Multiple resources limit plant growth and function in a saline-alkaline desert community

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Summary

1 We investigated resource limitations in a saltbrush scrub community along a salinity-alkalinity gradient in the Mojave Desert of North America. Previous studies have shown that, as productivity declines with increasing soil stress, there are parallel declines in leaf Ca and Mg, suggesting availability of these resources may limit growth in addition to water, N and P limitations expected in deserts.

2 To determine which soil resources limited growth of the dominant shrub, Atriplex parryi, and whether this differed along the soil stress gradient or among life stages, water and nutrients were applied in combination at different rates to plants at high- and low-stress sites. We developed and applied a conceptual model to identify resource limitations from this experiment. We also investigated how those limitations interacted to influence A. parryi growth and physiological function at the high-stress site.

3 Availability of soil N and P limited growth at the low-stress site and N, P and Mg limited growth at the high-stress site for both adult and juvenile life stages. There was no evidence that availability of water alone or K, Ca or other nutrients, or increasing soil Na and B, limited growth along the soil stress gradient.

4 When N, P, Mg and water were supplied in combination, plant growth increased more than 16-fold. Supply of these resources interacted to influence both plant growth and function. Because of the high demand for N relative to other resources, N supply rate was the major driver of these interactions, influencing the magnitude by which P and Mg affected growth. The major mechanism behind these growth responses was an increase in allocation to leaves relative to fine roots, rather than nutrient or water effects on water relations, photosynthesis or water use efficiency.

5 Multiple, interacting resources limit the growth and distribution of A. parryi on a saline, alkaline Mojave Desert site. Similar interactions between multiple limiting resources are likely to be instrumental in shaping community and species distributions along other abiotic stress gradients.

Key-words: alkalinity, Atriplex parryi, desert shrub, nutrient limitation, salinity

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Introduction

Resource limitations influence plant community properties, such as structure and species distribution, as well as ecosystem functions, such as productivity and nutrient cycling. Although multiple-factor limitations have long been recognized, few studies have investigated individual plant or community responses to such limitations (Chapin et al. 1987; Field et al. 1992; Shaw et al. 2002; Ho et al. 2004). This lack of information may be related to the large number of treatments needed to evaluate responses to both single resource limitations and their interactions with other factors. Additionally, individual species within a community may be limited by different resources, making community level and individual plant responses in species-rich communities difficult to interpret (Aerts & Chapin 2000; Drenovsky & Richards 2004). Despite these challenges, such insight is essential for understanding how individual species and communities are impacted following natural and anthropogenic perturbations, as these are inherently multifactorial (Chapin & Shaver 1985; Press et al. 1998; Shaver et al. 1998; Shaw et al. 2002).
Desert plant communities are excellent model systems in which to investigate multiple resource limitations to growth due to their simple structure, their low, but highly variable, annual productivity and their limited, heterogeneous supply of soil resources. Productivity patterns in deserts are thought to be driven mainly by low and infrequent precipitation inputs (Noy-Meir 1973; Hadley & Szarek 1981). In addition to the direct effect of precipitation on plant growth, low and variable water supply reduces soil nutrient availability by limiting the weathering of parent material, organic matter production and mineralization (Fisher et al. 1987; Burke 1989; Schlesinger 1997). Studies in several desert systems have shown that N or P can limit growth once water limitations are removed (Smith et al. 1997; Drenovsky & Richards 2004). Additionally, large temporal and spatial heterogeneity of soil resources compounds the effects of low soil nutrient supply on productivity. For example, soil inorganic N concentrations can vary three- to tenfold within a site through the season (Burke 1989; Ryel et al. 1996; Xie & Steinberger 2001; Z. Aanderud et al., unpublished data). Significant spatial variation has also been reported for N, P, Ca, Mg, pH and organic matter in a range of desert systems (Jackson & Caldwell 1993; Schlesinger et al. 1996; Cross & Schlesinger 1999).

While most research has focused on water limitations in deserts and how this interacts with low soil N availability, there is evidence that the availability of other soil resources may limit productivity in deserts, particularly in highly saline-alkaline systems. Topographic gradients across interior drainage basins in arid western North America are paralleled by gradients of decreasing soil fertility and increasing salinity, pH and toxic ion concentrations (e.g. Na, B) at lower positions. Thus, at lower topographic positions, productivity and diversity decline and, eventually, mono-specific stands develop at the most stressful sites (West 1983; Donovan & Richards 2000), probably as a combined result of several factors. Increasing salinity not only increases plant nutrient requirements, but it can interfere with uptake of nutrient cations such as K\(^+\), Ca\(^{2+}\) and Mg\(^{2+}\) (Flowers et al. 1977; Marschner 1995; Drenovsky & Richards 2003). Likewise, increasing alkalinity is expected to further reduce N availability through volatilization of mineralized NH\(_4\) and to decrease P, Ca and Mg solubility (Lajtha & Schlesinger 1988; Schlesinger & Peterjohn 1991; Lambers et al. 1998).

Evidence for multiple resource limitations in saline-alkaline deserts is, however, inconsistent. In a survey of widespread Great Basin and Mojave Desert species that establish on the lower portions of the topographic gradients (including *Atriplex parryi*, the species that we focus on here), Snyder et al. (2004) found that water addition alone had minimal effects on productivity or on physiological functions such as photosynthesis. When soil organic matter and nutrients are available, water addition should increase mineralization and nutrient mobility (Birch 1960; Fisher et al. 1987; Cui & Caldwell 1997), but no changes in leaf nutrient concentrations were observed. It was therefore suggested that plant growth was co-limited by soil nutrient availability. Other work supports the prediction that low nutrient availability regulates plant growth response to water in such environments. Along gradients of increasing soil salinity and alkalinity in the Great Basin and Mojave, both growth and leaf Ca and Mg concentrations of dominant shrubs, including *Sarcobatus vermiculatus* and *A. parryi*, declined in parallel with soil Ca and Mg availability (Richards 1994; Donovan et al. 1997).

