

Nutrient relations of the halophytic shrub, *Sarcobatus vermiculatus*, along a soil salinity gradient

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Abstract

Recent water level declines of a saline and alkaline lake (Mono Lake, California, USA) have exposed large areas of former lake bottom substrates that have been sparsely colonized by the halophytic shrub, *Sarcobatus vermiculatus*. To increase understanding of the interaction of salt and nutrient relations in halophytes we investigated spatial and seasonal patterns of leaf elemental composition and growth for *Sarcobatus* along an extreme salinity gradient using four sites varying in age since exposure. Soil and groundwater Na and EC increased from non-saline at the site farthest from the Lake to highly saline at the site closest to the Lake. Leaf and stem length growth declined along this same transect. In June, when shoot growth rates were maximal, leaf Na paralleled substrate availability and reached a high of 130 g kg⁻¹ leaf dry weight near the Lake. Through the remainder of the growing season, plants on the lower salinity site continued to accumulate increasing amounts of leaf Na, whereas plants at the highest salinity site reached a plateau earlier in the season. The similarity of high leaf Na at all sites by the end of the season indicates a dominance of Na nutrition over the entire gradient, and a possible upper bound of Na accumulation and tolerance for this species. In June, *Sarcobatus* leaf N, P were higher at sites further from the Lake and did not correspond to soil N (total) and P that were highest near the Lake. Leaf K, Ca, and Mg in June also did not match substrate availability, and were low enough to indicate marginal sufficiency for growth. However, the increasing substrate Na did not interfere with K, Ca and Mg uptake based on selectivity coefficients (e.g. (leaf K/leaf Na)/(soil K/soil Na)) that did not decline with increasing substrate salinity. Uptake and transport to leaves, of K and Ca relative to Na, remained proportional to what was in the soil across the entire gradient of soil salinity. Uptake and transport of Mg relative to Na increased dramatically in inverse proportion to declining soil availability near the Lake, indicating that Mg may be a critical limiting factor for tolerance of high salinity sites. The key determinants of *Sarcobatus* growth and ecological dominance along this extreme salinity gradient (non-saline to highly saline) are the propensity to accumulate large amounts of leaf Na over the entire gradient, and the ability to maintain adequate uptake of N, P, K, Ca, and Mg under highly variable substrate combinations of nutrients and Na.

Introduction

Leaf ion content and nutritional status of desert halophytes growing along ecological salinity gradients are influenced both by substrate characteristics and by plant ion physiology. Halophytes have evolved ion physiology characteristics that allow them to cope with

the multiple challenges of saline substrates: toxic ion effects, nutrient limitations, and osmotically reduced water availability (for reviews see Flowers et al., 1977; Osmond et al., 1980; Ungar, 1991). A major feature of the ion physiology of halophytes as compared to glycophytes is the quantitatively greater Na uptake and transport to leaves. Halophytes are thought to use high Na concentrations in leaves to create and maintain water potential gradients and turgor necessary for

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water uptake and growth, with Na sequestered primarily in vacuoles and osmotically balanced by compatible solutes in cytoplasm (Flowers et al., 1977; Gorham et al., 1980; Storey et al., 1977; Yeo, 1983). Greater Na uptake and transport to leaves in halophytes than in glycophytes involves lower selectivity against Na by membranes in the root and during ion transport from roots to leaves (Cheeseman, 1988; Niu et al., 1995; Reimann and Breckle, 1993). The halophyte need for uptake and accumulation of Na interacts with uptake of the cation macronutrients, K, Ca, and Mg, leading to relatively low leaf ratios of cation nutrient/Na (Albert and Popp, 1977; Gorham et al., 1980). This may result in cation nutrient deficiencies. In addition, desert halophytes often face additional stresses of low available N and P, and high B (Albert and Popp, 1977; Caldwell, 1974; Charley and West, 1975).

To increase understanding of the interaction of salt and nutrient relations in halophytes we analyzed leaves of the halophytic shrub *Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae; common name greasewood) and soil from an extreme soil salinity gradient on the north shore of Mono Lake, California. Mono Lake, one of the oldest lakes in the Great Basin of North America, is very saline and alkaline. Its water level has fluctuated due to long-term climate changes and has declined since 1940–41 due to anthropogenic influences, exposing large areas of extremely saline soils. The oldest site included in this study has been exposed for at least 500 years and the sand dune soils there have been leached of salts, making the site technically non-saline (Donovan et al., 1996; Schaber and Richards, 1995; Toft, 1995). This site supports a mixed shrub community where *Sarcobatus* is dominant. *Sarcobatus* is also the primary colonizer of the most recently exposed, highly saline lacustrine and shoreline substrates, where a salt crust is a visible component of the soil in some seasons (Richards et al., 1994). This salinity gradient is representative of saline soils and salt-tolerant vegetation common in western North America, where the desertification associated with post-glacial climate change has been recorded in the declining levels and even disappearance of many Pleistocene lakes in the Great Basin. Exposed shorelines and former lakebeds there are usually occupied by halophytic, chenopod shrubs (Gates et al., 1956; Vasek and Lund, 1980; Wallace et al., 1973; West, 1988).

Sarcobatus is a succulent-leaved, salt-tolerant, Na-accumulating shrub that is often, but not necessarily, associated with saline soils (Donovan et al., 1996; Fire-

man and Hayward, 1952; Gates et al., 1956; Shantz and Piemeisel, 1940). It is a halophyte according to the definition of Flowers et al. (1977), i.e. a plant that can survive and complete its life cycle on high salinity substrates. Although it is unclear whether *Sarcobatus* requires some low level of Na for optimal growth (Glenn and O'Leary, 1984; McNulty, 1969), it does tolerate high salinity in the field (soil electrical conductivity (EC) values for saturation extracts up to 23.8 dS m⁻¹; Gates et al., 1956) and under laboratory conditions (up to 1 M NaCl; Glenn and O'Leary, 1984; McNulty, 1969). *Sarcobatus* leaf cation status and soil salinity have been documented for isolated populations and in controlled experiments (Donovan et al., 1996; Eddleman and Romo, 1987; Fireman and Hayward, 1952; Glenn and O'Leary, 1984; McNulty, 1969; Richards, 1994; Rickard, 1965, 1982; Schaber and Richards, 1995; Wallace et al., 1973). However, salinity-nutrient relationships in *Sarcobatus*, especially along a natural salinity gradient, have not been investigated.

