Water relations and leaf chemistry of *Chrysothamnus nauseosus* ssp. *consimilis* (Asteraceae) and *Sarcobatus vermiculatus* (Chenopodiaceae)[1]

Lisa A. Donovan,[2] James H. Richards, and Matthew W. Muller

Department of Land, Air, and Water Resources, University of California, Davis, California 95616-8627

At Mono Lake, California, we investigated field water relations, leaf and xylem chemistry, and gas exchange for two shrub species that commonly co-occur on marginally saline soils, and have similar life histories and rooting patterns. Both species had highest root length densities close to the surface and have large tap roots that probably reach ground water at 3.4–5.0 m on the study site. The species differed greatly in leaf water relations and leaf chemistry. *Sarcobatus vermiculatus* had a seasonal minimum predawn xylem pressure potential (ψ_{pd}) of −2.7 MPa and a midday potential (ψ_{md}) of −4.1 MPa. These were significantly lower than for *Chrysothamnus nauseosus,* which had a minimum ψ_{pd} of −1.0 MPa and ψ_{md} of −2.2 MPa. *Sarcobatus* had leaf Na of up to 9.1 % and K up to 2.7 % of dry mass, and these were significantly higher than for *Chrysothamnus* which had seasonal maxima of 0.4% leaf Na and 2.4 % leaf K. The molar ratios of leaf K/Na, Ca/Na, and Mg/Na were substantially lower for *Sarcobatus* than for *Chrysothamnus.* Xylem ionic contents indicated that both species excluded some Na at the root, but that *Chrysothamnus* was excluding much more than *Sarcobatus.* The higher Na content of *Sarcobatus* leaves was associated with greater leaf succulence, lower calculated osmotic potential, and lower xylem pressure potentials. Despite large differences in water relations and leaf chemistry, these species maintained similar diurnal patterns and rates of photosynthesis and stomatal conductance to water vapor diffusion. *Sarcobatus* ψ_{pd} may not reflect soil moisture availability due to root osmotic and hydraulic properties.

Key words: Asteraceae; Chenopodiaceae; halophyte; nutrition; photosynthesis; root distribution; salinity; sodium; water relations.

In cold deserts of western North America, plant distribution on the landscape is often closely related to soil chemistry (Billings, 1949, 1951; West, 1988; Comstock and Ehleringer, 1992). In general, saline and alkaline soils at lower topographic positions in basins between mountain ranges are occupied by shrub species in the family Chenopodiaceae, while nonsaline, less alkaline soils are occupied by shrubs from the family Asteraceae (Gates, Stoddart, and Cook, 1956; West, 1988). At many locations, however, species from these families co-occur along broad gradients, and one commonly found association is *Chrysothamnus nauseosus* (Palla.) Britt. ssp. *consimilis* (E. Greene) H.M. Hall & Clements (Asteraceae; common name, salt rabbitbrush) and *Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae; common name, greasewood) (Shantz and Piemeisel, 1940; Robinson, 1958; Wiebe and Walter, 1972; Roundy, Young, and Evans, 1981; Robertson, 1983). These two species have similar life histories. They are winter deciduous shrubs with the C_3 photosynthetic pathway. Both produce leaves in early spring, have highest shoot growth rates in early summer, maintain high photosynthetic rates through summer, flower in mid-late summer, and senesce in late fall after producing large numbers of wind-dispersed seeds (Roundy, Young, and Evans, 1981; Robertson, 1983; Romo and Haferkamp, 1989; Donovan and Ehleringer, 1994a; Fort and Richards, 1995). The *consimilis* subspecies of *Chrysothamnus* is thought to be somewhat tolerant of alkaline and saline soils (Robinson, 1958; Rollins, Dylla, and Eckert, 1968; Roundy, Young, and Evans, 1981), whereas *Sarcobatus* is very salt and alkali tolerant (Shantz and Piemeisel, 1940; Fireman and Hayward, 1952; Gates, Stoddart, and Cook, 1956). Both shrub species are phreatophytic, indicating that they are generally rooted down to the capillary fringe of groundwater at depths of 2–12 m, and hence should have similar access to water (Robinson, 1958; Rollins, Dylla, and Eckert, 1968; Harr and Price, 1972; Branson, Miller, and Mc-Queen, 1976; Rickard and Warren, 1981). However, both species have been shown to respond to severe drought with either leaf drop, reduced canopy size, or increased mortality, indicating that access to water is not unlimited (Rickard and Warren, 1981; Toft, 1995).