Although N and P are expected to be limiting in deserts, no relationship was observed between growth and leaf N or P concentration. Macro- and micronutrient additions at one site, however, demonstrated that *S. vermiculatus* growth was stimulated by N (Drenovsky 2002), but not by P, Ca or Mg, supporting earlier experimental work in deserts (see Smith et al. 1997 for review).

The discord between these different approaches to determining resource limitations in deserts could be due to methodology. For example, nutrient addition may not significantly increase soil fertility if nutrients are fixed by soil chemical reactions (Chapin et al. 1986). Without dose-response curves it is not possible to determine if a lack of response is because the resource was not limiting or because supply rates were insufficient to overcome limitations or soil fixation. Of more fundamental importance, however, is the need to consider how multiple limitations may interact to influence plant response. Current models of allocation predict that multiple resources will be limiting, but differences in acquisition costs and absolute demand for resources should interact to influence plant response to changes in resource supply. In these models, small increases in resources that are in high demand, such as N, which is required in large quantities, result in significant reallocation to other functions (Bloom et al. 1985; Gleeson & Tilman 1992; Gleeson & Good 2003). The magnitude of this reallocation should therefore influence plant response to other resources or resource manipulation.

We determined whether single or multiple resources (water, N, P, Mg and Ca) limit productivity of *A. parryi* in the saltbrush scrub community it dominates. We had two specific objectives. The first was to determine experimentally which soil resources limit productivity of *A. parryi* and to evaluate if these limitations differed along a soil stress gradient or between life stages (reproductive adults vs. pre-reproductive juveniles). We applied resources in combination at different supply rates in two *A. parryi* stands, one at a high-stress site and the other at a more species-diverse, low-stress site. We then developed and applied a conceptual model of plant response to resource addition to evaluate patterns of nutrient limitations (Fig. 1). Treatments were applied to adult plants at both the low and high stress sites and to juvenile plants at the high stress site because juvenile plants may be less tolerant of soil stress (Donovan & Ehleringer 1994; Richards 1994).
Multiple resource limitations in deserts

The second objective was to investigate how resource limitations interact to influence plant growth and function. We used a full factorial approach to investigate how resource limitations identified in the first experiment interact to influence plant growth and function (biomass allocation, gas exchange, water relations) at the high-stress end of the gradient.

Materials and methods

SITE DESCRIPTION

Both experiments were conducted on the southwestern shore of Owens Lake, California, USA (36°21.5′ N, 118° W; 1085–1087 m a.s.l.). Owens Lake is in a closed hydrologic basin at the north-western edge of the Mojave Desert and has been dry since 1926 as a result of urban water diversion (Saint-Amand et al. 1986).

Previous soil sampling along transects in this basin, from the densely vegetated, non-saline dunes, through the historic shoreline, to the barren playa surface, has demonstrated steep gradients in soil nutrient availability, salinity and alkalinity (Dahlgren et al. 1997). Because the higher topographic sites have been exposed longer, soils generally have higher nutrient concentrations, lower pH and lower salinity levels. Sites located closer to the playa have very nutrient-poor soils that are quite saline and alkaline. Along the transects, soil NO₃ in the 10–40 cm depth layer, where the highest concentration of roots is found, ranges from 8 to less than 1 μg g⁻¹. In saturated paste extracts, soil P ranges from 5.1 to 0.01 mM, K from 40 to 1 mM, Ca from 6 to 1 mM and Mg from 0.45 to 0.05 mM. Soil salinity (Na concentration) increases from less than 10 to over 500 mM and soil pH increases from 8.5 to over 10 (Dahlgren et al. 1997). The mean annual precipitation is 149 mm year⁻¹, with over 80% of the precipitation occurring between October and April. Total precipitation in 2001 and 2002 was 196 and 138 mm. From January to August 2003 precipitation totalled 164 mm.

Two sites that differed in soil stress were selected along an E-W transect. The low-stress site on the historic shoreline of Owens Lake (Shoreline) and the high-stress site below it on the recently exposed playa surface (Playa) encompass the ecological range of Atriplex parryi S. Watson in this community. This C₄, non-mycorrhizal shrub, forms a sparse (6% cover) but monospecific stand at the high-stress site and is the dominant species (23% cover) at the low-stress site (Table 1). At the low-stress site, the less stress-tolerant shrubs Sarcobatus vermiculatus, Atriplex confertifolia and Distichlis spicata add 4% perennial cover and quickly replace A. parryi at higher topographic positions, while at lower locations no vegetation is able to establish. These sites correspond to the LM4 and LM7 sampling locations of Richards (1994) and Dahlgren et al. (1997).

EXPERIMENTAL DESIGN AND RESOURCE ADDITION

Experiment 1

To determine which resources limit growth, we selected 40 widely spaced, similar-sized adult A. parryi shrubs (canopy dimensions c. 20 × 20 × 35 cm and c.10 × 10 × 10 cm at the low- and high-stress sites) at each site in spring 2001. Additionally, 40 subplots, consisting of three juvenile A. parryi plants (c. 5 × 5 × 8 cm each), were selected at the Playa site. We selected shrubs and subplots that had no neighbouring plants present within a 1-m² area. There were insufficient similar-sized juveniles at the Shoreline site to allow treatment replication there, but it was more important to compare the response of the two different life stages at the high-stress site because juveniles may be more sensitive to soil stress than adult plants (Donovan & Ehleringer 1994; Richards 1994). In each of five blocks, eight treatments (control, water, three rates of NPK addition with water and three different Ca : Mg ratios with NPK and water, Table 2) were randomly assigned to the eight adult plants and eight juvenile subplots. Slow-release KNO₃ fertilizer was used to control the duration of N and K availability and limit NO₃ leaching (Apex® 12-0-42, Simplot, Lathrop, CA, USA). Nutrients were applied in spring of 2001 and 2002 in the same locations in two 40-cm-deep holes on opposite sides of the canopy of each adult plant and by auguring one 40-cm-deep hole in the centre of each cluster of juvenile plants. The nutrients were mixed with the excavated soil and holes back-filled. Treatments receiving water were drip-irrigated bi-weekly throughout the growing season (March–June). The average amount of water applied
Nutrient limitations can only be confidently assessed if geochemical processes that reduce nutrient availability are saturated, allowing plant nutrient requirements to be met (Chapin et al. 1986). To overcome geochemical fixation in these highly alkaline soils, we applied high rates of P, Ca and Mg so that a small amount of the added resources would remain in a soluble form long enough to be accessed by the shrubs. Fertilizer addition increased nutrient availability to levels within ranges sampled in adjacent upland stands that are dominated by less stress-tolerant vegetation. Similarly, applying water at a high rate ensured that water