The objective of this study was to use spatial and seasonal patterns of variation in *Sarcobatus* nutrient physiology over a gradient of abiotic conditions from non-saline to seasonal salt crust sites to improve understanding of salinity-nutrient relationships in halophytes and to provide insight into physiological characteristics of *Sarcobatus* that may allow it to be ecologically dominant under both high and low salinity conditions. Based on *Sarcobatus* and typical halophyte characteristics, we hypothesized that: 1) *Sarcobatus* would accumulate Na in leaves in proportion to Na available in the substrate, 2) higher soil and plant Na would lead to deficiencies in cation nutrients (K, Ca, Mg), reflected in absolute leaf concentrations, leaf cation/Na ratios, and declining selectivity coefficients [(leaf cation/Na)/(soil cation/Na)], and 3) *Sarcobatus* N and P would reflect soil availability patterns, with greater deficiency indicated when the substrate was more saline or alkaline.

Materials and methods

This study was conducted on the north shore of Mono Lake, California, USA, (38°5' N, 118°58' W). Mono Lake is in a closed hydrologic basin at the western edge of the Great Basin biogeographic province. Climate at the site is arid (mean annual precipitation = 163 mm; Toft, 1995), with precipitation of 205 and 210 mm during 1993 and 1994, respectively. This study is part of a larger ecosystem study being conducted on a 0.7 by

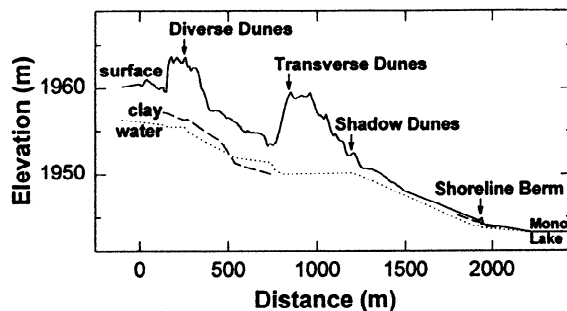


Figure 1. Elevation transect of the study plot on the north shore of Mono Lake, CA, USA showing topography, sampling site locations (labelled arrows), depth to lacustrine clay and depth to groundwater. Transect extends from north (0 m) to south (2400 m).

2.4 km plot, where elevations range from 1943 to 1963 m a.s.l. (Figure 1). The four sampling sites represent substrates exposed by receding Mono Lake waters for differing amounts of time.

The Diverse Dunes sampling site at 250 m along the N-S transect (Figure 1), furthest from the Lake, has not been inundated by the Lake for at least 500 years. This site supports the most diverse flora (at least 41 species) and has the most variable topography among our four study sites. The dominant shrub species are *Sarcobatus* and *Chrysothamnus nauseosus* (Palla.) Britt. ssp. *consimilis* (E. Greene) H.M. Hall and Clements, with 5.2% and 2.2% cover, respectively. Other less abundant species include the shrubs *C. viscidiflorus* (Hook.) Nutt. ssp. *viscidiflorus*, *Tetradymia tetrameres* (S.F. Blake) Strother, *T. canescens* DC., *T. glabrata* Torrey and A. Gray, *Atriplex canescens* (Pursh) Nutt., *A. confertifolia* (Torrey and Fremont) S. Watson, as well as saltgrass, *Distichlis spicata* (L.) E. Greene, and several perennial and annual herbaceous species.

The three other sites, Transverse Dunes, Shadow Dunes and Shoreline Berm, at 850, 1200, and 1900 m along the transect, are progressively younger and closer to Mono Lake (Figure 1). *Sarcobatus* canopy cover at these three sites is 2.5%, 0.4% and 0.05%, respectively. *D. spicata* is the only other perennial plant species at the Transverse and Shadow Dunes sites. The Transverse Dunes site is a recently sand-covered offshore bar that formed when the Lake level was higher, and was last inundated 70–80 years ago. Shadow Dunes formed behind former shoreline ridges built by Mono Lake in 1955–1957, i.e. about 40 years ago. The Shoreline Berm at 1900 m was formed in 1984–6 and was 1.5–2 m elevation above the Lake in 1993–4 during the course of this study. The Shoreline Berm

site represents an isolated population of plants that is approximately 700 m downslope from the nearest other *Sarcobatus* plants at the Shadow Dunes (Richards et al., 1994). As a phreatophyte, *Sarcobatus* has extensive deep roots capable of reaching groundwater at depths to 13 m (Harr and Price, 1972; Robinson, 1958), and it is rooted to groundwater at each of the sites in this study (see Figure 1 for groundwater depths). Thus, *Sarcobatus* has the potential to acquire nutrients and salts from both groundwater and soil.

Groundwater access holes were installed at each site in 1994. Soils were collected with a bucket-auger at 50 cm depths from the surface to groundwater to determine stratigraphy. Groundwater depth and electrical conductivity (EC, dS m^{-1}) were measured on eight dates in 1994 and 1995 and groundwater pH was determined once in 1994. Groundwater was sampled in mid-1994 and mid-1995 for elemental analysis. B and P were measured on an inductively-coupled-plasma atomic-emission spectrophotometer (ICP-AES, Thermo Jarrell Ash Corp., Franklin, MA, USA), and Na^+ , K^+ , Mg^{2+} , Ca^{2+} , SO_4^{2-} , NO_3^- , NH_4^+ were determined with a Dionex 4500 ion chromatograph (Sunnyvale, CA, USA).

Soils were collected from beneath three shrubs at each site. *Sarcobatus* has a dense shallow root system in addition to its deep taproot (Donovan et al., 1996), so we sampled soils at 5, 25 and 200 cm depths, at the Diverse, Transverse, and Shadow Dunes sites, in fall 1992. A compressed profile was sampled at the Shoreline Berm (summer 1993) because there was only a 30–50 cm rooting zone above anaerobic, saturated substrates. Soil data from the different sampling dates were combined for statistical analysis because other soil analyses at this site indicated that fall 1992 and summer 1993 were not significantly different (Schaber and Richards, 1995). Soils were water-extracted to assure dissolution of all soluble salts (1 part dry soil to 5 parts water, weight:weight). The 1:5 soil extract was analyzed for EC and pH, and for Na, K, Ca, Mg, B, S, and P on the ICP-AES. Data are presented as g element per kg dry soil. Values for saturation extracts were 14.1 times greater than values for the 1:5 extracts (linear $r^2 = 0.99$; Schaber and Richards, 1995). Total soil N was determined using a Carlo Erba NA1500 nitrogen analyzer (Milan, Italy).