Relationships to soil chemistry and water potentials have been investigated for both *Chrysothamnus* and *Sarcobatus,* but only for non-co-occurring populations. *Sarcobatus* can accumulate Na in its leaves, and create a salt-enriched microsite under its canopy due to leaching of salt from shed leaves. In contrast, soils under the canopy of *Chrysothamnus* and other shrubs in the Asteraceae, such as *Artemisia tridentata,* do not differ in salt content from soils in interspaces between shrubs (Fireman and

[2] Author for correspondence, current address: Department of Botany, University of Georgia, Athens, GA 30602-7271.

Hayward, 1952; Rickard, 1964, 1965; McNulty, 1969; Rickard, Cline, and Gilbert, 1973; Wallace, Romney, and Hale, 1973; Cline and Rickard, 1974; Glenn and O'Leary, 1984; Eddleman and Romo, 1987). Leaf elemental contents for *Chrysothamnus* on saline soils have not been reported, but other species in the same family have been shown to accumulate some Na (Glenn and O'Leary, 1984). Field values of xylem pressure potentials for adult *Chrysothamnus* range from -1.0 to -4.0 MPa (Branson, Miller, and McQueen, 1976; Donovan and Ehleringer, 1994b), and values of xylem pressure potentials for *Sarcobatus* are generally more negative, reported to range from -1.5 to -6.5 MPa (Detling and Klikhoff, 1973; Branson, Miller, and McQueen, 1976; Romo and Haferkamp, 1989). Although xylem pressure potentials for woody plants are generally related to minimum water availability in the soil column (Branson, Miller, and McQueen, 1976; Hinckley, Lassoie, and Running, 1978; Davis and Mooney, 1986), xylem pressure potentials of *Chrysothamnus* and *Sarcobatus* appear to be independent of moisture in surface soil layers, presumably because they are phreatophytic. When co-occurring shrubs are phreatophytic, differences in water relations and leaf chemistry may reflect physiological responses to groundwater and soil chemistry, not differences in rooting depths and soil moisture availability.

In this study we compared the seasonal water relations and leaf chemistry of mature individuals of *Chrysothamnus* and *Sarcobatus* where they co-occur on dunes near Mono Lake, CA. Although these shrubs have similar rooting zones and similar life histories, we expected them to differ in seasonal water relations and leaf chemistry due to their different physiological mechanisms for salinity tolerance. We assessed the causes and consequences of different xylem pressure potentials by examining diurnal gas exchange, xylem chemistry, root distribution, and soil and groundwater chemistry.

MATERIALS AND METHODS

The study site (38° 5' N, 118° 58' W, 1958 m elevation) is located ≈2 km from the northeast shore of Mono Lake, CA. The climate is arid, with annual precipitation at the site averaging 160 mm (Toft, 1995). From October 1993 to March 1994 precipitation totalled 93 mm and an additional 54 mm fell at the beginning of the growing season in April and May 1994. No precipitation occurred during the summer (June-August 1994) when the study was conducted. The site was a 100 × 100 m area of late Holocene semistabilized dunes (described by Toft, 1995). At the site 2.0–3.6 m of aeolian sand overlies lacustrine clay, with the free groundwater surface at depths of 3.4–5.0 m, depending on the thickness of the overlying sand deposit. Six interspecific pairs of *Chrysothamnus* and *Sarcobatus* shrubs were chosen within the site. Each shrub was a discrete individual, separate from other individuals by at least 2 m, and shrubs were paired for canopy size, measured as height and canopy volume. In spring 1994, soils were collected at 50 cm depths from a hole augured to groundwater in a shrub interspace. Electrical conductivity (EC, dS/m) and pH were determined for groundwater and saturated soil extracts. Groundwater was also analyzed for Na, Ca, K, P, B, S, and Mg on an inductively coupled plasma–atomic emission spectrophotometer (ICP-AES; Thermo Jarrell Ash Corp., Franklin, MA).