**Table 1** Comparison of plant community and soil characteristics at the Shoreline (low-stress) and Playa (high-stress) sites and effects of water addition on soil characteristics. Soil samples were collected during August 2001 (5 months after start of water treatments). Analyses were performed on saturated paste extracts. Soil values (mean ± SE, n = 5) are from 10 to 40 cm depth. All elemental data are in mg L⁻¹. N is inorganic N (NO₃⁻ + NH₄⁺) and P is inorganic P (H₂PO₄⁻ + HPO₄²⁻). Different letters within a soil characteristic (e.g. pH) indicate significantly different mean values as determined by ANOVA and subsequent multiple range tests.

<table>
<thead>
<tr>
<th>Plant community characteristics</th>
<th>Shoreline</th>
<th>Playa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total cover (%)</td>
<td>27 ± 2</td>
<td>6 ± 1</td>
</tr>
<tr>
<td>A. parryi cover (%)</td>
<td>23 ± 2</td>
<td>6 ± 1</td>
</tr>
<tr>
<td>A. parryi density (plants m⁻²)</td>
<td>2.1 ± 0.4</td>
<td>0.8 ± 0.1</td>
</tr>
<tr>
<td>A. parryi height (cm)</td>
<td>36 ± 2</td>
<td>10 ± 2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Soil characteristics</th>
<th>pH</th>
<th>Control</th>
<th>Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>8.58 ± 0.05b</td>
<td>9.04 ± 0.04a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.39 ± 0.13b</td>
<td>8.47 ± 0.03b</td>
</tr>
<tr>
<td>EC (dS m⁻¹)</td>
<td>C</td>
<td>2.41 ± 0.67b</td>
<td>6.33 ± 0.61a</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>0.85 ± 0.25b</td>
<td>1.32 ± 0.22b</td>
</tr>
<tr>
<td>Na</td>
<td>C</td>
<td>27.28 ± 8.13b</td>
<td>78.38 ± 7.47a</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>9.73 ± 3.71b</td>
<td>14.71 ± 2.53b</td>
</tr>
<tr>
<td>B</td>
<td>C</td>
<td>1.020 ± 0.381b</td>
<td>2.605 ± 0.196a</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>0.644 ± 0.413b</td>
<td>0.945 ± 0.201b</td>
</tr>
<tr>
<td>N</td>
<td>C</td>
<td>0.111 ± 0.052a</td>
<td>0.036 ± 0.008a</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>0.079 ± 0.024a</td>
<td>0.171 ± 0.049a</td>
</tr>
<tr>
<td>P</td>
<td>C</td>
<td>0.032 ± 0.011b</td>
<td>0.063 ± 0.006a</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>0.014 ± 0.006b</td>
<td>0.019 ± 0.005b</td>
</tr>
<tr>
<td>Mg</td>
<td>C</td>
<td>0.027 ± 0.003a</td>
<td>0.029 ± 0.005a</td>
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<tr>
<td></td>
<td>W</td>
<td>0.091 ± 0.057a</td>
<td>0.076 ± 0.018a</td>
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<tr>
<td>Ca</td>
<td>C</td>
<td>0.166 ± 0.031a</td>
<td>0.155 ± 0.016a</td>
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<td></td>
<td>W</td>
<td>0.061 ± 0.012a</td>
<td>0.097 ± 0.027a</td>
</tr>
<tr>
<td>K</td>
<td>C</td>
<td>3.05 ± 0.56b</td>
<td>4.72 ± 0.45a</td>
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<tr>
<td></td>
<td>W</td>
<td>0.95 ± 0.09c</td>
<td>0.86 ± 0.11c</td>
</tr>
</tbody>
</table>

**Table 2** Fertilizer addition rates for treatments in experiments 1 and 2. Values are g of nutrient replicate⁻¹ year⁻¹. The three different NPK and Ca : Mg doses are indicated by L (low), M (mid) and H (high) rates. Soil NO₃⁻ samples were collected 5 months after fertilization. Values are in µg N as NO₃⁻ per g dry soil (mean ± SE, n = 10). In experiment 1 all treatments except control received water (W).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N(KNO₃)</th>
<th>P(P₂O₅)</th>
<th>K(KNO₃)</th>
<th>Mg(MgSO₄)</th>
<th>Ca(CaSO₄)</th>
<th>Soil N (NO₃⁻)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult</td>
<td>Juvenile</td>
<td>Adult</td>
<td>Juvenile</td>
<td>Adult</td>
<td>Juvenile</td>
</tr>
<tr>
<td>Control</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>W</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>W + LNPK</td>
<td>20</td>
<td>4</td>
<td>9</td>
<td>2</td>
<td>70</td>
<td>14</td>
</tr>
<tr>
<td>W + MNPK</td>
<td>60</td>
<td>12</td>
<td>30</td>
<td>6</td>
<td>210</td>
<td>42</td>
</tr>
<tr>
<td>W + HNPK</td>
<td>120</td>
<td>24</td>
<td>60</td>
<td>12</td>
<td>420</td>
<td>84</td>
</tr>
<tr>
<td>W + HNPK + LCa : Mg</td>
<td>120</td>
<td>24</td>
<td>60</td>
<td>12</td>
<td>420</td>
<td>84</td>
</tr>
<tr>
<td>W + HNPK + MCa : Mg</td>
<td>120</td>
<td>24</td>
<td>60</td>
<td>12</td>
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<td>W + HNPK + HCa : Mg</td>
<td>120</td>
<td>24</td>
<td>60</td>
<td>12</td>
<td>420</td>
<td>84</td>
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<tr>
<td>Experiment 2</td>
<td>N</td>
<td>24</td>
<td>0</td>
<td>84</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>P</td>
<td>0</td>
<td>12</td>
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<td>Mg</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>65</td>
<td>0</td>
<td>0</td>
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</tbody>
</table>