Sarcobatus phenology was recorded in 1993 and 1994 and was similar. Leaf and shoot lengths were measured for 8 reproductively mature shrubs at each site on five dates during the 1994 growing season. Leaf elemental composition was determined for each shrub

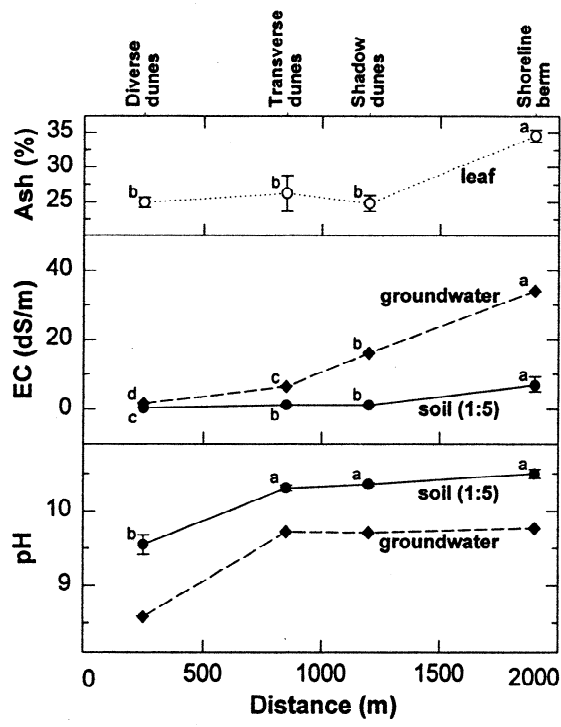


Figure 2. EC and pH for 1:5 soil extracts and groundwater, and % leaf ash for *Sarcobatus vermiculatus* leaves in June 1993 at the four sampling sites along the transect. Site means with the same letter are not significantly different. Data are means \pm SE. For each point, $n=3-4$ for leaf ash, $n=8-9$ for soil EC, soil pH, and groundwater EC, and $n=1$ for groundwater pH. Results of statistical analyses are in Table 1.

sampled on June 23, September 16, and October 16, 1993. The June samples were mature leaves collected at the peak of the growing season, September samples were mature leaves collected just prior to or in initial stages of senescence, and October samples were senescent leaves collected just prior to being shed. After drying at 60 °C, ground leaves were extracted with acid dissolution and microwave digestion (Sah and Miller, 1992). Extracts were analyzed for Na, K, Ca, Mg, B, S and P on the ICP-AES. Leaf tissue was also analyzed for N with the Carlo Erba nitrogen analyzer, and for % ash by combustion for 6 hrs at 520 °C.

Site effects for June leaf elemental composition and extractable soil elements were analyzed statistically with ANOVA, and mean separations were determined with the REGWF multiple-range test (SAS, 1989). The soil analysis included depth nested within each site. Seasonal leaf elemental composition and leaf and shoot growth involved repeated sampling of individual plants, and were analyzed with repeated-measures

ANOVA (SAS, 1989; Von Ende, 1993). The between-subjects effect was site: Diverse Dunes, Transverse Dunes, Shadow Dunes, and Shoreline Berm. Within-subjects effects were time and the time by site interaction. Univariate analyses and Huynh-Feldt (H-F) adjusted p values were used for testing within-subjects effects for leaf elemental composition. Mauchly's criterion was used to test for sphericity and indicated no significant departure from compound symmetry for most chemical variables. For the variables where there was a significant departure, the results of the H-F adjusted p concurred with unadjusted p values (Von Ende, 1993). Results of multivariate analyses were used for the growth analyses because of sphericity problems, but the results concurred with the univariate results. When necessary variables were log transformed to meet assumptions of: normality, equivalent variance of residuals, and/or Mauchly's criterion for sphericity. For these variables, back-transformed means and standard errors are presented.

Results

Along the transect from the Diverse Dunes site towards Mono Lake the depth of dune sand overlying the buried lacustrine clay layer and depth to groundwater decreased (Figure 1). Accompanying this decrease in depth to groundwater was a significant increase in groundwater EC, up to 34.0 dS m⁻¹ at the Shoreline Berm, where groundwater was only ~70 cm beneath the surface (Figure 2). Mono Lake water had an EC of 64.7 dS m⁻¹ at the time of this study. The pH of groundwater also varied, increasing from 8.6 in the Diverse Dunes to 9.7 at the Shoreline Berm.

The sampling sites also differed in EC and pH of soil extracts (Figure 2). From Diverse Dunes to Shoreline Berm, the EC of 1:5 soil extracts increased significantly from 0.36 to 6.89 dS m⁻¹, and the pH increased significantly from 9.6 to 10.5. Although there were also significant differences in EC, pH and elemental composition of the soil extracts for the three depths at each site, depth accounted for <15% of the variation, with the exception of P (Table 1).

The concentrations of potentially toxic Na and B increased in the soil and groundwater with increasing proximity to the Lake (Figure 3, Table 1). This same pattern was found in the leaves of *Sarcobatus* in June, with leaves at the Shoreline Berm having accumulated Na to 130 g kg⁻¹ leaf of the dry weight. This was significantly higher than the 64 to 86 g kg⁻¹ Na in

Table 1. Analysis of variance for soil extract elemental composition (effects are site and depth nested within site), groundwater elemental composition (effect is site), and June 1993 leaf elemental composition (effect is site). Presented for each effect are an *F* statistic, significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ^{ns} $p > 0.05$), and degrees of freedom for numerator (dfn) and denominator (dfd). Means and SEs for the variables compared here are in Figures 2–4