Shrub stem xylem pressure potentials were determined with a pressure chamber (PMS Inc., Corvallis, OR). When plants were still leafless on 22 April, only midday xylem pressure potentials (ψ_{md}) were deter-

mined. On 20 May, 7 July, 17 August, and 20 September, stems were also measured for predawn xylem pressure potential (ψ_{pd}). Additional diurnal ψ measurements were made on 7 July and 17 August, to accompany measurements of gas exchange. Rates of photosynthesis (A) and stomatal conductance (g) were determined for stems with leaves, with a LI-COR 6200 portable photosynthesis system (LI-COR., Lincoln, NE) and a quarter-litre chamber. The leaf-to-air vapor pressure deficit was calculated from air temperature and relative humidity assessed with the chamber open to the atmosphere, and leaf temperatures were assumed to be the same as air temperature because both shrub species have small linear leaves. For individual plants, the maximum rate of A on each date was used to calculate A/g and instantaneous water-use efficiency or WUE (A/E, mmol CO_2/mol H_2O, where E is transpiration), and photosynthetic nitrogen-use efficiency or NUE (A/N, μmol $CO_2 \cdot$mol $N^{-1} \cdot s^{-1}$, where N is leaf nitrogen content per unit area) (Field, Merino and Mooney, 1983). Leaf areas were measured with a Delta-T system (Decagon Devices, Pullman, WA).

Leaf chemistry was determined for mature leaves that were collected from each plant at the time of ψ_{pd} sampling in May, July, and August. After air drying at 60°C, a portion of ground leaf material was extracted with acid dissolution and microwave digestion (Sah and Miller, 1992). Extracts were analyzed for Na, Ca, K, P, B, S, and Mg on the ICP-AES. The remaining leaf tissue was analyzed for percentage N by Dumas combustion with a Carlo Erba NA1500 elemental analyzer (Milan, Italy), and for percentage ash by combustion for 6 h at 520°C. Leaf water and mass per area characteristics were determined for leaves prior to senescence in early October. Ten leaves were collected at sunrise from each shrub, and fresh mass, area, and dry mass were determined. Estimates of leaf osmotic potentials were calculated for each species on the basis of leaf Na, K, H_2O, and dry mass (Storey, Ahmad, and Wyn Jones, 1977).

Xylem sap was extracted from 0.3 m long, 0.5 cm diameter, woody stem segments collected at sunrise and at midday on 17 August from four shrubs of each species. Upon collection, stem segments were wrapped in parafilm and stored cold until extraction of sap within 6–48 h after severing. For extraction, bark and phloem were removed from each end of the stem. Plastic tubing was attached to the top of the stem, and a 2-m column of water and acid fuchsin dye solution (0.5%) was used to displace xylem sap. Volume collected varied from 2 to 9 mL. Evaporative loss during collection was minimized by exposing sap to a small volume of air in parafilm-sealed, 15-mL vials, and by keeping collection vials on ice. Xylem extracts were analyzed for Na, Ca, K, P, B, S, and Mg on the ICP-AES. For each species, morning and midday samples did not differ significantly for any element ($P > 0.05$ for all comparisons), and data from the two collection times were combined for subsequent statistical analysis.

Root density and depth distribution were determined in pits at the canopy edge of each shrub at the end of the growing season. Soil cores (180 cm³) were taken at 0.25, 0.50, 0.75, and 1.0 m depths and roots were elutriated onto fine screens. Root lengths were determined for a subset of cores with a Comair root length scanner (Hawker De Havilland Victoria Limited, Melbourne, Australia). Root dry masses after 48 h at 60°C, were determined for all samples. Root mass per volume of soil (rwd; g/m³) was converted to root length density (rld; m/m³) from the regressions: for *Chrysothamnus* rld = rwd·165.87 $-$ 1.82 ($N = 12$, $r^2 = 0.86$, $P < 0.05$), and for *Sarcobatus* rld=rwd·146.52 $-$ 0.93 ($N = 13$, $r^2 = 0.87$, $P < 0.05$).