per replicate per year was equivalent to 330 mm of rainfall for adult plants and 310 mm of rainfall for juvenile plants. Nutrient limitations can only be confidently assessed if geochemical processes that reduce nutrient availability are saturated, allowing plant nutrient requirements to be met (Chapin et al. 1986). To overcome geochemical fixation in these highly alkaline soils, we
limitations were removed, allowing additional effects of nutrient limitations to growth to be determined. The sandy, well-drained soils and wide plant spacing prevented soil resources from overlapping into other treatments.

Experiment 2

To determine how multiple resource limitations interact to influence *A. parryi* growth and function, we selected 80 similar-sized juvenile plants at the Playa site in March 2003. Neighbouring plants within a 1-m² area around the target shrubs were removed. Four soil resources (water, N, P, Mg), each at two levels (+ or −), were applied in a complete factorial design. The control treatment received no additional resources (i.e. water, N, P, Mg). The 16 treatment combinations were randomly assigned to plants in each of five blocks. Fertilizer and irrigation applications and rates were similar to those applied in experiment 1 (Table 2) but application rates per plant were therefore three times higher in this second experiment.

PLANT TISSUE SAMPLING AND ANALYSIS

Biomass and tissue nutrient samples were collected in July 2002 for experiment 1 and July 2003 for experiment 2. In experiment 1 leaf biomass was sampled by harvesting one-quarter of the hemispherical canopy from each adult plant (Messina et al. 2002; Snyder et al. 2004). In experiment 2 the entire canopy was harvested and roots were sampled by excavating a 45 cm wide × 45 cm deep hole around each plant. Previous sampling demonstrated that *A. parryi* rooting density is highest in this soil layer (Dahlgren et al. 1997). All excavated soil was placed in a basin and washed to separate roots from the sandy soil. Before grinding and analysis, root samples were triple rinsed with deionized water and all coarse roots (> 2 mm), dead roots and non-root material were removed. A similar triple rinsing procedure was followed for leaf samples to remove dust and surface salts. Plant tissue was analysed for N content by micro-Dumas combustion with a Carlo Erba NA1500 elemental analyser (Milan, Italy). For all other elements, samples were microwave digested with nitric acid following the method of Sah & Miller (1992) and analysed by inductively coupled-plasma atomic-emission spectrophotometry (Thermo Jarrell Ash Corp., Franklin, MA, USA).

SOIL SAMPLING AND ANALYSIS

Soils were sampled from the 10–40 cm depth layer in experiment 1 in all treatments. Three subsample cores were taken directly under the edge of the canopy of each adult plant and combined. Soil characteristics were measured on saturated paste extracts. Na⁺ and K⁺ were analysed by atomic absorption spectrophotometry and Ca²⁺ and Mg²⁺ by atomic emission spectrophotometry. Soil NO₃⁻ and NH₄⁺ were analysed following Carlson (1978), P and B were analysed colourimetrically following Murphey & Riley (1962) and Keren (1996).

INSTANTANEOUS GAS EXCHANGE AND PLANT WATER POTENTIAL

Instantaneous gas exchange and predawn (Ψₚ₀) and midday (Ψₚ₉) water potentials were measured on juvenile plants in experiment 2 only. Leaf gas-exchange was measured from 09.00 to 11.00 hours on all treatments using a LI-6400 (LiCor Inc., Lincoln, NE, USA) in mid-spring (23 and 24 May) and early summer (1 and 2 July) 2003. Sample CO₂ was 370 µ mol mol⁻¹. PPFD was maintained at an average ambient rate for the sampling period (1800 µ mol m⁻² s⁻¹), cuvette temperature was set to 28 °C, and relative humidity tracked ambient levels. Leaves within the cuvette were excised and scanned for leaf area using a desktop scanner and image analysis software (Scion Corp., 2000, Frederick, MD, USA, and Win RHIZO vs. 5.0 A software, Regent Instruments Inc., Saint-Foy, Canada). Treatment effects on gas exchange and on Ψₚ₀ and Ψₚ₉ were assessed only for the Control, Water, NPMg and Water + NPMg treatments. Measurements of plant water status were made on terminal leafy stems with a Scholander-type pressure chamber (PMS, Corvallis, OR, USA) following the procedures of Turner (1988) to minimize errors. Water potential measurements were made on the same days and plants used for gas exchange measurements.

STATISTICAL ANALYSIS

The main objective of the first experiment was to determine which resources were limiting plant growth by fitting treatment effects on leaf biomass and nutrient concentration to a conceptual model (Fig. 1). In this model the primary focus is how the relationship between individual nutrients and biomass changes across resource addition treatments rather than the interaction of all five response variables. Although this univariate approach allows for a direct application of our conceptual model, we first evaluated treatment effects on all leaf response variables (i.e. leaf biomass, N, P, K, Ca and Mg concentration) using multivariate analysis of variance (MANOVA) and contrasts because the response variables were strongly correlated. Because these comparisons were not orthogonal, sequential Bonferroni corrections were made to maintain an experiment-wise error rate of α = 0.05 (Rice 1989). When these MANOVA contrasts indicated significant differences between treatments, univariate ANOVA models were run on each of the five leaf response variables followed by univariate contrasts (Scheiner 1993; Tabachnick & Fidell 1996). Normality of residuals was evaluated using Shapiro Wilk tests on individual univariate models. Because MANOVA is robust against heterogeneity of covariance matrices (Scheiner 1993), particularly when cell sizes are equal (Tabachnick & Fidell 1996), no remedial measures were taken to correct univariate
heterogeneity of variance in the MANOVA models. However, when univariate approaches were used, the ANOVA models were weighted by the inverse of the variance to correct for heterogeneous variances among treatments (Neter et al. 1990).

