

PLANT RESPONSES TO AN EDAPHIC GRADIENT ACROSS AN ACTIVE SAND DUNE/DESERT BOUNDARY IN THE GREAT BASIN DESERT

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In arid ecosystems, variation in precipitation causes broad-scale spatial heterogeneity in soil moisture, but differences in soil texture, development, and plant cover can also create substantial local soil moisture heterogeneity. The boundary between inland desert sand dunes and adjacent desert habitats exhibits abrupt changes in soil and vegetation characteristics that may be associated with differences in plant-available water and nutrients. We hypothesized that differences in plant water status between habitats would mirror changes in soil texture and vegetation cover. Because the dunes have higher water availability, we predicted that plants on dunes would have higher plant water potential (Ψ) and be less water use efficient than plants off dunes. We tested these predictions for three species—*Psoralidium lanceolatum* (a C₃ perennial N-fixing subshrub), *Stipa hymenoides* (a C₃ perennial bunchgrass), and *Salsola iberica* (a C₄ annual)—on actively moving desert dunes and adjacent stabilized dunes at Little Sahara Dunes, Utah. Plants on the dunes maintained higher predawn (Ψ_{pd}) water potentials (>-1.5 MPa) throughout the summer season, whereas off-dune plants were water stressed from July on ($\Psi_{pd} < -1.5$ MPa). Midday water potential (Ψ_{md}) generally mirrored Ψ_{pd} . As predicted, off-dune plants were more water use efficient, on the basis of leaf carbon isotope ratios ($\delta^{13}C$) for the C₃ species. The observed differences in soil particle size, soil water content, and the concomitant effect on soil Ψ likely explain the observed differences in Ψ_{pd} . Soil N was significantly lower on dunes, while soil P was similar across habitats. In contrast, leaf N was similar across habitats, but leaf P was significantly higher on dunes, possibly because of species-specific differences in nutrient relations or differences in habitat nutrient availability. Abrupt changes in water and nutrient availability associated with soil texture are likely to be important selective forces shaping plants' strategies in this and other desert boundary communities.

Keywords: soil texture, water relations, sand dune, desert, nitrogen, phosphorus, carbon isotope.

Introduction

Spatially heterogeneous resources affect numerous plant ecological processes, including the distribution of plant communities, the structuring of plant populations, and the establishment and recruitment of individuals (Harper 1977; Polis 1991; Kadmon 1993; Smith et al. 1997). Differences in natural selection resulting from spatially heterogeneous resources can lead to phenotypic divergence between populations (Hedrick 1986; Dudley 1996; Nagy 1997). Such population differentiation has been associated with changes in water and inorganic nutrient availability, even over very small spatial scales (Snaydon and Davies 1972; Stewart and Schoen 1987; Lechowicz and Blais 1988). Although researchers can measure environmental changes, it is often difficult to determine which aspects of the natural environment are most critical in determining the distribution of a given plant population. The

abrupt transition between actively moving desert sand dunes and adjacent stabilized dunes (hereafter referred to as “on-dune” and “off-dune” habitats, respectively) provides a natural laboratory to study the effects of resource heterogeneity on desert plants (Chadwick and Dalke 1965; Hennessy et al. 1985; Lei 1998). However, the extent to which plant water status, nutrient status, and water use efficiency change in response to resource differences in this habitat boundary is poorly understood. Here we test the hypothesis that desert sand dune habitats are mesic islands in an otherwise arid ocean.

In desert ecosystems, small-scale variation in vegetation, soil surface cover, and soil texture can change the amount of water and nutrients available to plants (Whitford 2002). Soil texture is particularly important to plant and soil water relations in arid systems (Alizai and Hulbert 1970; Noy-Meir 1973), because there should be more plant-available water in sandy soils than in finer-textured clay soils (McAuliffe 1994; Hamerlynck et al. 2000, 2002). Sandy soils allow precipitation to infiltrate more quickly, leaving less capillary water in the topsoil, compared with clay soils. Although clay soils hold more water than sandy soils, water is more tightly bound to the fine clay particles than to the larger sand particles. This causes a sandy soil to have a greater water potential (Ψ) than a clay soil at a somewhat low relative water content (Nilsen and Orcutt 1996). At greater soil Ψ , plants can extract more soil water, leading to better plant water

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status. Thus, the generally lower clay content and coarser texture of sand dune soils, coupled with relatively low soil moisture content in deserts, indicate that plant Ψ should be greater on dunes than off. We therefore expect dune plants to use water less conservatively than similar plants off dunes (Ehleringer and Cooper 1988; Donovan and Ehleringer 1994; Sandquist and Ehleringer 2003).

Plant Ψ on desert sand dunes has been variously reported as higher than, similar to, or lower than that in adjacent off-dune habitats (Pavlik 1980; Forseth et al. 1984). Hennessy (1985) concluded that sand dune soils hold less plant-available water than adjacent interdune soils, although plant responses were not reported. An accurate comparison of plant responses to soil moisture heterogeneity in dune habitats requires simultaneous evaluation of soil and plant water status both on and off the dunes. These questions are particularly interesting in light of ongoing work assessing ecological and evolutionary divergence in two wild annual sunflower species, *Helianthus anomalous* and *Helianthus deserticola*, that are restricted to on- and off-dune habitat patches, respectively (Schwarzbach et al. 2001; Rosenthal et al. 2002; Rieseberg et al. 2003).

To assess the on- and off-dune habitats, we measured aspects of the physical environment, including soil water content and soil Ψ . However, we also used extant individuals of three species that occur both on and off dunes as “phytometers” (Clements and Goldsmith 1924). Although past phytometer studies (Antonovics et al. 1987; Miller et al. 1995) have planted common genotypes into different environments and measured only performance, here we measured traits associated with plant water relations and nutrient status *in situ* on naturally occurring plants. Simply measuring performance is not an adequate method to assess habitat water availability, because on- and off-dune habitats also differ in soil texture and stability, vegetation cover, and nutrient availability. Using *in situ* individuals does not control for potential effects of age, habitat choice, or genetics on phenotypic differentiation. However, by using three species with different life histories and independent environmental responses, we obtained a more generalizable measure. We could then ask how the plant responses differed between habitats and whether these differences reflected soil water availability and nutrient status.

In this study, we measured soil and plant Ψ and soil and plant nutrient concentrations for five pairs of on-dune and off-dune sites. We predicted that plant water status would be higher on the active dunes than off and that plant Ψ could be explained in terms of habitat soil characteristics. We predicted that on-dune plants would use water less efficiently because higher seasonal plant water availability should be associated with lower water use efficiency (Ehleringer and Cooper 1988). Finally, we predicted that plant nutrient content would reflect differences in soil nutrient levels, with less nutrients available on dune than off dune.