Data were analyzed with repeated-measures analysis of variance for variables that involved repeated sampling of individual plants through the season, through the day, or at several depths, and for which there were few missing values, i.e., seasonal xylem pressure potentials and leaf chemistry, diurnal xylem pressure potentials, rates of gas exchange, and root length density (Gurevitch and Chester, 1986; SAS, 1989; Potvin, Lechowicz, and Tardif, 1990; von Ende, 1993). Between-subject effects were block (shrubs paired for canopy size) and species. Within-subject effects were repeated interval (either month, hour, or depth),

TABLE 1. One-way analysis of variance comparisons between *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* growing at Mono Lake, CA in 1994 for plant canopy size, leaf ash content, leaf mass and area (N = 6), and xylem sap chemistry (N = 4). For each variable: mean ± 1 SE, F statistic and significance. * P < 0.05, ** P < 0.01, *** P < 0.001, and NS is not significant.

	Chrysothamnus	*Sarcobatus*	F
Canopy size (18 August)			
Canopy height (m)	1.3 ± 0.2	1.3 ± 0.4	0.1NS
Canopy volume (m³)	3.6 ± 1.0	4.7 ± 2.8	0.6NS
Leaf ash content			
20 May (%)	16.6 ± 6.5	22.4 ± 4.2	0.3NS
7 July (%)	11.9 ± 3.4	29.1 ± 1.1	23.3***
17 August (%)	9.9 ± 0.6	33.3 ± 0.6	694.3***
Leaf mass and area (10 October)			
Fresh mass/area (g/m²)	492.3 ± 16.1	1 125.7 ± 61.3	99.9***
Dry mass/area (g/m²)	207.0 ± 6.0	212.3 ± 8.0	0.3NS
Organic dry mass/area (g/m²)	186.5 ± 5.5	142.3 ± 7.7	48.4***
Water/area (g/m²)	283.0 ± 16.0	905.0 ± 58.0	196.1***
Fresh mass/dry mass	2.4 ± 0.1	5.3 ± 0.2	235.7***
Xylem chemistry (17 August)			
B (mg/L)	3.2 ± 0.4	3.7 ± 0.6	0.6NS
Ca (mg/L)	66.2 ± 5.7	21.2 ± 6.1	29.2***
K (mg/L)	219.2 ± 18.6	227.5 ± 46.8	0.3NS
Mg (mg/L)	21.5 ± 1.73	12.8 ± 1.1	18.0***
Na (mg/L)	21.6 ± 4.2	141.9 ± 16.2	83.0***
P (mg/L)	13.3 ± 1.4	17.3 ± 4.4	1.1NS
S (mg/L)	5.9 ± 0.9	17.7 ± 3.5	22.1***

interval by species interactions, and interval by block interactions. Univariate analyses and Huynh-Feldt (H-F) adjusted P values were used for testing within-subject effects. Mauchly's criterion was used to test for sphericity and indicated no significant departure from compound symmetry for most variables. For the variables where there was a significant departure (photosynthetic rates in July and August, and leaf chemistry molar ratios), the results of the H-F adjusted P concurred with unadjusted P values (von Ende, 1993). For all variables except root length density, the block effect (between subject), and block by interval interaction effect (within subject) were not significant (P > 0.05 for all analyses) and these block effects are not presented in the ANOVA tables.

One-way analysis of variance was used to determine species differences for variables sampled only on one date, i.e., canopy size, xylem chemistry, and leaf mass characters. One-way ANOVA was also used

for percent ash on each sampling date because it had many missing values and hence was inappropriate for repeated-measures analysis (SAS, 1989). Variables were log transformed, when necessary, to meet assumptions of normality and equivalent variance of residuals. For these variables, back-transformed means and standard errors (averaged) are presented.