Measured variables in experiment 2 that did not involve repeated sampling (i.e. biomass and nutrient concentrations) were analysed using ANOVA. Assumptions of ANOVA were tested and corrected following the same procedures used in experiment 1. Repeated-measures ANOVA was used for variables that involved repeated sampling of individual plants through the season (i.e. gas exchange and water potential) (Gurevitch & Chester 1986). Between-subject effects were block, water and NPMg. Within-subject effects were season and the interactions of season with the between-subject effects. Univariate analyses were used to test within-subject effects. When there were more than two levels of the within-subject factor and assumptions of sphericity were violated, Huynh-Feldt adjusted P-values were used to evaluate within-subject effects. Data were analysed with SAS (SAS Institute 2001).

Results

EXPERIMENT 1

Soils

Soil salinity (EC and Na), B and pH were higher at the Playa site than the Shoreline site (P < 0.05, Table 1). Values for soil stress factors and nutrient concentration in the control plots are similar to those previously reported from this study site (Dahlgren et al. 1997). Water addition lowered pH, EC, Na and B in both plots, reducing differences in soil stress factors between sites. Soil nutrient concentrations were low at both sites and were generally unaffected by water addition. An exception to this was the relatively high inorganic P found in soil solution at both sites. Due to the high soil pH, however, the majority of this P was in the form of $\text{H}_2\text{PO}_4^-$ as opposed to the more plant available $\text{H}_3\text{PO}_4^-$ (Kochian 2000). Application of slow-release KNO$_3$ created large differences in soil NO$_3^-$ availability (Table 2), and at the highest dose saturated paste K$^+$ increased from 0.95 to 6.23 mM. At the highest P dose, saturated paste inorganic P increased from 0.014 to 0.06 mM. Saturated paste concentrations of Ca and Mg rose from 0.09 to 0.2 mM and from 0.06 to 0.3 mM, respectively, when these elements were added. These increases in soil nutrient levels are within the range documented in adjacent, upland stands that are dominated by less stress-tolerant vegetation.

Plant growth and nutrient relations

Multivariate comparison of treatment effects on adult and juvenile plants within sites Because limitations within sites were of primary interest, treatment effects on the leaf response variables (i.e. total leaf biomass, and leaf N, P, K, Mg and Ca concentrations) were analysed separately for the Shoreline and Playa sites (Table 3). Control and watered adult plants did not differ significantly at either site and this comparison was therefore excluded from the subsequent univariate analyses. Both NPK supply and soil Ca : Mg and addition rates, however, significantly affected the leaf response variables of adult plants at both sites. Juvenile plants showed similar responses to both water and nutrient addition.

Univariate responses of leaf N, P, K, Mg and Ca and relationship with leaf biomass Univariate contrasts were run on the six leaf response variables (i.e. leaf biomass,

<table>
<thead>
<tr>
<th>Site</th>
<th>Stage</th>
<th>Treatment comparison</th>
<th>Wilks’ lambda</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoreline</td>
<td>Adult</td>
<td>Control vs. Water</td>
<td>0.768</td>
<td>1.45</td>
<td>0.2435</td>
</tr>
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<td>Water vs. average NPK</td>
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<td>Playa</td>
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and leaf N, P, K, Mg and Ca concentrations) and treatment effects on these responses were fitted to our conceptual model to evaluate nutrient limitations (Fig. 1).

At the Shoreline site, leaf N and leaf biomass both increased with higher rates of NPK supply (Fig. 2a). Both biomass and N concentration increased up to the mid rate of N supply but further increases in leaf biomass were not associated with concurrent increases in leaf N, indicating that N limitations had been overcome. Leaf biomass and P concentration also increased at higher rates of NPK supply, but the increase was only significant at the highest rate, indicating that P availability continued to limit growth. Both biomass and leaf Mg concentrations increased significantly with increasing soil Mg supply (i.e. decreasing soil Ca : Mg), suggesting that Mg was limiting growth once N and P limitations were removed. Increased plant growth due to increased NPK supply also resulted in a significant dilution of leaf Mg, with Mg concentrations declining over 1.6-fold with NPK addition. Increasing soil K and Ca again had no effect, suggesting that, as at the Shoreline site, they were not limiting growth.

Adult plants at the Playa site increased both leaf biomass and N and P concentrations when NPK was added at the lowest rate (Fig. 2b). Further increases in NPK supply resulted in increased growth but not leaf N, indicating that N supply was sufficient at the lowest rate, whereas leaf P continued to increase, indicating that P availability continued to limit growth. Both biomass and leaf Mg increased at higher soil Mg supply rates (i.e. decreasing soil Ca : Mg), suggesting that Mg was limiting growth once N and P limitations were removed. Increased plant growth due to increased NPK supply also resulted in a significant dilution of leaf Mg, with Mg concentrations declining over 1.6-fold with NPK addition. Increasing soil K and Ca again had no effect, suggesting that, as at the Shoreline site, they were not limiting growth.

Juvenile plants at the Playa plot increased leaf biomass and leaf N and P concentrations when soil NPK supply was increased (Fig. 2c), but the effect was only significant at the highest rate. It was not therefore
possible to determine if N and P limitations were overcome. The addition rates per plant may have been too low to create a significant dose response (adult leaf N concentrations exceeded 2%, even at the mid N supply rate, while juvenile concentrations never exceeded 1.5%). At the highest rate of NPK supply leaf Mg increased but no significant growth responses were observed, suggesting low N and P availability continued to be the primary growth limitation. Consistent with the adult plants, increasing soil K and Ca did not result in any significant change in leaf nutrient concentrations or biomass, suggesting soil K and Ca was not limiting growth.