	<i>F</i>		<i>F</i>	
	Site	dfn, dfd	Depth (site)	dfn, dfd
<i>Soil</i>				
pH	39.9***	3,35	1.5 ^{ns}	8,35
EC (dS m ⁻¹)	173.7***	3,35	15.5***	8,35
N (g kg ⁻¹)	117.3***	3,35	6.7***	8,35
Na (g kg ⁻¹)	165.6***	3,35	12.9***	8,35
K (g kg ⁻¹)	133.8***	3,35	25.2***	8,35
Ca (g kg ⁻¹)	6.4**	3,35	1.9 ^{ns}	8,35
Mg (g kg ⁻¹)	45.7***	3,35	4.6**	8,35
B (g kg ⁻¹)	129.0***	3,35	6.7***	8,35
P (g kg ⁻¹)	14.6***	3,35	23.6***	8,35
S (g kg ⁻¹)	97.8***	3,35	8.2***	8,35
K/Na (molar ratio)	93.4***	3,35	0.9 ^{ns}	8,35
Ca/Na (molar ratio)	125.2***	3,35	6.1***	8,35
Mg/Na (molar ratio)	63.2**	3,35	3.0*	8,35
<i>Groundwater</i>				
EC (dS m ⁻¹)	326.7***	3,29		
N (mM)	0.3 ^{ns}	3,5		
Na (mM)	12.7**	3,5		
K (mM)	10.8*	3,5		
Mg (mM)	8.8*	3,5		
B (mM)	34.6**	3,4		
P (mM)	99.4***	3,4		
S (mM)	8.4*	3,5		
K/Na (molar ratio)	5.7*	3,5		
Mg/Na (molar ratio)	1.7 ^{ns}	3,5		
<i>Leaf (June)</i>				
Ash (%)	9.5**	3,14		
N (g kg ⁻¹)	14.6***	3,14		
Na (g kg ⁻¹)	16.2***	3,14		
K (g kg ⁻¹)	6.7**	3,14		
Ca (g kg ⁻¹)	10.2**	3,14		
Mg (g kg ⁻¹)	0.5 ^{ns}	3,14		
B (g kg ⁻¹)	12.2***	3,14		
P (g kg ⁻¹)	6.6**	3,14		
S (g kg ⁻¹)	4.4*	3,14		
K/Na (molar ratio)	11.6***	3,14		
Ca/Na (molar ratio)	25.9***	3,14		
Mg/Na (molar ratio)	6.5**	3,14		

leaves at the other sites in June. Na was the primary contributor to the increased leaf ash content (%) at sites closer to the Lake (Figure 2, Table 1).

Total soil N was very low ($<0.2 \text{ g kg}^{-1}$) at the Diverse, Transverse, and Shadow Dunes sites (Figure 3, Table 1). It was significantly higher (2.0 g kg^{-1}) at the Shoreline Berm. Groundwater N, determined as NO_3^- since no NH_4^+ was detected, was also relatively low, but did not vary significantly among the sites along the transect. In June, *Sarcobatus* leaf N was lowest at the Diverse Dunes (22 g kg^{-1}), and was exceptionally high for plants at the Transverse Dunes where it reached 42 g kg^{-1} . This is the site where growth started earliest (see below). The site variability in leaf N did not reflect the patterns in soil or groundwater N, as the highest leaf N was associated with the site that had the lowest soil N and groundwater N did not vary significantly between sites. Soil and groundwater P were both maximal at the Shoreline Berm, opposite the pattern of June leaf P which was minimal at that site. Soil, groundwater and June leaf S were lowest at the Diverse Dunes and were highest at the Shoreline Berm.

The major cation macronutrients, K, Mg, and Ca, differed in their availability patterns across the site (Figure 3, Table 1). Soil and groundwater K were lowest at the Diverse Dunes and increased towards the Lake. June leaf K was highest at the Diverse Dunes and significantly lower at all remaining sites, a pattern opposite to substrate K availability and leaf Na concentrations. Soil Mg was high at the Diverse and Transverse Dunes sites, and then declined significantly with increasing proximity to the Lake. Groundwater Mg was opposite that of the soil, with lowest values found at the Diverse Dunes and significantly greater values towards the Lake. The variability in soil and groundwater Mg availability appeared to be integrated by *Sarcobatus*, for which the June leaf Mg values did not differ significantly among sites. Soil Ca was less consistent across sites, and was lowest at the Shadow Dunes. Groundwater Ca was very low at Diverse Dunes, Shadow Dunes and Shoreline Berm sites, but sites could not be compared statistically since Ca was sampled only once. Leaf Ca varied across the sites with Transverse Dunes and Shoreline Berm values significantly lower than the other two sites.

Nutritional status of *Sarcobatus* relative to site salinity was examined by calculating molar ratios of cation elements in leaves: K/Na, Mg/Na, Ca/Na. All three molar ratios for *Sarcobatus* leaves were highest at the Diverse Dunes and decreased significantly

with increased proximity to the Lake (Figure 4, Table 1). The significant site differences in soil molar ratios showed the same pattern, with the highest values at the Diverse Dunes.

Selectivity coefficients for K, Mg, and Ca relative to Na, $S_{[\text{K,Na}]}$, $S_{[\text{Mg,Na}]}$, $S_{[\text{Ca,Na}]}$, are the quotients of leaf molar ratio divided by the appropriate soil molar ratio. As calculated here, these selectivities represent an integrated, ecological measure of acquisition of each of the cations into leaves under differing levels of Na (and the nutrient) in the soil and result from selectivity at multiple locations in the plant. Since the decline in the K/Na molar ratio in leaves and soil were proportional, the resulting $S_{[\text{K,Na}]}$ was remarkably constant (approximately 2) for all of the sites (Figure 4, Table 1). The value of $S_{[\text{Ca,Na}]}$ also remained fairly constant, 3–5, across the sites. In contrast, the $S_{[\text{Mg,Na}]}$ increased greatly with proximity to the Lake, especially at the Shoreline Berm, indicating that the decline in Mg uptake to leaves relative to Na uptake was not proportional to the decline in Mg availability relative to Na in the soil. Thus, for growing *Sarcobatus* leaves in June $S_{[\text{K,Na}]}$ and $S_{[\text{Ca,Na}]}$ were relatively stable across the four sites, but $S_{[\text{Mg,Na}]}$ increased dramatically.

Variation in seasonal nutrient status of *Sarcobatus* leaves was examined to determine if the patterns established by June were maintained. Significant site differences observed in June leaf elemental composition were generally confirmed in the repeated measures ANOVA that took into account all three sampling dates (Figure 5, Table 2). However, there were also significant time effects and time by site interactions, which indicated seasonal changes and different seasonal patterns among the sites. Overall, leaf N declined through the season, but the decline was smallest at Shoreline Berm. While leaf Na, B, Ca, and Mg generally rose through the season, differences among sites became greater for B, Ca, and Mg. As the season progressed the sites became more similar for leaf Na. Seasonal variation in leaf K was not significant.