Relationships between photosynthetic rates and conductances were determined with a linear regression and subsequent F test for each species on each sampling date. Differences in regression coefficients were determined with the Tukey-Kramer method (Sokal and Rohlf, 1981).

RESULTS

The depth of the free groundwater surface did not change through the 1994 growing season, remaining 3.4–5.0 m below the sand surface, depending on the sand depth at the sampled shrubs. Groundwater contained 475 mg/L (ppm) Na, 3 mg/L B, 5 mg/L Ca, 47 mg/L K, 1 mg/L P, and 51 mg/L S, and had an EC of 1.5 dS/m and pH of 8.6. EC of saturated soil extracts ranged from 1.0 to 1.5 dS/m and pH ranged from 7.8 to 9.2. Since most of the salt in the soil at this site is NaCl (J.H. Richards and L.A. Donovan, unpublished data), the soil solutions at saturation had a range of Na concentrations from 230 to 345 mg/L and osmotic potentials from −0.05 to −0.07 MPa.

The average height and canopy volume of the reproductively mature *Chrysothamnus* and *Sarcobatus* did not differ (Table 1). The species differed in root length density, with *Sarcobatus* having 46% higher root length density than *Chrysothamnus* in the 0–1.0 m rooting zone (between subject, species effect), but both species showed a similar pattern of decrease in root length density with increasing depth (within subject, species by depth interaction) [(Fig. 1, Table 2)]. Roots of both species penetrate much deeper than 1 m and were occasionally found in augered holes at 3–5 m depths.

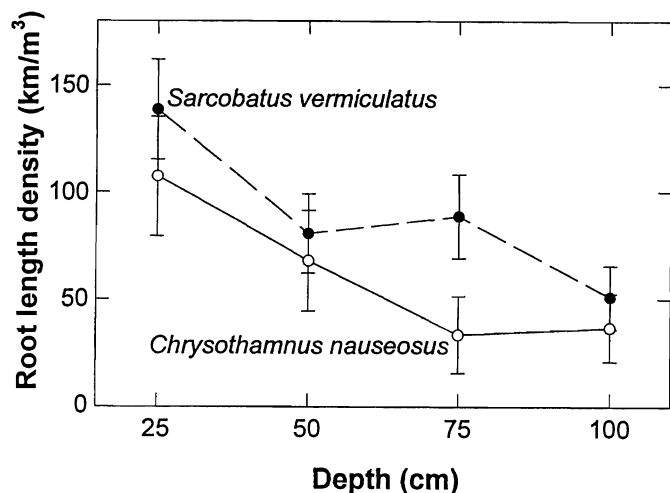*Chrysothamnus* and *Sarcobatus* had different seasonal

Fig. 1. Profile of root length density in the 0–1 m soil layer for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* at Mono Lake, CA at the end of the 1994 growing season; mean ± 1 SE, N = 6 (for statistics see Table 2).

TABLE 2. Results of repeated measures analysis of variance for comparisons of characteristics of *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* at Mono Lake, CA in 1994. Between-subject effect is species, and within-subject effects are the repeated interval (month, time of day, or depth) and interval by species interaction. Presented for each effect are an F statistic, significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$), and degrees of freedom for numerator and denominator (df). Means and SEs for the variables compared here are in Figs. 1–4.