Cation selectivity

Cation selectivity coefficients are an integrated measure of nutrient acquisition and allocation to leaves in different soil environments, such as declining nutrient availability and/or increasing salinity (Donovan et al. 1997). Selectivity coefficients are calculated as the leaf molar ratio of an elemental pair divided by their soil molar ratio (e.g. \( S_{\text{Mg,Na}} = \frac{\text{Leaf}_{\text{Mg,Na}}}{\text{Soil}_{\text{Mg,Na}}} \)). In control plants, \( S_{\text{Mg,Na}} \), \( S_{\text{Ca,Na}} \) and \( S_{\text{K,Na}} \) increased five-, four- and twofold between the Shoreline and Playa sites, indicating that plant uptake and allocation of Mg\(^{2+}\), Ca\(^{2+}\) and K\(^+\) to leaves relative to Na\(^+\) increased as relative soil availability declined (Fig. 3). \( S_{\text{Ca,Mg}} \) remained constant between the sites.

EXPERIMENT 2

Above-ground biomass

Plant growth was significantly affected by factorial alteration of the four soil resources \( (P < 0.0001) \). Over one growing season above-ground biomass of juvenile \( A. \text{parryi} \) increased over 16-fold when the supplies of water, N, P and Mg were increased (Fig. 4). These growth responses were driven by both effects of single resource manipulations and the interaction of multiple resource additions.

Effects of single resource manipulations Increasing N, P or Mg supply without water addition significantly increased shoot mass \( (P < 0.0001, P = 0.02, P = 0.0004, \text{Fig. 4}) \). There was no significant effect of water addition alone on shoot mass \( (P > 0.05) \).

Interaction of resources The effects of increasing supply of any resource on shoot mass depended on the supply rate of other soil resources (Fig. 5a–d; all four three-way interactions were significant, \( W \times N \times P (P = 0.03), W \times P \times Mg (P < 0.001), N \times P \times Mg (P < 0.001), W \times N \times Mg (P = 0.01) \), while the four-way interaction was not significant \( (P = 0.35) \)). For example, Mg addition significantly increased growth at both low and high rates of N and P supply \( (P = 0.0001, P < 0.0001, \text{Fig. 5a}) \) but the response was greater when both N and P were supplied at high rates relative to when either was supplied at lower rates \( (P < 0.0001) \). Similarly, the response to Mg addition was greatest when high rates of water and P were combined \( (P < 0.0001) \).

Although all the soil resources interacted to influence growth, soil N availability, as determined both by the rate of N and water supply, had the largest effect and was thus a major driver of most interactions (Fig. 5b,d).
Multiple resource limitations in deserts

For example, when both N and water were supplied, Mg addition resulted in a 1.6-fold increase in growth but Mg addition had no effect on growth when N supply was increased without water addition (Fig. 5b).

Tissue nutrient and toxic ion concentrations

N, P and Mg addition all significantly increased concentration of the respective element in leaf tissue, but in general, leaf nutrient concentrations depended on what other resources were manipulated concurrently (see data in Appendix S1 and statistics in Appendix S2 in Supplementary Material). Plants receiving water and N had 1.5-fold higher leaf N concentration than plants only receiving N, but water alone had no effect on leaf P and Mg. Increasing soil Mg predictably lowered leaf Ca : Mg but this decline was due to both an increase in leaf Mg concentration and a decline in leaf Ca. Leaf K increased in treatments receiving water and N (N was supplied as KNO₃). These resource effects on leaf K, however, were moderate, increasing less than 1.2-fold. Treatment effects on root nutrient concentrations were less pronounced than effects on leaf nutrient concentrations. N addition did not alter root N concentration significantly ($P > 0.05$, Appendices S1 and S2), although P and Mg additions raised root concentrations of these elements ($P < 0.0001$, $P = 0.01$). Altering soil Ca : Mg supply did not change root Ca : Mg and there were no consistent treatment effects on root Ca or K concentrations.

Leaf and fine root Na and B concentrations significantly decreased with water addition ($P < 0.0001$) but there was no effect of increasing N, P or Mg supply, either with or without water, on leaf and root Na or B. Leaf concentrations of Na and B, respectively, were: –W, 75.2 ± 1.0 g kg⁻¹ and 305 ± 8 mg kg⁻¹; +W 65.2 ± 1.2 g kg⁻¹ and 219 ± 9 mg kg⁻¹ (means ± SE, $n = 40$). Root Na and B concentrations, respectively, were: –W, 8.3 ± 0.5 g kg⁻¹, 138 ± 10 mg kg⁻¹, +W 6.2 ± 0.2 g kg⁻¹, 80 ± 3 mg kg⁻¹. Storage patterns were similar between treatments and elements; leaf tissue had > nine- and twofold higher Na and B concentrations than roots.

Effects of salinity on leaf cation nutrition were examined by calculating molar ratios of cation nutrients, Mg and Ca, relative to Na. Leaching of Na through irrigation increased leaf Mg : Na and Ca : Na (see data and statistics in Appendices S1 and S2). Treatment differences beyond the irrigation effects were mainly due to the differential effects of N, P and Mg addition on leaf nutrient status, rather than differences in leaf Na.

Leaf and fine root allocation

Plant leaf : fine root biomass was significantly affected by soil water and NPMg availability and this effect differed depending on the rate of water and NPMg supply ($P = 0.005$, Fig. 6). All plants receiving treatments without NPMg had a significantly lower leaf : fine root biomass than plants that received NPMg addition ($P < 0.0001$). Furthermore, plants that received NPMg and water had a significantly higher leaf : fine root biomass than plants that received NPMg alone ($P = 0.005$). Water addition alone, however, had no effect on leaf : fine root biomass ($P > 0.05$).
either May or July ($P > 0.05$) (Fig. 7). Photosynthesis increased with NPMg addition ($P = 0.01$) but this effect was similar regardless of water addition ($P > 0.05$) and did not differ between May and July sampling periods ($P > 0.05$). Changes in photosynthetic rate were small, increasing approximately 1.2-fold with NPMg addition. Photosynthetic water use efficiency (WUE) significantly increased with both water and NPMg addition ($P \leq 0.05$). These resource effects on WUE were similar across the season ($P > 0.05$) and were moderate, with approximately 1.5-fold increases in treatments receiving NPMg only relative to control plants. Water addition significantly improved $\Psi_{pd}$ and $\Psi_{md}$ in both May and June ($P < 0.05$); there was no effect of plant nutrient status on $\Psi_{pd}$ and $\Psi_{md}$ at either high or low water supply ($P > 0.05$) (Fig. 7). Although there was a significant decline in both $\Psi_{pd}$ and $\Psi_{md}$ through the season (main effect of season, $P < 0.001$) there was not a significant season $\times$ treatment interaction ($P = 0.29$), indicating plants experienced similar changes in $\Psi_{pd}$ and $\Psi_{md}$ through the season in all treatments.

