrate availability and its effect of leaf gas exchange. This study strongly suggests that N cycling must be incorporated into conceptual and quantitative models of woody encroachment following hydrological change. Studies that examine groundwater depth, plant water sources, and water relations without consideration of interactions with nutrient availability will be unlikely to provide a predictive capacity for determining the response of local communities to future hydrologic change.

Student Support

	Total Project Funding		Supplemental Awards	Total
	Federal Funding	State Funding		
Undergrad.	3			
Masters				
PhD.	1			
Post-Doc.				
Total	4			

This project provided a summer stipend, travel expenses, and supplies for Ph.D. student Christine Goedhart from May to Sept. 2006. The project also provided funds for three undergraduate students to travel to our field sites in Bishop, CA to collect data during the 2006 growing season.

Publication citations associated with the project

Peer-reviewed manuscripts

Pataki DE, Billings SA, Naumburg E, Goedhart CM. 2007. Water sources and nitrogen relations of grasses and shrubs in phreatophytic communities of the Great Basin Desert. In review.

Goedhart CM, Pataki DE, Billings SA. In preparation. Controls on plant gas exchange across a grassland to shrubland gradient in Owens Valley, California.

Conference presentations

Goedhart CM, Pataki DE, Billings SA. Controls on plant gas exchange across a grassland to shrubland gradient in Owens Valley, California. Ecological Society of America meeting, San Jose, CA, August 2007.

Pataki DE, Billings SA, Naumburg E, Goedhart CM. Water sources and nitrogen relations of grasses and shrubs in phreatophytic communities of the Great Basin Desert. Ecological Society of America meeting, San Jose, CA, August 2007.

Goedhart CM, Pataki DE, Billings SA. 2007. Controls on plant gas exchange across a grassland to shrubland gradient in Owens Valley, California. Annual Meeting of the Southern California Academy of Sciences, Fullerton, California.

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