| | Between-subject effect | | Within-subject effects | | | |
| | Species | | Month | | Month × species | |
	F	df	F	df	F	df
Season variables						
ψ_{pd}	69.5***	1,5	65.8***	3,15	39.6***	3,15
ψ_{md}	297.5***	1,5	63.7***	4,20	21.2***	4,20
ψ_{md}-ψ_{pd}	15.2*	1,5	10.5***	3,15	6.8**	3,15
Leaf N	16.6**	1,5	232.8***	2,10	1,3	2,10
Leaf B	5.1	1,5	31.4***	2,10	2.6	2,10
Leaf Ca	0.1	1,5	17.8***	2,10	0.2	2,10
Leaf K	6.6*	1,5	3.5	2,10	1.8	2,10
Leaf Mg	7.4*	1,5	12.0**	2,10	2.2	2,10
Leaf Na	335.7***	1,5	67.7***	2,10	84.2***	2,10
Leaf P	51.5***	1,5	13.1**	2,10	1.3	2,10
Leaf S	3.5	1.5	7.5	2,10	8.0**	2,10
Leaf K/Na	23.8**	1,5	2.5	2,10	3.1	2,10
Leaf Ca/Na	19.6**	1,5	5.4*	2,10	5.4*	2,10
Leaf Mg/Na	26.2**	1,5	8.9**	2,10	9.2**	2,10
	Species		Time of day		Time of day × species	
	F	df	F	df	F	df
Diurnal variables						
July ψ	131.7***	1,5	225.5***	5,25	30.0***	5,25
July A	11.9*	1,5	27.2***	3,15	1.2	3,15
July g	9.0*	1,5	19.8***	3,15	2.0	3,15
Aug ψ	416.8***	1,5	133.5***	5,25	2.0	5,25
Aug A	0.2	1,5	37.8***	4,20	0.7	4,20
Aug g	1.6	1,5	12.6***	4,20	3.8*	4,20
	Species		Depth		Depth × species	
	F	df	F	df	F	df
Spatial variable						
Root length density	7.9*	1,5	9.0***	3,15	0.8	3,15

courses of ψ_{pd}, ψ_{md}, and ψ_{md}-ψ_{pd} (the difference between midday and predawn water potentials), as indicated by a significant species effect in the between-subject analysis (Fig. 2, Table 2). *Chrysothamnus* had consistently much less negative ψ_{pd} and ψ_{md} values throughout the season. The first sampling date was prior to leaf out, and represented late-winter dormant conditions. After leaves were produced in May, both species showed significant seasonal declines in both ψ_{pd} and ψ_{md} (within-subject, time effect), but the shapes of the seasonal curves were different as indicated by a significant species by time interaction in the within-subject analysis (Table 2).

The seasonal species differences in xylem pressure potentials were accompanied by seasonal differences in leaf chemistry for N, P, K, Mg, and Na, but not for Ca, B, and S (Fig. 3, Table 2). *Chrysothamnus* had higher leaf N, P, and Mg, but lower leaf K and Na than *Sarcobatus*. There was a significant seasonal (month) effect for all elements except K and S (even when the species effects were not significant) and a significant time by species interaction for Na. *Sarcobatus* leaves accumulated Na to 9.1 % of dry mass while *Chrysothamnus* Na content fell through the season to 0.2 % (Fig. 3). Na was the primary cation contributing to the significant species difference in ash content by the end of the growing season (Fig. 3, Table 1). The species also differed significantly for molar

ratios of K/Na, Ca/Na, and Mg/Na in leaf tissues (Table 2). Throughout the season, K/Na molar ratios were > 3.8 for *Chrysothamnus* and < 0.3 for *Sarcobatus*. In addition, Ca/Na molar ratios were > 1.6 for *Chrysothamnus* and < 0.06 for *Sarcobatus*, while Mg/Na molar ratios were > 0.9 for *Chrysothamnus* and < 0.4 for *Sarcobatus*. Species differences in leaf chemistry were generally paralleled by differences in xylem sap chemistry in August: *Chrysothamnus* had much lower xylem Na and S than *Sarcobatus*, while the reverse was true for Ca and Mg (Table 1). The species did not differ in B, K, and P contents in the xylem sap.

Sarcobatus leaves were more succulent than those of *Chrysothamnus*, based on a higher fresh mass/area ratio, higher H_2O/area ratio, and lower organic dry mass per unit area (Table 1). The greater leaf succulence of *Sarcobatus* is consistent with the higher leaf Na and ash contents per unit leaf area. Calculated leaf osmotic potential, based on total leaf Na, K, and water per gram dry mass and ignoring compartmentation effects, were −1.8 and −4.6 MPa for *Chrysothamnus* and *Sarcobatus*, respectively.