Leaf growth of *Sarcobatus* began earliest at the Transverse Dunes site, but by June there was no difference in leaf length or extension rate for the three sites farthest from the Lake (Figure 6, Table 2). By the end of the season leaf lengths varied among the sites, with the longest leaves at the sites farthest from the Lake. Shoot extension was maximal in June, after the still expanding leaves had reached 54–71% of their final lengths. Leaf and shoot growth were lower in June and through most of the growing season at the Shoreline Berm site. By continuing shoot growth after

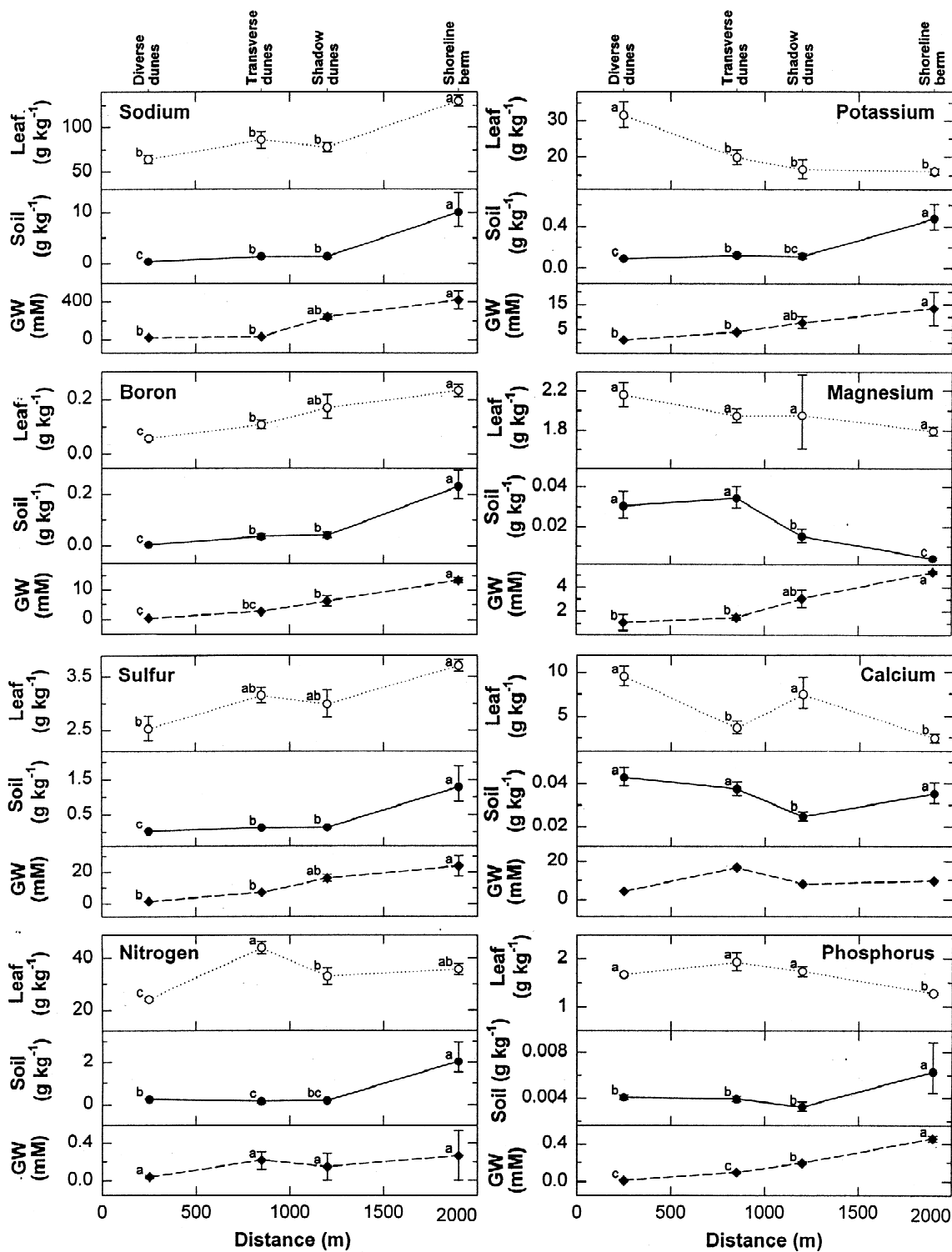


Figure 3. Elemental composition of *Sarcobatus vermiculatus* leaves (June 1993), 1:5 soil extracts (average across depths), and groundwater at the four sampling sites along the transect. Nitrogen values are total N in leaves or soil, but nitrate-N in groundwater (ammonium was negligible). Site means with same letter are not significantly different. Data are means ± 1 SE. For each point, $n=3-4$ for leaves, $n=8-9$ for soils, and $n=2-3$ for groundwater except for groundwater Ca where $n=1$. Results of statistical analyses are in Table 1.

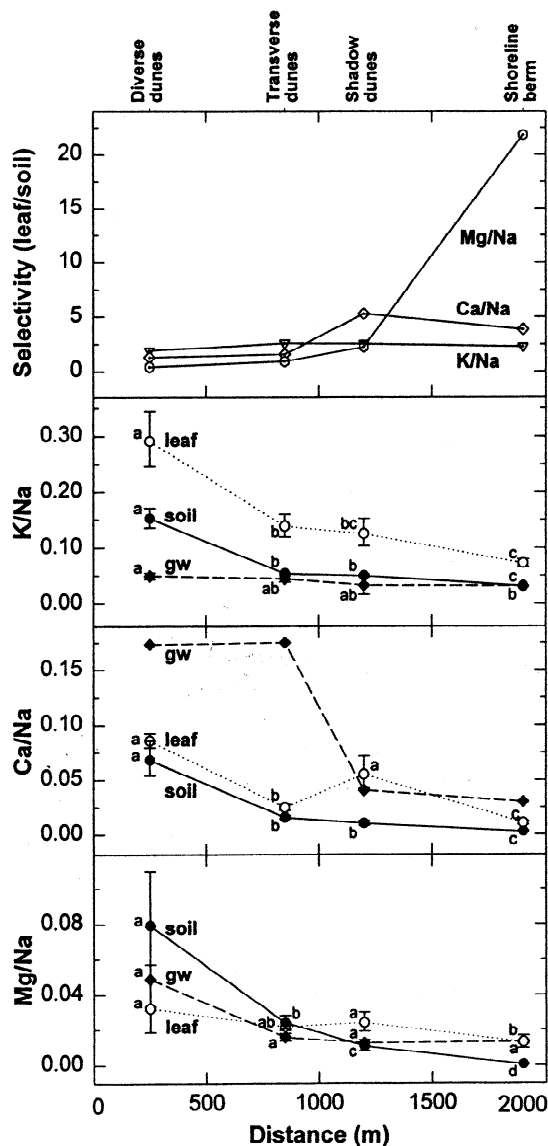


Figure 4. Selectivity coefficients for elemental pairs (upper panel) and molar ratios of K/Na, Ca/Na, and Mg/Na for soil, groundwater, and *Sarcobatus vermiculatus* leaves (June 1993) at the four sampling sites along the transect. Selectivity coefficients for each elemental pair were calculated as leaf molar ratio/soil molar ratio (see text). Site means with same letter are not significantly different. Data are means \pm 1 SE. For each molar ratio point, $n=3-4$ for leaf, $n=8-9$ for soil, $n=2-3$ for groundwater except for groundwater Ca/Na where $n=1$. For selectivity coefficients, $n=1$. Results of statistical analyses are given in Table 1.

growth had stopped at the other sites, however, the plants at this site achieved final shoot lengths not different from shoot lengths at the Transverse and Shadow

Dunes sites. Maximum shoot lengths were nearly 50% greater at the Diverse Dunes than at the other sites.