Material and Methods

Study Site

The study was conducted in Little Sahara Recreation Area, Juab County, Utah (lat. 39°44'N, long. 112°18'W). The cli-

mate is typical of the Great Basin Desert, with the majority of precipitation occurring as snow or rain during the cold winter and cool spring months (Smith et al. 1997). The summers are characterized by a significant drought, usually beginning in June and lasting until August. Mean annual precipitation is 312 mm, making this an arid zone according to the UNESCO (1977) classification. Annual precipitation was well below average the year of the study (2002; 110 mm) and the preceding year (2001; 191 mm). Given that only four small rain events (each <6.0 mm) occurred from June to August 2002, it is likely that the study plants relied predominantly on soil moisture derived from winter and early spring rather than from summer precipitation (Ehleringer et al. 1991).

We chose the three focal species because they occurred on actively moving dunes as well as off the dunes in stabilized sand substrates. *Psoraleidum lanceolatum* var. *stenostachys* (Pursh.) Rydb. (Fabaceae), the dune scurfpea, is an endemic N-fixing perennial rhizomatous herb. *Salsola iberica* Sennen & Pau, Russian thistle, is a widespread weedy annual herb. *Stipa hymenoides* R. & S., Indian ricegrass, is a widespread dune-colonizing perennial bunchgrass. Scientific names and nomenclature follow Welsh et al. (1987).

In order to encompass the environmental heterogeneity of active sand dunes and the adjacent off-dune habitat, we established a pair of on- and off-dune experimental plots at each of five replicate sites (blocks), for a total of 10 plots. For each on- and off-dune pair, plots were 50–75 m apart, and the five sites ranged from 1 to 7 km apart. Plant cover was estimated around each plot on June 24–28, 2002, using line transects and a modified step-point method appropriate for relatively uniform communities of low-stature vegetation (Barbour et al. 1987). Briefly, we established a 30-m baseline transect along a north-south or an east-west axis by coin toss. At each garden, two 50-m transects were set up perpendicular to the baseline at two randomly selected points along the 30-m baseline. We collected cover data by placing a 0.9-m steel pin perpendicular to the baseline and vertically lowering the pin until it intersected plants, bare ground, or litter. Pin hits were recorded every 20 cm on each 50-m transect. Percent cover is determined as the proportion of hits for a given species or cover category within the total number of pin hits. Although this method tends to underestimate taxa with low cover values (Barbour et al. 1987), it is well suited to quantify common taxa in these communities.

Soil Characterization and Analyses

We sampled soils at all 10 plots at depths of 0, 25, 50, 75, 100, 150, and 200 cm (June 6, July 1, July 30, August 30). We measured soil water content (SWC) gravimetrically (Rundel and Jarrell 1989). We then estimated soil Ψ from the relationship between the SWC and soil Ψ . These soil moisture release curves were generated in the lab for each depth/site combination (soil collected July 30) using a thermocouple psychrometer system (SC-10, Decagon Devices, Logan, UT) to measure soil Ψ . The curves were fitted using a three-parameter exponential model: soil $\Psi = y_0 + a(1 - b^{\text{SWC}})$. We determined soil texture (percent sand, percent silt, and percent clay) using the hydrometer method (Bouyoucos 1962). Presence of soil carbonates was confirmed by applying several drops of 10% hydrochloric acid to soil samples.

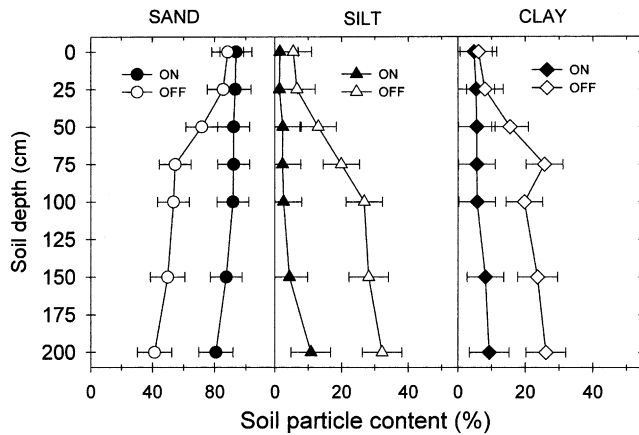


Fig. 1 Soil sand, silt, and clay fractions for on-dune (filled symbols) and off-dune (open symbols) habitats at 0-, 25-, 50-, 75-, 100-, 150-, and 200-cm depths. Symbols represent model-adjusted means \pm SE for five plots per habitat.

Plant Water Potential

We measured plant predawn (Ψ_{pd}) and midday (Ψ_{md}) water potentials with a pressure chamber (PMS Instruments, Corvallis, OR) on the same dates as the soil sampling. We sampled fully expanded, mature, nonsenescent leaves from two individuals of each species on each of the 10 plots (five on-dune and five off-dune). Although soil Ψ and plant Ψ_{pd} may not equilibrate for some plants, the magnitude of predawn soil-plant Ψ disequilibrium generally appears to be small for nonsaline herbaceous species similar to those in this study (Donovan et al. 2001, 2003). In addition, predawn disequilibrium due to nighttime transpiration is likely to be greater in less water-stressed plants, potentially minimizing habitat differences being investigated here. Thus, intraspecific differences in plant Ψ_{pd} are a conservative comparative estimate of habitat soil Ψ differences for this study.

Soil and Leaf Elemental Analyses

We collected mature leaves for each species (eight to 10 individuals per species bulked per plot) on June 13, dried them at 60°C, and ground them (SPEX 8000, SPEX CertiPrep, Metuchen, NJ). Double acid extracts of ashed leaf tissue (Allen 1989) were analyzed for total P on an inductively coupled plasma-atomic emission spectrophotometer (Jarrel-Ash 965 ICP-AES). Ground leaf and soil samples were analyzed for total N and C by Micro-Dumas combustion analysis on an elemental analyzer (Carlo Erba NA 1500, Milan, Italy). Soil P was estimated from acid persulfate extracts (Nelson 1987) using Alpkem continuous-flow colorimetry. The carbon isotopic composition ($\delta^{13}C$) of dried leaves was determined using continuous flow mass spectrometry (Stable Isotope/Soil Biology Laboratory, University of Georgia). Under similar atmospheric conditions, more negative leaf $\delta^{13}C$ are generally interpreted as lower integrated leaf-level water use efficiency for C_3 plants (Farquhar et al. 1989). *Salsola iberica* was not included in this analysis because variation in $\delta^{13}C$ does not estimate water use efficiency for C_4 species (Farquhar et al. 1989).