**Discussion**

**RESOURCE LIMITATIONS IN SALINE-ALKALINE DESERTS**

Water, N and P limitations to plant growth in deserts have been demonstrated (Smith *et al.* 1997; Drenovsky & Richards 2004). Our results are consistent with N and P limitations but demonstrate an additional limitation of Mg at the most saline-alkaline site. Although Ca limitations were predicted by earlier studies in this community and in a similar system in the Great Basin (Richards 1994; Donovan *et al.* 1997), increasing Ca supply did not result in Ca accumulation or growth at either site or life stage. A similar lack of effect of K addition suggests that low soil K, or high soil Na$^+$ relative to K$^+$, was not limiting growth. Although there was no direct manipulation of other plant macro- or micronutrients, no significant changes of these elements occurred with plant growth, suggesting their availability did not limit growth (data not presented). Although there were gradients in soil toxic ions (Na and B) through the community, the high leaf concentrations of these elements do not appear to be major limiting factors to *A. parryi* growth. Leaching of soil Na and B in the water addition treatment decreased Na and B concentrations in juvenile *A. parryi* leaves as well as in adults (data not presented) but no positive effect on growth was observed. Leaf toxic ion levels in all treatments, for all life stages, were well below tolerance limits measured in sand culture (Richards 1994).

Unlike other work in deserts, our results suggest that water availability alone does not limit growth (Noy-Meir 1973; Fisher *et al.* 1988; Smith *et al.* 1997; Reynolds *et al.* 1999; but see Hooper & Johnson 1999). Experiment 1 encompassed wet and dry years, but no significant effects of water addition on growth or leaf nutrient concentrations were observed. Significant improvement in pre-dawn water status confirms that plants acquired water but did not use it to increase growth. A parallel
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study indicates that nutrient, but not water, addition increased *A. parryi* seed production and viability (A.N. Breen and J.H. Richards, unpublished data) and that seeds produced by fertilized plants were larger, germinated faster and resulted in seedlings that had higher survival rates under stressful soil conditions. Nutrients, N, P and Mg, which limit growth in this system, are therefore likely also to play a role in establishment and survival of seedlings.

The concept of resource limitations was developed in agricultural systems and has been utilized in many ecological studies to understand the major factors limiting individual plant, community and ecosystem processes. This approach requires high rates of resource addition to overcome soil biogeochemical fixation and abiotic loss, allowing enough resources to remain available to meet plant resource demand. However, measured responses represent the maximum potential for resource limitation, and resource manipulations must be compared with the natural resource dynamics of the study system. Our water additions in both experiments represented more than twice the amount of rainfall normally received but the absence of effects on growth, allocation or leaf-level physiology makes it likely that smaller, more ecologically relevant increases in water availability would not affect *A. parryi* performance. Although we applied nutrients at a high rate, water extractable nutrient pools only increased moderately. Soil $\text{NO}_3^-$ increased approximately sixfold from the low N addition rate (which was sufficient to saturate plant N demand) and the observed increase in soil $\text{NO}_3^-$ was similar to what occurs following spring precipitation pulses and N mineralization preceded by several drought years (Cui & Caldwell 1997; Z. Aanderud et al., unpublished data). The other nutrients (P, K, Ca, Mg) that are mainly supplied through weathering of parent material also increased (approximately four-, six-, five- and twofold, respectively) well within documented levels. Although a detailed understanding of community nutrient dynamics requires both measurements of pool sizes and estimates of pool turnover rates, our results indicate that changes in soil N availability that occur seasonally with varying precipitation inputs may interact strongly with changes in P and Mg availability that occur over successional time periods to influence the distribution of *A. parryi* specifically and the species composition and structure of saline-alkaline desert plant communities in general.

**RESOURCE INTERACTIONS DETERMINE PLANT GROWTH AND NUTRIENT STATUS**

At the high-stress site, plant growth increased when the three nutrients, N, P and Mg were added individually (Fig. 4), as predicted by the model and experiment 1 results (Figs 1 and 2). While some treatment combinations, such as N Mg, resulted in growth that was similar to the average response when N and Mg were supplied individually, factorial application of nutrients and water demonstrated that effects of resource addition on *A. parryi* growth were not strictly additive (Fig. 5). The supply rate of N, as determined by both rate of N addition and soil water availability, appeared to be a primary driver of these interactions, and therefore a major determinant of plant response to other resource limitations. For example, when NPMg was supplied, growth increased more than 3.5-fold relative to PMg addition. When water was supplied with NPMg, there was an additional threefold increase in growth. In general, the effect of Mg and P on growth depended on the supply rate of N, which in turn was influenced by soil water status. Not all interactions were positive. Some treatment combinations, such as PMg, resulted in lower growth responses than if either resource was supplied individually. These results demonstrate that the magnitude of response to altering the supply of one resource can influence plant response to other resource manipulations.