Discussion

The sampling sites differ in time since exposure by receding Mono Lake waters and represent a typical spatial sequence radiating out from Great Basin saline, alkaline lakes and playas. Soil and groundwater EC, pH, and Na and B concentrations were lowest at the Diverse Dunes and increased towards Mono Lake to levels detrimental to plant growth. This overall salinity gradient was reflected in *Sarcobatus* growth, with greatest shoot growth observed at the longest exposed, least saline site (Diverse Dunes). The soils along the sampling gradient range from non-saline by agricultural standards (Richards, 1954) to among the most saline recorded for *Sarcobatus*. As expected, *Sarcobatus* accumulated Na in its leaves, to levels associated with decreased growth in controlled environment studies (Glenn and O'Leary, 1984; Richards, 1994). Our highest leaf Na values of 150 g kg^{-1} exceed previous reports for *Sarcobatus* (Glenn and O'Leary, 1984; Richards, 1994; Rickard, 1965, 1982; Rickard and Keough, 1968). As hypothesized, leaf Na in June, when shoot growth rates were maximal, roughly paralleled substrate availability along the ecological salinity gradient at Mono Lake (Figures 3 and 6).

Seasonal increases in leaf Na at several sites, which are consistent with one previous report for *Sarcobatus* (Rickard and Keough, 1968), changed this relationship, however. The seasonal increase in Na and ash content has been shown to be accompanied by an increase in leaf succulence for *Sarcobatus* plants sampled near the Diverse Dunes in 1994 (Donovan et al., 1996). Plants at the Shoreline Berm were unique in achieving extremely high Na early in the season, and then maintaining the same approximate leaf Na concentration and steady leaf and shoot growth through the season. These seasonal patterns of Na accumulation led to results that contrasted with expectations of plant Na paralleling substrate Na; plants at all sites had leaf Na $> 115 \text{ g kg}^{-1}$ late in the growing season and thus were remarkably similar given the underlying salinity gradient (Figures 3 and 5). Although leaves may have been shed after reaching such high Na concentrations, we did not observe substantial leaf fall at our sites during the growing season.

High substrate Na, in addition to any direct toxic effects, presents both a water relations and a nutrition-

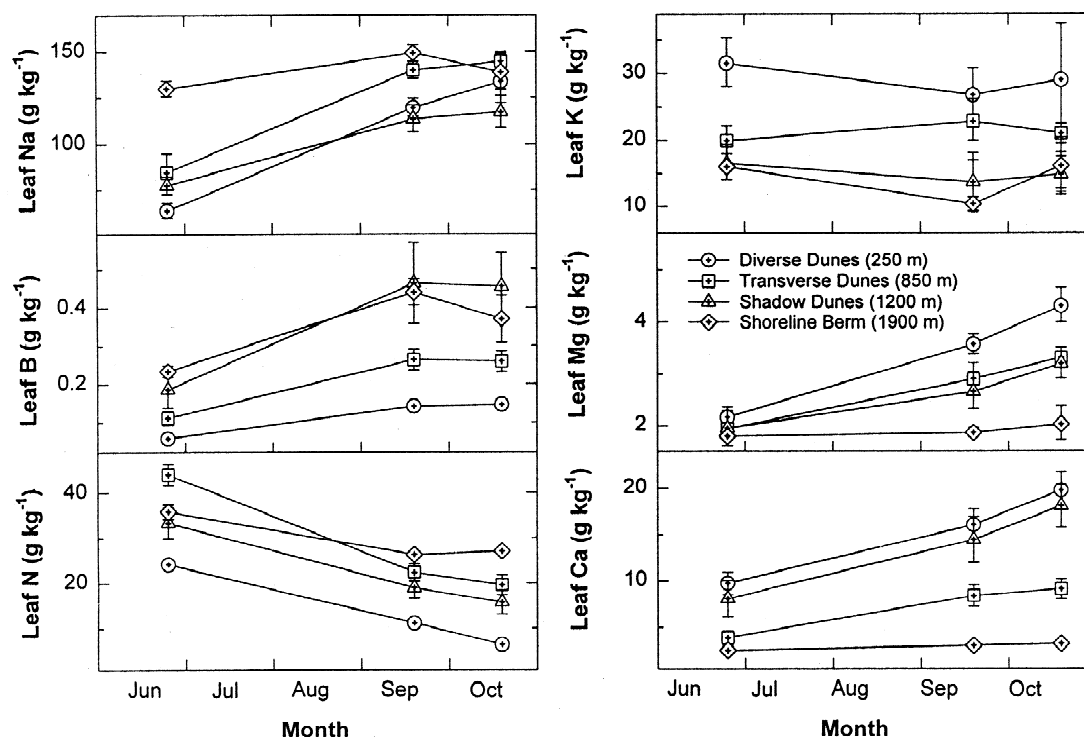


Figure 5. Seasonal changes in elemental composition of *Sarcobatus vermiculatus* leaves at each of four sampling sites. Data are means \pm 1 SE, $n=3-5$ for each point. Results of repeated-measures statistical analyses are given in Table 2.