Statistical Analyses

The sampling design consisted of five sites, with one on-dune and one off-dune plot at each site. Site was treated as a random (block) effect and habitat and species as fixed effects for all analyses. Soil depth, soil water content, leaf Ψ , and nutrient status were dependent variables. The MIXED procedure (SAS Institute 2001) was used for all analyses. Seasonal plant Ψ and soil water content data were analyzed as repeated measures, and denominator degrees of freedom were calculated using a Satterthwaite approximation (SAS Institute 2001). Variables were transformed as needed to meet model assumptions. Simple effects tests (LSMEANS/Slice) were implemented to dissect significant two-way interactions (e.g., $A \times B$) (SAS Institute 2001). This procedure tests for the simple main effects of A for B , which are calculated by extracting the appropriate rows from the coefficient matrix for the $A \times B$ LSMEANS and using them to form an F -test. Means and standard errors presented in figures are model-adjusted means unless stated otherwise. Multiple and individual linear regressions (SAS Institute 2001) were used to estimate the significance of the relationship between $\delta^{13}C$ and Ψ_{pd} and tissue N.

Results

Habitat Measures

Vegetation cover was significantly lower on dunes (12.3%) than off dunes (67.8%, $F_{1,10} = 631.9$, $P < 0.0001$). The focal species, *Psoralidium lanceolatum*, *Salsola iberica*, and *Stipa hymenoides*, were the most common species on the dune (37.1%, 16.9%, and 14.6% cover, respectively) and occurred at lower frequencies off the dune (2.3%, 8.5%, and 3.5% cover, respectively). Other common taxa off the dunes were *Bromus tectorum*, *Artemisia tridentata* var. *tridentata*,

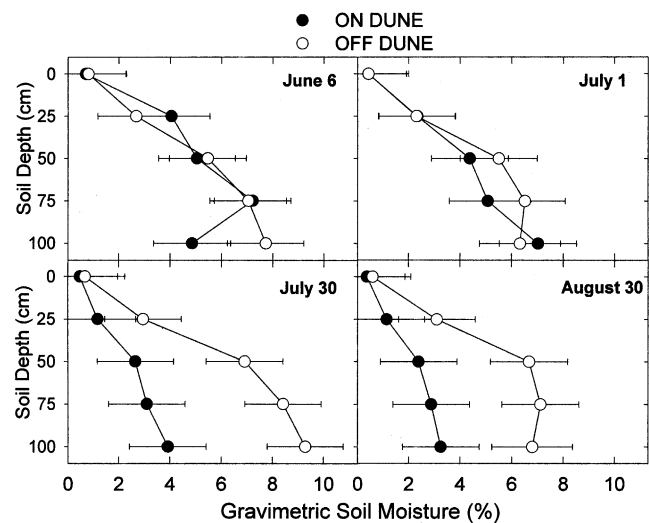


Fig. 2 Gravimetric soil moisture at 0-, 25-, 50-, and 100-cm depths on four sampling dates for on-dune (filled circles) and off-dune (open circles) habitats. Circles represent model-adjusted means \pm SE for five plots per habitat.

Table 1

Repeated-Measures Mixed Model for the Effects of Habitat (On-Dune vs. Off-Dune), Depth, and Day of Year (Date) on Gravimetric Soil Water Content

Effects	df	F	P
Habitat	1, 4.01	2.04	0.2259
Depth	4, 16.1	96.77	<0.0001
Habitat × depth	4, 15.2	0.24	0.9086
Date	3, 114	53.82	<0.0001
Date × habitat	3, 114	17.32	<0.0001
Date × depth	12, 114	10.38	<0.0001
Habitat × depth × date	12, 114	0.80	0.6523

Note. Five on-dune and five off-dune sites. See also figure 2. Site effects and all appropriate interactions were modeled as random effects. Significant effects are shown in boldface.

and *Agropyron* sp. (47.8%, 14.7%, and 14.4% cover, respectively). Litter was far less abundant on dunes than off dunes (6.4% ± 0.8% vs. 45.5% ± 1.7% cover, respectively). The vast majority of off-dune litter was identifiable as *B. tectorum*.

The on-dune habitat had a higher soil sand fraction but a lower clay fraction than the off-dune habitat (fig. 1). Changes in particle distribution by depth were habitat specific. On the dunes, only the silt fraction increased with depth ($F_{6,21} = 2.72$, $P < 0.05$). Off the dunes, the sand fraction decreased and the clay content increased as a function of depth ($F_{6,21} = 5.04$, $P < 0.005$ and $F_{6,21} = 2.75$, $P < 0.05$, respectively).

Overall, soil water content increased with depth and decreased over time. Differences between the habitats varied with sampling date (fig. 2; table 1). Soil water content was similar between habitats on June 6 and July 1 but significantly lower on dunes on July 30 and August 30 (simple effect test: $F_{1,114} = 8.28$, $P < 0.01$ and $F_{1,114} = 6.65$, $P < 0.05$, respectively). On July 30, soil Ψ was extremely low (<−10 MPa) at 0 and 25 cm depths both on and off dunes, but soil Ψ increased substantially below 25 cm and rose to ≥−1.5 MPa at 50 cm on dunes and at 75 cm off dunes (table 2).

Soil N was extremely low for both habitats. However, on-dune soil N was consistently low at all depths, while off-dune soil N decreased with depth (fig. 3; table 3). Soil P did not differ overall between habitats, although the depth profile did differ between habitats (fig. 3). On the dunes, soil P was lowest at the soil surface and highest at 75 cm. This trend was reversed off the dunes, where soil P was highest at the soil surface and decreased to its minimum at 75 cm. Soil total C : N ratio was significantly greater on dunes than off ($F_{1,4.02} = 20.84$, $P < 0.05$), with these differences being primarily driven by N rather than C. For example, at the soil surface the total C : N ratio was 201 ± 17 on dunes and 53 ± 17 off dunes (fig. 3). C : N ratios also decreased significantly with depth on dunes, but the trend was opposite off dunes (treatment × depth: $F_{6,43.8} = 12.57$, $P < 0.0001$). Soil carbonates (CaCO_3) were not detected in any of the on-dune soils. Off-dune soils had detectable amounts of carbonates at 75 cm and lower at all sites.

Plant Responses

Plant Ψ_{pd} and Ψ_{md} were significantly higher on the sand dunes than off the dunes for all species and sampling dates except for the first sampling date (June 6), when Ψ was similar for all sites (fig. 4; table 4). Plant Ψ_{pd} and Ψ_{md} decreased significantly with sampling date but at a slower rate on dune than off dune. Individually, species' Ψ_{pd} and Ψ_{md} differed depending on habitat, but species ranks did not change over time.