Low nutrient availability in desert soils is compounded by salinity and pH effects on nutrient availability (Lajtha & Schlesinger 1988; Marschner 1995; Lambers et al. 1998). While nutrient sufficiency levels are not well established for desert plants, leaf N and P levels in control plants were low relative to other reported values for desert plants (El-Ghony et al. 1978; Wentworth & Davidson 1987; Donovan et al. 1997). Although addition of limiting nutrients resulted in significant increases in leaf nutrient concentrations of the respective elements, there were both synergistic and antagonistic effects of nutrient addition on concentrations of other nutrients. For example, N addition stimulated P and Mg acquisition but P addition decreased Mg and Ca concentrations. Similar nutrient interactions are widely documented in agricultural systems but poorly understood in natural systems (Marschner 1995). In this experiment, it was not possible to determine if these responses were due to changes in soil chemical properties as a result of fertilization or plant physiological responses to nutrient imbalance. Concentrations of cation macronutrients relative to Na were consistent with reported values for other halophytic desert shrubs (Donovan et al. 1997), supporting the conclusion that salinity per se has little effect on growth, nutrient status or other plant functions in this system dominated by salt-tolerant halophytes.

**PLANT FUNCTIONAL RESPONSES**

Increasing levels of the four soil resources in this experiment resulted in over a 16-fold increase in above-ground biomass in a single growing season. The major mechanism driving these growth responses appears to be changes in biomass allocation between leaves and fine roots. The ratio of leaf to fine root biomass is a sensitive measure of functional allocation because it quantifies the amount of resource dedicated to instantaneous leaf photosynthetic rate relative to nutrient and water absorption in these perennial shrubs. In this study, water addition alone did not change allocation between leaf
and fine roots, while NPMg addition resulted in a four-fold increase in allocation to leaves relative to fine root biomass. When water was added with N, allocation to leaves increased over sixfold.

In contrast, changes in leaf level responses do not appear to be key mechanisms contributing to these growth responses. Although increasing soil water availability improved plant water status through the growing season, it did not increase instantaneous leaf photosynthetic rate or conductance. Increasing nutrient availability stimulated instantaneous leaf photosynthetic rate only slightly (c. 20%). For plants not receiving water, instantaneous WUE increased 1.5-fold in fertilized plants. Photosynthetic nitrogen use efficiency (PNUE) declined, however, because leaf N concentration increased 1.4-fold with only small changes in instantaneous leaf photosynthetic rate. This is consistent with the expected trade-off between leaf-level WUE and PNUE (Field et al. 1983). These changes in instantaneous WUE, like instantaneous photosynthesis, were moderate, consistent with the expectation of tight internal controls on photosynthesis in desert environments (Smith et al. 1997).

Taken together, these results suggest both that soil nutrient availability is the major driver of leaf vs. fine root allocation patterns and that changes in allocation appear to be much more important than changes in photosynthetic rates per unit leaf area or leaf level instantaneous WUE. A key functional trait of stress-tolerant plants, according to life-history theory, is slow, tightly regulated growth, in order to balance plant demand with the low resource supply rates typical in stressful systems. While similar nutrient-driven responses are well documented in systems dominated by fast-growing plants (Marschner 1995; Aerts & Chapin 2000), the magnitude of changes observed in allocation in this nutrient-poor environment were substantially greater than expected based on traditional life-history theory (Aerts & Chapin 2000; Grime 2001). However, similar large changes (threefold) in above-ground/below-ground allocation were also observed in transplants of *Sarcobatus vermiculatus* grown for 2 years at sites differing in nutrient availability in a Great Basin playa ecosystem (Donovan & Richards 2000).

**Implications**

Our results are consistent with current models that predict optimal allocation will balance resource supply and plant demand, resulting in multiple resource limitations (Bloom et al. 1985; Gleeson & Tilman 1992; Gleeson & Good 2003; Ho et al. 2004). A hierarchy of limiting resources, with N limitations producing the largest growth responses and P and Mg limitations producing equivalent, substantially smaller, growth responses, was apparent. A large N response, as reflected in both significant plant growth and increases in leaf : fine root biomass, is not surprising given the high demand and acquisition costs of N and extremely low N concentrations in desert soils.

Increased allocation to root growth to minimize N limitations might be expected to increase capture of the less limiting resources P and Mg, potentially resulting in a single limitation. However, nutrient-specific components to allocation have been demonstrated in nutrient-poor soils (Marschner 1995; Hinsinger 2001) and, although not directly quantified, may well occur in our system. For example, although high concentrations of Na and K can drastically reduce Mg uptake, *A. parryi* minimized limitation along the soil stress gradient by increasing selectivity for Mg relative to Na, similar to the cold desert halophyte *S. vermiculatus* (Donovan et al. 1997). Likewise, when all nutrients were supplied simultaneously, Ca uptake did not increase, while uptake of P and Mg did. This supports the idea that plant demand regulates nutrient uptake through changes in selectivity and that root growth does not necessarily result in simultaneous capture of multiple nutrients (Marschner 1995).

These observed patterns of resource limitations have major implications for understanding arid ecosystem responses to environmental change. Although there is strong evidence that soil nutrient availability is the major limitation to plant growth, our results suggest that the various nutrients interact to influence plant growth, physiology and allocation patterns. This suggests that perturbations that change nutrient availability will have the largest impacts on these desert plant communities, contrasting with expectations that changes in water availability or efficiency of water utilization will be most important in altering community and ecosystem properties (Melillo et al. 1993; Brown et al. 1997; Smith et al. 2000). It is therefore likely that desert plant community responses to accelerated N deposition, such as changes in productivity, stability and invasibility, will strongly depend on the relative availability of water and other nutrients. Multiple interacting resources limit the growth and distribution of *A. parryi* at our Mojave Desert site. We predict that similar interactions between multiple limiting resources may be instrumental in shaping community and species distributions along other abiotic stress gradients and are potentially important in defining ecotonal areas between major communities in resource-poor ecosystems.

**Supplementary material**

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC948/JEC948sm.htm

**Appendix S1** Experiment 2 treatment effects on *Atriplex parryi* leaf and fine root nutrient concentrations and nutrient cation molar ratios.

**Appendix S2** Experiment 2 treatment effects of water, N, P and Mg addition (source) on *Atriplex parryi* shoot mass, leaf elemental concentrations and leaf cation molar ratios.
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