Table 2. Results of repeated-measures analysis of variance for 1993 seasonal leaf elemental analysis and ash content and for 1994 leaf and shoot length measurements. Between-subjects effect is site, and within-subjects effects are the time (month) and time by site interaction. See methods for more on the repeated-measures analyses. Presented for each effect are an F statistic, significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ^{ns} $p > 0.05$), and degrees of freedom for numerator (dfn) and denominator (dfd). Means and SEs for most of the variables compared here are in Figures 5–6. Seasonal values for S, P, molar ratios, and ash are not shown

	Between-subjects		Within-subjects		F	
	F	dfn, dfd	F	dfn, dfd	Time \times site	dfn, dfd
Leaf length (mm)	103.2***	3,28	5272.2 ***	4.25	9.1***	12,81
Shoot length (cm)	15.7***	3,28	1424.6***	4.25	6.8***	12,81
Ash (%)	3.3 ^{ns}	3,12	92.1***	2.24	6.4***	6,24
N (g kg^{-1})	20.2***	3,12	252.3***	2.24	9.0***	6,24
Na (g kg^{-1})	10.9***	3,12	83.4***	2.24	7.4***	6,24
K (g kg^{-1})	5.2*	3,12	3.1 ^{ns}	2.24	1.9 ^{ns}	6,24
Ca (g kg^{-1})	16.0***	3,12	134.8***	2.24	15.8***	6,24
Mg (g kg^{-1})	7.0**	3,12	47.3***	2.24	3.6*	6,24
B (g kg^{-1})	7.4**	3,12	58.2***	2.24	3.4*	6,24
P (g kg^{-1})	2.3 ^{ns}	3,12	138.1***	2.24	6.6***	6,24
S (g kg^{-1})	4.9**	3,12	149.1***	2.24	6.5***	6,24
K/Na (molar ratio)	6.5**	3,12	60.1***	2.24	13.3***	6,24
Ca/Na (molar ratio)	53.2***	3,12	8.8***	2.24	2.1 ^{ns}	6,24
Mg/Na (molar ratio)	15.3***	3,12	2.8 ^{ns}	2.24	0.2 ^{ns}	6,24

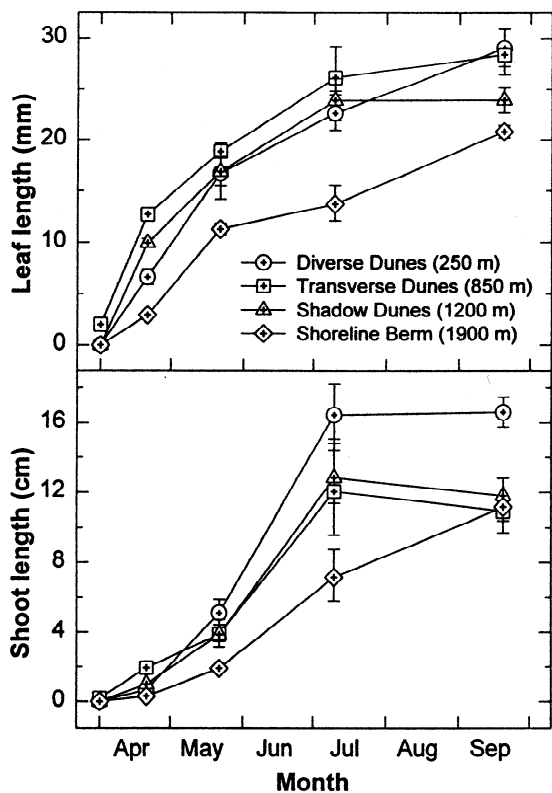


Figure 6. Seasonal pattern of *Sarcobatus vermiculatus* leaf and shoot growth at the four sampling sites. Data are means \pm 1 SE, $n=8$ for each point. Results of repeated-measures statistical analyses are given in Table 2.

al challenge for plants (Flowers et al., 1977; Niu et al., 1995). For *Sarcobatus*, Na uptake necessary for osmoregulation can start as soon as seedlings germinate, allowing the seedlings to maintain water uptake, turgor, and growth (Eddleman and Romo, 1987; Romo and Haferkamp, 1987). On the basis of controlled environment experiments over short time periods, Glenn and O'Leary (1984) previously classified *Sarcobatus* as an osmoconformer, i.e. a plant that regulates Na to maintain plant osmotic potential proportional to water potential of the substrate. In our study, the end-of-season similarity of leaf Na for plants on soils varying in salinity suggests more of an osmoregulator capacity for *Sarcobatus*. Although we can not adequately distinguish between osmoconforming and osmoregulation without additional soil and plant water relations data, our results suggest that *Sarcobatus* takes up more Na than required to maintain water potential gradients sufficient for water uptake and growth. These high leaf Na levels raise the question as to whether *Sarcobatus*

predawn water potentials are in approximate equilibrium with the wettest soil layers or groundwater accessed by its roots (Donovan et al., 1996).

In saline and alkaline soils, availability of the cation macronutrients -K, Ca, Mg- may also be limited (Marschner, 1995; Vasek and Lund, 1980). Leaf K, Ca, and Mg at Mono Lake were all consistent with previous reports for *Sarcobatus* (Glenn and O'Leary, 1984; Rickard, 1982; Rickard and Keough, 1968; Wallace et al., 1973). Although nutrient sufficiency levels are not well established for wildland plants, our lowest nutrient cation values were all at the lower limits of sufficiency for agricultural plants (Marschner, 1995), or reported for *Sarcobatus* growing in non-saline nutrient solutions (Glenn and O'Leary, 1984; Richards, 1994).

The cation macronutrients are also important in terms of concentration relative to Na, because of interactions during uptake and in other plant functions. The ability of plants to maintain K uptake when Na is high is a key character of salinity tolerance (Cheeseman, 1988; Flowers et al., 1977; Niu et al., 1995; Reimann and Breckle, 1993, but see Glenn et al., 1992). Influx of Na across root plasma membranes is generally thought to be passive, and apparently interacts with K carriers at the membrane level (see Niu et al., 1995 for review). Glycophytes tend to have greater selectivity for K and end up with K/Na leaf values greater than one. In contrast, halophytic plants such as *Sarcobatus* take up large amounts of Na while still maintaining K uptake, and end up with leaf K/Na values less than one (Albert and Popp, 1977; Glenn and O'Leary, 1984; Gorham et al., 1980). *Sarcobatus* leaf K/Na values of 0.3 at the Diverse Dunes and lower towards the Lake were consistent with values for halophytes (Figure 4).

Selectivity coefficients provide a means of comparing nutrient and Na concentrations in the plant relative to availability of both cations in the substrate: i.e. the ratio of nutrient to toxic ion in some plant compartment over the same ratio for the substrate (e.g. $S_{[K,Na]} = (K_{plant})/(Na_{plant}) / (K_{substrate}/Na_{substrate})$). Selectivity coefficients were initially used to examine ion uptake selectivity across root plasma membranes in solution culture experiments, and subsequently used for whole plant or shoot ion concentrations relative to solution concentrations (Läuchli, 1990; Pitman, 1976; Reimann and Breckle, 1993). The selectivity coefficient for K, designated by $S_{[K,Na]}$, is the one primarily discussed due to interactions between K^+ and Na^+ at membrane-bound transporters. The $S_{[Ca,Na]}$ is important because Ca participates in signal transduction for cellular responses to the environment, and Ca affects membrane integrity

and permeability to Na, K/Na uptake ratios, and salinity tolerance (Greenway and Munns, 1980; Läuchli, 1990; Rengel, 1992; Niu et al., 1995): For halophytes, there have been few investigations of Ca and salinity tolerance, although it is still presumed to play a large role. $S_{[Mg,Na]}$ is also potentially important because Mg is involved in membrane transport and other cellular processes. Decreased cover of *Atriplex parryi* was highly correlated with decreased leaf Mg/Na along a large salinity gradient at Owens Lake, CA, suggesting that Mg was limiting in that environment (Richards, 1994).