Leaf N was similar across habitats, although species differed significantly (table 3). Leaf N ranks were *P. lanceolatum* > *S. iberica* > *S. hymenoides*. Mean leaf P was significantly higher on dunes (0.2317% ± 0.0106%) than off dunes (0.1935% ± 0.0118%) and differed significantly among species (*S. iberica* > *P. lanceolatum* > *S. hymenoides*; table 3). The tendency for leaf P to differ across habitats was strongest for *S. hymenoides* and weakest for *P. lanceolatum* (fig. 5).

Carbon isotope ratio ($\delta^{13}\text{C}$) was significantly more negative for on-dune plants than for off-dune plants (fig. 5; table 3). When data from both species are pooled, multiple regression analysis of $\delta^{13}\text{C}$ against Ψ_{pd} and percent N showed that these significantly affected $\delta^{13}\text{C}$ (adjusted $R^2 = 0.36$, $F_{2,15} = 3.82$, $P < 0.05$), with both variables contributing significantly to the relationship (Ψ_{pd} : $t = -3.37$, $P = 0.0056$; percent N: $t = 2.89$, $P = 0.013$). However, when species are analyzed individually, multiple regression showed that neither Ψ_{pd} nor percent N explained the variation in $\delta^{13}\text{C}$ for *S. hymenoides*, whereas Ψ_{pd} and that percent N explained 93% of the variation in $\delta^{13}\text{C}$ for *P. lanceolatum* (adjusted $R^2 = 0.93$, $F_{3,3} = 29.41$, $P < 0.01$). Notably, only Ψ_{pd} contributed significantly to this relationship for *P. lanceolatum*.

Discussion

We show that plants growing on desert sand dunes have consistently higher water potentials than plants of the same species growing off dunes, probably driven largely by differences in soil texture. More importantly, we show that on-dune plants use water less conservatively (more negative $\delta^{13}\text{C}$) than similar plants of the same species off dunes. Our results are consistent with those of Hamerlynck et al. (2004), who found that *Larrea tridentata* on dunes used water less

Table 2
Soil Water Potential (Ψ) for On-Dune and Off-Dune Habitats on July 30, 2002

Soil depth (cm)	On-dune Ψ_{soil} (MPa)	Off-dune Ψ_{soil} (MPa)
25	−10.36 (3.85)	−29.37 (11.56)
50	−1.35 (1.34)	−4.82 (1.29)
75	−1.33 (1.29)	−1.51 (0.44)
100	−0.91 (0.87)	−1.00 (0.40)
150	−0.59 (0.55)	−2.10 (0.23)

Note. Soil Ψ was estimated from the relationship between soil water content and soil Ψ from soil moisture release curves generated in the lab for each depth/site combination. Values are means for two on-dune and three off-dune sites, with SE in parentheses.

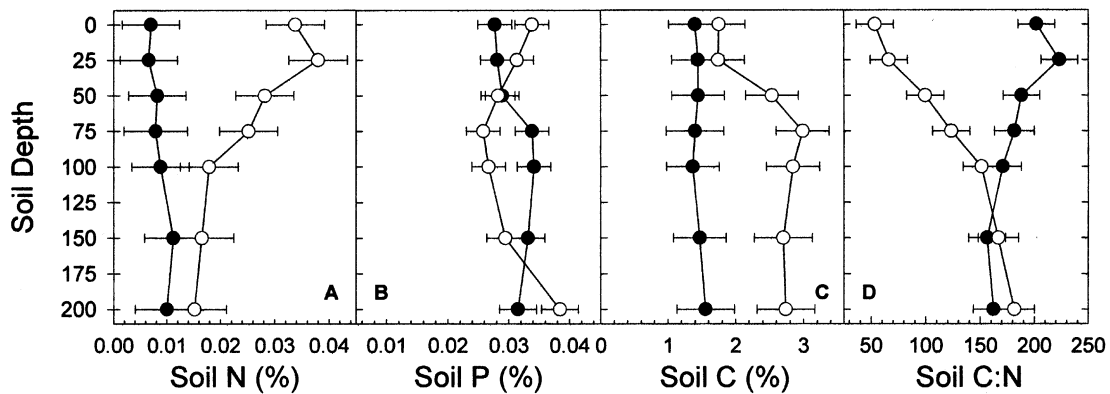


Fig. 3 Soil total N (A), P (B), C (C), and C : N ratio (D) at 0-, 25-, 50-, 75-, 100-, 150-, and 200-cm depths for on-dune (filled circles) and off-dune habitats (open circles). Circles represent model-adjusted means \pm SE for five plots per habitat.

conservatively than plants in four other more developed Mohave Desert soils (Hamerlynck et al. 2004). The greater plant Ψ on the dunes and associated lower integrated water use efficiency attest to the potential for different selective forces to act in these contrasting habitats.

Despite large differences in habitat N, species leaf nutrient contents do not reflect overall habitat nutrient differences and, in some species, differ in the opposite direction. We show a previously undescribed heterogeneity in and complex interactions between soil texture, moisture availability, and nutrient availability along this sand dune/desert boundary. This supports a growing body of literature on the importance of effects of soil texture on water and nutrient relations in arid and semiarid ecosystems (McAuliffe 1994; Hamerlynck et al. 2000, 2002; Hook and Burke 2000; Barrett and Burke 2002). Finally, the similarity in leaf N within species, coupled with differences in patterns of covariation between $\delta^{13}\text{C}$ with Ψ_{pd} and leaf N between species, indicates that stomatal closure appears to drive differences in $\delta^{13}\text{C}$. This supports recent modeling and empirical work demonstrating that stomatal response to Ψ_{pd} , not mesophyll demand, largely controls differences in water use strategies in desert shrubs (Ogle and Reynolds 2002; Hamerlynck et al. 2004).

Plant and Soil Water Relations

It has long been assumed that plant distribution and community structure in arid ecosystems are a consequence of precipitation inputs. In this way, vegetation distribution and primary production will vary predictably along precipitation gradients (Noy-Meir 1973). However, recent studies along a soil chronosequence in the Mohave Desert have demonstrated that when precipitation inputs are similar among habitats, plant performance can be tightly coupled with soil age and horizon development (McAuliffe 1994; Hamerlynck et al. 2000, 2002).

Theory predicts that in arid systems, coarse-textured soils in general and sand dunes in particular should capture and store precipitation more efficiently than finer-textured soils (Noy-Meir 1973). Our plant Ψ data support this assertion. Hennessy et al. (1985) studied a *Prosopis glandulosa* coppice dune community in southern New Mexico and compared

vegetated dunes and interdune sites, which parallel the soil textural differences of on- and off-dune soils, respectively. They reported that there was significantly less water available above -1.5 MPa on vegetated dunes than in interdune sites and concluded that vegetated dunes store water less efficiently than interdune habitats. Although the interdune soils had more clay and held more water by volume than sandier soils, Hennessy et al. (1985) did not provide plant Ψ or other plant physiological data to confirm their conclusions. In another comparison, winter annuals on dunes did not have Ψ significantly different from that of similar plants off dunes (Forseth et al. 1984). However, our results tend to agree with

Table 3

Mixed-Model ANOVA Results of the Effect of Habitat and Depth on Soil N and P and Habitat and Species Effects on Leaf N, P, and $\delta^{13}\text{C}$ (C_3 Species Only)

Effect	df	F	P
Soil N:			
Habitat	1, 3.92	32.29	0.0050
Depth	6, 43.2	0.42	0.8648
Habitat \times depth	6, 43.2	4.20	0.0020
Soil P:			
Habitat	1, 4.12	0.04	0.8487
Depth	6, 20.8	2.00	0.1111
Habitat \times depth	6, 20.6	4.26	0.0060
Leaf N:			
Habitat	1, 19	0.35	0.5606
Species	2, 19	57.54	<0.00001
Habitat \times species	2, 19	1.04	0.3736
Leaf P:			
Habitat	1, 7.14	5.79	0.0464
Species	2, 11.1	77.74	<0.0001
Habitat \times species	2, 7.14	2.68	0.1120
Leaf $\delta^{13}\text{C}$:			
Habitat	1, 11	7.2	0.0213
Species	1, 11	0.25	0.6239
Habitat \times species	1, 11	0.18	0.6827

Note. For five on-dune and five off-dune habitats. Soil and leaf data were sampled on one date. Site effects and appropriate interactions were modeled as random effects. See also figures 3 and 5. Significant effects are shown in boldface.

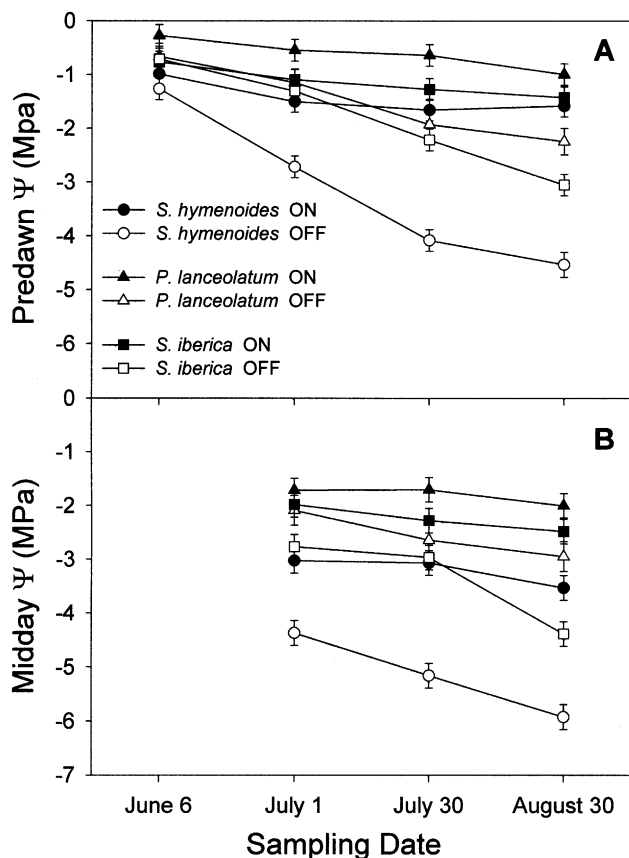


Fig. 4 Seasonal predawn water potential (Ψ_{pd}) and midday water potential (Ψ_{md}) for plants at on-dune (filled symbols) and off-dune (open symbols) sites. Each symbol represents a model-adjusted mean \pm SE for $n = 6-10$ individuals.

those of Pavlik (1980), who reported that seasonal water status for *Stanleya pinnata*, a drought deciduous shrub, was greater for individuals in on-dune habitats than for those in adjacent off-dune habitats.

Significant differences in soil texture can account for the apparent discrepancy between plant Ψ and soil water content differences reported here (Noy-Meir 1973; Hennessy et al.

1985; Hacke et al. 2000). On July 30 and August 30, 2001, soil water content was significantly higher off dunes, but plant Ψ was significantly greater for all three species on dunes. The increase in the amount of clay in the soil from on- to off-dune habitats reported here is likely to be associated with decreased plant Ψ (Hamerlynck et al. 2000). Water is more tightly bound to clay than to sand particles, so soils with higher clay content have greater resistance to water movement and lower Ψ than comparable soils with lower clay content (Bristow et al. 1984; Nilsen and Orcutt 1996). It is likely, then, that the higher soil clay content offsets any benefit of greater soil water content off dunes, thus leading to higher realized plant Ψ on dunes. Furthermore, the relatively small change in soil texture in the top 50 cm of soil indicates that moisture in the deeper soil layers plays a key role in annual and forb plant performance in these systems, as Hammerlynck et al. (2002) found in their work. We note that evapotranspiration is positively associated with vegetation cover (Branson et al. 1976). Therefore, greater vegetation cover and associated competition for water off dunes cannot be ruled out as additional factors associated with lower attained plant Ψ off dunes.

Plant and Habitat Nutrient Differences

Total soil C and N are greater off dunes and were negatively correlated with soil sand fractions (figs. 1, 3). Soil C and N covaried in a similar fashion along shortgrass steppe soil catenas in Colorado (Schimel et al. 1985; Hook and Burke 2000) and across a Mohave sand dune desert ecotone (Lei 1998). Soil organic matter and total N also tend to be positively correlated with nitrogen availability (Schimel et al. 1985; Hook and Burke 2000; Whitford 2002), and leaf nutrient concentrations tend to increase with increasing habitat nutrient availability (Chapin 1980; Aerts and Chapin 2000). However, leaf N levels in this study did not covary with soil N levels. Leaf tissue nutrient concentrations of wild plants tend to be less sensitive indicators of nutrient availability than that in crop species (Chapin 1980). Nevertheless, it is surprising, given the threefold difference in soil N between habitats, that leaf N is not higher in the off-dune habitats. It may be that higher soil C : N ratios off dunes, which tend to be associated with low N mineralization and increased N

Table 4

Repeated-Measures Mixed-Model ANOVA of the Response of Predawn (Ψ_{pd}) and Midday (Ψ_{md}) Water Potential to the Effects of Species, Habitat (On-Dune vs. Off-Dune), and Day of Year (Date)

Effect	df	Ψ_{pd}		df	Ψ_{md}	
		F	P		F	P
Habitat	1, 3.92	72.31	0.0011	1, 4.15	67.87	0.0010
Species	2, 193	115.68	<0.0001	2, 8.14	130.46	<0.0001
Habitat \times species	2, 193	14.96	<0.0001	2, 7.35	6.30	0.0254
Date	3, 190	117.66	<0.0001	2, 128	48.72	<0.0001
Date \times habitat	3, 190	24.29	<0.0001	2, 128	8.78	0.0003
Date \times species	6, 190	1.12	0.3524	4, 128	1.26	0.2877
Date \times habitat \times species	6, 190	2.00	0.0674	4, 128	2.30	0.0618

Note. For five on-dune and five off-dune habitats. See figure 4. Site effects and all appropriate interactions were modeled as random effects. Significant effects are shown in boldface.