For our study, $S_{[K,Na]}$, $S_{[Ca,Na]}$, and $S_{[Mg,Na]}$ refer to leaf ion molar ratios relative to soil extract ion molar ratios. This is an integrated, ecological measure of plant response to the relative amount of these cations in the rooting substrate and depends on selectivity at many locations within the plant. Along the salinity gradient at Mono Lake, the decline in leaf K/Na was proportional to that in the soil, so $S_{[K,Na]}$ was remarkably constant, ranging only from 1.9 to 2.6 (Figure 4). This means that the K/Na in the plants remained proportional to the K/Na in the soil, even as Na and K varied widely across the site in absolute and relative substrate availability (Figure 3). These results contrast with those for halophytes in controlled environment studies; with increased substrate NaCl, $S_{[K,Na]}$ of *Suaeda maritima* increased (Yeo and Flowers, 1986), but $S_{[K,Na]}$ of young *Sarcobatus* decreased (Glenn and O'Leary, 1984). The difference between our field study and these controlled environment studies may be due to differences in absolute concentrations of the substrate cations or interactions with Ca availability. However, it is likely that the constant $S_{[K,Na]}$ we observed reflects the resilience of K uptake by *Sarcobatus* under variable field conditions, even when substrate and plant Na are high and Ca low. At the Shoreline Berm, *Sarcobatus* may be limited by the low absolute amount of K in the soil, but K uptake does not appear to be limited by interference from high Na. Similarly, *Sarcobatus* $S_{[Ca,Na]}$ also remained relatively constant, ranging from 1.3 to 5.3. This suggests, again, that while leaf Ca may have been deficient at the sites closer to the Lake, the low Ca was due to lack of Ca in the rooting substrate as opposed to Na interference with Ca uptake. Unlike selectivity for K or Ca, *Sarcobatus* $S_{[Mg,Na]}$ increased dramatically across the gradient from 0.4 at the Diverse Dunes to 21.8 at the Shoreline Berm, a 54-fold increase. This suggests, yet again, that high Na at the Shoreline Berm did not interfere with plant Mg uptake. In fact high

salinity and alkalinity were associated with enhanced uptake of Mg relative to Na, consistent with a Mg nutrient deficiency. Maintaining leaf Mg may be especially necessary at the highest salinity site because it is a cofactor for tonoplast ATPases (Marschner, 1995), the activity of which is needed to maintain vacuolar compartmentation of Na for osmoregulation (Yeo, 1983). Maintaining leaf Mg may also be necessary for protein translation in the presence of high Na (Flowers and Dalmond, 1992). Overall, variation in *Sarcobatus* selectivity coefficients across the salinity gradient at Mono Lake strongly suggest: 1) that high substrate Na did not reduce selectivity for K, Ca, and Mg and 2) that this species responded to low availability of Mg (and perhaps Ca) at the most alkaline and saline site with increased selectivity for this (these) cations. These patterns contrast sharply with effects of high Na on selectivity for cation macronutrients in glycophytes.

Against the background of high substrate pH, EC, Na and B, *Sarcobatus* also needs to take up adequate N and P. With the exception of the Shoreline Berm, overall N availability for the plants was very low across the site, which is typical of many desert ecosystems (Caldwell, 1974; Charley and West, 1975). However, *Sarcobatus* had very high leaf N at all sites, especially considering the high leaf ash contents, and the site with the highest leaf N did not have the highest soil or groundwater N. High leaf N has previously been found for other halophytes and non-halophytes in the Chenopodiaceae (Osmond et al., 1980; Rozema et al., 1983), indicating efficient N uptake and utilization. Many halophytes in the Chenopodiaceae invest a large proportion of N in compatible solutes such as glycinebetaine for cytoplasmic osmoregulation (Gorham and Wyn Jones, 1983; Rozema et al., 1983; Storey et al., 1977), and high leaf N may be associated with greater salinity tolerance. For *Sarcobatus* in a greenhouse study, Richards (1994) found that increased substrate NaCl resulted in decreased leaf N and P. Other investigations of N nutrition and salinity in desert halophytes indicate no effect of NaCl on NO_3^- uptake or leaf N concentration (Black, 1956; Osmond et al., 1980). Phosphorus was also relatively low in the substrates at our study site, but the *Sarcobatus* leaf P levels were comparable to sufficiency levels for agricultural plants, again considering the high ash contents (Marschner, 1995).

In addition to the high soil Na, desert halophytes are often exposed to soils with high levels of B (Caldwell, 1974; Marschner, 1995). Although the high soil B levels in this system were potentially toxic, the extremely

high pH values make it difficult to determine actual B availability to plants. In a controlled environment study *Sarcobatus* grew in substrate B concentrations up to 44.8 μM (added to alkalized modified Hoagland's solution) and accumulated up to 1.7 g kg^{-1} leaf B (Richards, 1994), greatly exceeding leaf B concentrations we found at Mono Lake. In the controlled environment study, increasing substrate and leaf B were associated with decreased leaf Ca and P, but did not show any clear interaction with leaf Na, N, K, or Mg. At Mono Lake, *Sarcobatus* responses to increased site Na and B did not differ markedly from studies where only elevated Na was examined, suggesting that high B levels at Mono Lake were not a primary limitation to *Sarcobatus* growth.

Comparison of substrate and *Sarcobatus* leaf elemental composition across a large salinity gradient at Mono Lake illustrated the importance of salinity/nutrient interactions in determining the salinity tolerance, nutrient deficiency responses, and probably distribution of that halophytic species. Na dominated the leaf composition of *Sarcobatus* along the entire gradient, even on technically non-saline sites. A remarkable similarity of leaf Na content from that site to highly saline sites, suggests that the key determinants of *Sarcobatus*, and perhaps other halophytes, growth and distribution are in the relation of Na to the highly variable combinations of other nutritional ions (N, P, K, Ca, and Mg) on ecological salinity gradients.

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