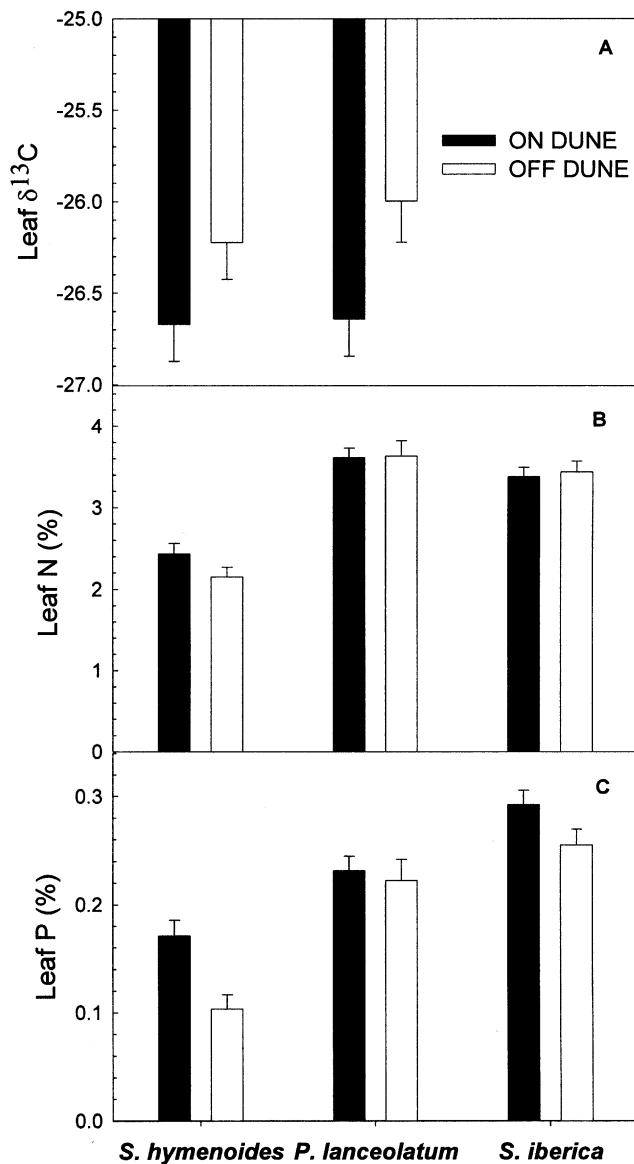


Fig. 5 Leaf $\delta^{13}\text{C}$ (A), N (B), and P (C) for *Stipa hymenoides*, *Psoralidium lanceolatum*, and *Salsola iberica*. Leaf $\delta^{13}\text{C}$ is not reported for *S. iberica* because it is a C_4 species (see "Material and Methods" for details). Bars represent adjusted means \pm SE for five plots per habitat.

immobilization (Schimel et al. 1985; Barrett and Burke 2000), reduce available N in spite of the greater total N off dunes. Also, N mineralization off dunes could be further reduced because of lower soil Ψ off dunes (Paul et al. 2003). Indeed, mean annual precipitation was well below average the year preceding and the year of the study.

Habitat soil P did not differ, but overall, leaf P was greater on dunes (table 3; fig. 5). However, unlike total N, total soil P is not necessarily a good predictor of plant-available P (Lajtha and Schlesinger 1988a). Lower leaf P off dunes may be the result of the complementary effects of lower soil Ψ and higher clay content on diffusion, because P acquisition is pri-

marily limited by diffusion, which tends to be lower in higher clay soils (Cox and Barber 1992; Marschner 1995). Lower leaf P off dunes may be lower in part because of soil chemistry. Clay particles frequently have higher P concentrations than other soil fractions because organic P and PO_4 are adsorbed to clays (Srivasta and Pathak 1971; Dong et al. 1983; Atalay 2001). Furthermore, CaCO_3 is only found at off-dune sites. This may indicate that soil pH plays a role in limiting P acquisition and uptake off dunes (Lajtha and Schlesinger 1988b), because P tends to be chemically bound and unavailable to plants in alkaline soils (Lajtha and Schlesinger 1988a).

Significant species differences in leaf N content within habitats reflect inherent species differences in nutrient uptake ability and metabolism (Marschner 1995; Aerts and Chapin 2000). For example, only *Stipa hymenoides* had significant differences in leaf N between habitats, but again they were contrary to our expectations. Rhizosheaths improve water status around the roots of *S. hymenoides* and enhance water uptake from the rhizosphere (Bristow et al. 1985; Wullstein 1991). The presence of symbiotic N fixers in rhizosheaths, coupled with seasonally higher plant water availability on the dunes, may explain higher leaf N for *S. hymenoides* on versus off dunes (Wullstein et al. 1979).

Alternatively, nutrient resorption triggered by senescence may have lowered leaf N and P for *S. hymenoides*, compared with the other species (Aerts and Chapin 2000). *Stipa hymenoides* in off-dune habitats experienced significantly lower water potentials than the other species in either habitat (fig. 4) and had been experiencing lower plant Ψ for 3 wk when leaves were collected for elemental analysis. Moreover, some *S. hymenoides* individuals off dunes were already beginning to senesce, while *Salsola iberica* and *Psoralidium lanceolatum* were not (D. M. Rosenthal, personal observations).

Consequences for Plant Strategies

When viewed together, soil and plant Ψ indicates that on-dune plants are rooted more deeply than those off dune. Indeed, deep taproots are characteristic of many desert dune plants and are presumed to be adaptive under the constant threats of dune deflation and soil moisture depletion (Bowers 1982; Danin 1991), and recent studies show that some shrubs and trees tend to be more shallowly rooted in fine-textured soils (loam) than in coarse soils (sand) (Hacke et al. 2000; Sperry and Hacke 2002). At our sites, both soil water content and soil Ψ increased with depth, so we would expect plants with less negative Ψ to be more deeply rooted. Using this analogy, species ranks for rooting depths for this study are *S. hymenoides* < *S. iberica* < *P. lanceolatum*. The relative ranks of *S. hymenoides* and *P. lanceolatum* make sense, because we would expect a bunchgrass (*S. hymenoides*) to have the majority of its roots higher in the soil profile than a shrub (*P. lanceolatum*) in similar habitats (Jackson et al. 1996). The tendency to root more deeply on the dunes is evident from the plant and soil Ψ on July 30, and the trends are consistent for the species studied here. For example, the observed Ψ_{pd} for *P. lanceolatum* could only have been achieved by having access to soil water at 75 cm off dunes but at least 100 cm on dunes (table 2). For the preceding discussion, we

assume that Ψ_{pd} is in equilibrium with soil Ψ ; therefore, Ψ_{pd} should reflect either the wettest soil the plant sees or a depth-weighted average of soil water potential (Breda et al. 1995; Sperry and Hacke 2002; but see Donovan et al. 2003).

The small spatial scale differences in soil water availability documented in this study with the phytometer method may drive differences in selection on plant water use characters along this and other sand dune/desert boundary communities (Antonovics and Bradshaw 1970). For our study species that grew both on and off the dunes, this difference in environment may have driven ecotypic differentiation, which could have confounded our results. However, the differences in water status between on- and off-dune habitats were robust across all three species, indicating that for these species any ecotypic variation would likely be a minor effect.

For other species that are more restricted in their habitat tolerances and distributions, differences in water availability between these habitats may be particularly important. For example, two species of annual sunflowers, *Helianthus anomalus* and *Helianthus deserticola*, are specialized to on- and off-dune habitats, respectively, at Little Sahara Dunes, Utah. For the on-dune endemic *H. anomalus*, Ψ_{md} and Ψ_{pd} are greater than or similar to those of *P. lanceolatum*, which has the highest Ψ of all the plants on all the dates presented here, indicating that *H. anomalus* has a deep root system to access stored water (D. M. Rosenthal, unpublished data). *Helian-*

thus anomalus persists throughout the summer growing season and reproduces in late summer and fall, which is an unusual strategy for a desert summer annual. In contrast, *H. deserticola* is endemic to the lower water availability off-dune habitat and appears to follow a more traditional desert annual strategy, flowering significantly earlier and completing its life cycle before soil moisture limitations become extreme (Rosenthal et al. 2002; Gross et al. 2004). The differences in flowering phenology between the *H. anomalus* and *H. deserticola* habitats may reflect differing adaptive strategies in light of the seasonal difference in soil and plant water status.

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Literature Cited

- Aerts R, FS Chapin 2000 The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67.
- Alizai HA, LC Hulbert 1970 Effects of soil texture on evaporative loss and available water in semi-arid climates. *Soil Sci* 110:328–332.
- Allen SE 1989 Chemical analysis of ecological materials. Blackwell, Boston.
- Antonovics J, AD Bradshaw 1970 Evolution in closely adjacent plant populations. 8. Clinal patterns at a mine boundary. *Heredity* 25: 349–362.
- Antonovics J, K Clay, J Schmitt 1987 The measurement of small-scale environmental heterogeneity using clonal transplants of *Anthoxanthum odoratum* and *Danthonia spicata*. *Oecologia* 71: 601–607.
- Atalay A 2001 Variation in phosphorus sorption with soil particle size. *Soil Sediment Contam* 10:317–335.
- Barbour MG, JH Burk, WD Pitts 1987 Terrestrial plant ecology. Benjamin, Menlo Park, CA.
- Barrett JE, IC Burke 2000 Potential nitrogen immobilization in grassland soils across a soil organic matter gradient. *Soil Biol Biochem* 32:1707–1716.
- 2002 Nitrogen retention in semiarid ecosystems across a soil organic-matter gradient. *Ecol Appl* 12:878–890.
- Bouyoucos GJ 1962 Hydrometer method improved for making particle size analyses of soils. *Agron J* 54:464–465.
- Bowers JE 1982 The plant ecology of inland dunes in Western North America. *J Arid Environ* 5:199–220.
- Branson FA, RF Miller, IS McQueen 1976 Moisture relationships in 12 northern desert shrub communities near Grand Junction, Colorado. *Ecology* 57:1104–1124.
- Breda N, A Granier, F Barataud, C Moyne 1995 Soil-water dynamics in an oak stand. 1. Soil-moisture, water potentials and water-uptake by roots. *Plant Soil* 172:17–27.
- Bristow CE, GS Campbell, LH Wullstein, R Neilson 1985 Water-uptake and storage by rhizosheaths of *Oryzopsis hymenoides*: a numerical-simulation. *Physiol Plant* 65:228–232.
- Bristow KL, GS Campbell, C Calissendorff 1984 The effects of texture on the resistance to water-movement within the rhizosphere. *Soil Sci Soc Am J* 48:266–270.
- Chadwick HW, PD Dalke 1965 Plant succession on dune sands in Fremont County, Idaho. *Ecology* 46:765–780.
- Chapin FS 1980 The mineral-nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–260.
- Clements FE, GW Goldsmith 1924 The phytometer method in ecology. *Carnegie Inst Washington Publ* 356:1–106.
- Cox MS, SA Barber 1992 Soil-phosphorus levels needed for equal P-uptake from 4 soils with different water contents at the same water potential. *Plant Soil* 143:93–98.
- Danin A 1991 Plant adaptations in desert dunes. *J Arid Environ* 21: 193–212.
- Dong A, GV Simsiman, G Chesters 1983 Particle-size distribution and phosphorus levels in soil, sediment, urban dust and dirt samples from the Menomonee River Watershed, Wisconsin, USA. *Water Res* 17: 569–577.
- Donovan LA, JR Ehleringer 1994 Potential for selection on plants for water-use efficiency as estimated by carbon-isotope discrimination. *Am J Bot* 81:927–935.
- Donovan LA, MJ Linton, JH Richards 2001 Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. *Oecologia* 129:328–335.
- Donovan LA, JH Richards, MJ Linton 2003 Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. *Ecology* 84:463–470.
- Dudley SA 1996 Differing selection on plant physiological traits in response to environmental water availability: a test of adaptive hypotheses. *Evolution* 50:92–102.

- Ehleringer JR, TA Cooper 1988 Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76: 562–566.
- Ehleringer JR, SL Phillips, WSF Schuster, DR Sandquist 1991 Differential utilization of summer rains by desert plants. *Oecologia* 88: 430–434.
- Farquhar GD, JR Ehleringer, KT Hubick 1989 Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537.
- Forseth IN, JR Ehleringer, KS Werk, CS Cook 1984 Field water relations of Sonoran Desert annuals. *Ecology* 65:1436–1444.
- Gross BL, NC Kane, C Lexer, F Ludwig, DM Rosenthal, LA Donovan, LH Rieseberg 2004 Reconstructing the origin of *Helianthus deserticola*: survival and selection on the desert floor. *Am Nat* 164:145–156.
- Hacke UG, JS Sperry, BE Ewers, DS Ellsworth, KVR Schafer, R Oren 2000 Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124:495–505.
- Hamerlynck EP, TE Huxman, JR McAuliffe, SD Smith 2004 Carbon isotope discrimination and foliar nutrient status of *Larrea tridentata* (creosote bush) in contrasting Mojave Desert soils. *Oecologia* 138: 210–215.
- Hamerlynck EP, JR McAuliffe, EV McDonald, SD Smith 2002 Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. *Ecology* 83:768–779.
- Hamerlynck EP, JR McAuliffe, SD Smith 2000 Effects of surface and sub-surface soil horizons on the seasonal performance of *Larrea tridentata* (creosote bush). *Funct Ecol* 14:596–606.
- Harper JL 1977 The population biology of plants. Academic Press, New York.
- Hedrick PW 1986 Genetic polymorphism in heterogeneous environments: a decade later. *Annu Rev Ecol Syst* 17:535–566.
- Hennesy JT, RP Gibbens, JM Tromble, M Cardenas 1985 Mesquite (*Prosopis glandulosa* Torr.) dunes and interdunes in southern New Mexico: a study of soil properties and soil-water relations. *J Arid Environ* 9:27–38.
- Hook PB, IC Burke 2000 Biogeochemistry in a shortgrass landscape: control by topography, soil texture, microclimate. *Ecology* 81: 2686–2703.
- Jackson RB, J Canadell, JR Ehleringer, HA Mooney, OE Sala, ED Schulze 1996 A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411.
- Kadmon R 1993 Population-dynamic consequences of habitat heterogeneity: an experimental study. *Ecology* 74:816–825.
- Lajtha K, WH Schlesinger 1988a The biogeochemistry of phosphorus cycling and phosphorus availability along a desert soil chronosequence. *Ecology* 69:24–39.
- 1988b The effect of CaCO₃ on the uptake of phosphorus by two desert shrub species *Larrea-tridentata* (DC) Cov and *Parthenium-incanum* Hbk. *Bot Gaz* 149:328–334.
- Lechowicz MJ, PA Blais 1988 Assessing the contributions of multiple interacting traits to plant reproductive success: environmental dependence. *J Evol Biol* 1:255–273.
- Lei SA 1998 Soil properties of the Kelso sand dunes in the Mojave Desert. *Southwest Nat* 43:47–52.
- Marschner H 1995 Mineral nutrition of higher plants. Academic Press, New York.
- McAuliffe JR 1994 Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. *Ecol Monogr* 64:111–148.
- Miller RE, JMV Hoef, NL Fowler 1995 Spatial heterogeneity in eight central Texas grasslands. *J Ecol* 83:919–928.
- Nagy ES 1997 Selection for native characters in hybrids between two locally adapted plant subspecies. *Evolution* 51:1469–1480.
- Nelson NS 1987 An acid-persulfate digestion procedure for determination of phosphorus in sediments. *Commun Soil Sci Plant Anal* 18:359–369.
- Nilsen ET, DM Orcutt 1996 Physiology of plants under stress: abiotic factors. Wiley, New York.
- Noy-Meir I 1973 Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–51.
- Ogle K, JF Reynolds 2002 Desert dogma revisited: coupling of stomatal conductance and photosynthesis in the desert shrub, *Larrea tridentata*. *Plant Cell Environ* 25:909–921.
- Paul KI, PJ Polglase, AM O'Connell, JC Carlyle, PJ Smethurst, PK Khanna 2003 Defining the relation between soil water content and net nitrogen mineralization. *Eur J Soil Sci* 54:39–47.
- Pavlik BM 1980 Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. *Oecologia* 46: 147–154.
- Polis GA 1991 The ecology of desert communities. University of Arizona Press, Tucson.
- Rieseberg LH, O Raymond, DM Rosenthal, Z Lai, K Livingstone, T Nakazato, JL Durphy, AE Schwarzbach, LA Donovan, C Lexer 2003 Major ecological transitions in wild sunflowers facilitated by hybridization. *Science* 301:1211–1216.
- Rosenthal DM, AE Schwarzbach, LA Donovan, O Raymond, LH Rieseberg 2002 Phenotypic differentiation between three ancient hybrid taxa and their parental species. *Int J Plant Sci* 163:387–398.
- Rundel PW, M Jarrell 1989 Water in the environment. Pages 29–56 in RW Percy, J Ehleringer, HA Mooney, PW Rundel, eds. *Plant physiological ecology: field methods and instrumentation*. Chapman & Hall, London.
- Sandquist DR, JR Ehleringer 2003 Carbon isotope discrimination differences within and between contrasting populations of *Encelia farinosa* raised under common-environment conditions. *Oecologia* 134:463–470.
- SAS Institute 2001 SAS/STAT user's guide, version 8.01. SAS Institute, Cary, NC.
- Schimel D, MA Stillwell, RG Woodmansee 1985 Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology* 66: 276–282.
- Schwarzbach AE, LA Donovan, LH Rieseberg 2001 Transgressive character expression in a hybrid sunflower species. *Am J Bot* 88: 270–277.
- Smith SD, RK Monson, JE Anderson 1997 Physiological ecology of North American desert plants. Springer, Berlin.
- Snaydon RW, MS Davies 1972 Rapid population differentiation in a mosaic environment. 2. Morphological variation in *Anthoxanthum odoratum*. *Evolution* 26:390–405.
- Sperry JS, UG Hacke 2002 Desert shrub water relations with respect to soil characteristics and plant functional type. *Funct Ecol* 16: 367–378.
- Srivasta OP, AN Pathak 1971 Available phosphorus in relation to soil texture. *Agrochimica* 15:255–258.
- Stewart SC, DJ Schoen 1987 Pattern of phenotypic viability and fecundity selection in a natural population of *Impatiens pallida*. *Evolution* 41:1290–1301.
- UNESCO 1977 World map of arid regions. United Nations Educational, Scientific, and Cultural Organization, New York.
- Welsh SL, ND Atwood, S Goodrich, LC Higgins 1987 A Utah flora. *Great Basin Nat Mem* 9:1–894.
- Whitford WG 2002 Ecology of desert systems. Academic Press, San Diego, CA.
- Wullstein LH 1991 Variation in N₂ fixation (C₂H₂ Reduction) associated with rhizosheaths of Indian ricegrass (*Stipa hymenoides*). *Am Midl Nat* 126:76–81.
- Wullstein LH, ML Bruening, WB Bollen 1979 Nitrogen fixation associated with sand grain root sheaths (rhizosheaths) of certain xeric grasses. *Physiol Plant* 46:1–4.