Diurnal courses of ψ, A, and g differed between *Chrysothamnus* and *Sarcobatus* in July, but in August only ψ was significantly different (Fig. 4, Table 2). Both species had significant differences associated with time for all of
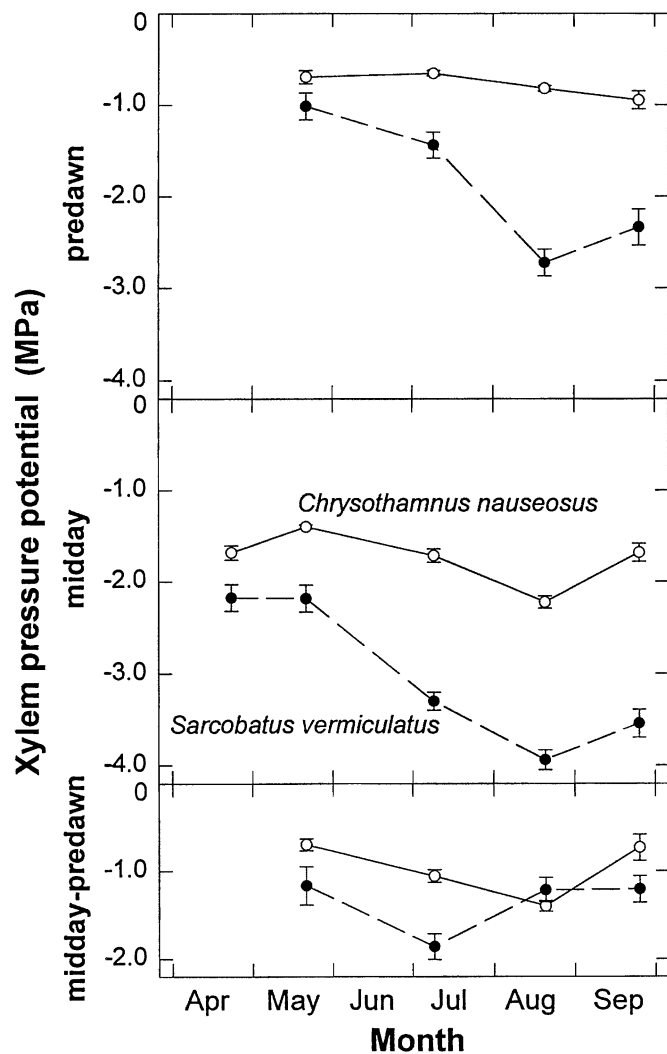
Fig. 2. Seasonal courses of xylem pressure potentials for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* at Mono Lake, CA in 1994: predawn (ψ_{pd}), midday (ψ_{md}), and the difference between midday and predawn (ψ_{md}-ψ_{pd}); mean ± 1 SE, $N = 6$ (for statistics see Table 2).

the diurnal variables on both dates, and the shapes of the curves differed for species (indicated by significant time by species interaction) for ψ in July and for g in August.

There was a significant positive linear relationship between A and g for each species on each sampling date (Fig. 5; $F > 19.6$ and $P < 0.05$ for each test). Comparing the slopes of the relationships between A and g indicated that the species did not differ in July ($P > 0.05$), but did differ significantly in August ($P < 0.05$), with *Chrysothamnus* having the steeper slope. *Chrysothamnus* and *Sarcobatus* did not differ for instantaneous WUE (A/E) nor instantaneous NUE (A/N) in either July or August (Table 3).

DISCUSSION

The co-occurring shrub species, *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus*, differ substantially in their diurnal and seasonal water relations, with *Sarcobatus* having much more negative ψ_{pd} and ψ_{md} through-

out the season. The large differences in ψ_{pd}, especially late in the summer (Fig. 2), between *Sarcobatus* and *Chrysothamnus* would conventionally be interpreted as an indication of differential access to moist soil layers. This does not appear to be the case in this situation, however. Rather, evidence from this study, the literature, and stable hydrogen isotope analyses suggests that these co-occurring shrub species have root systems that are exposed to a similar belowground environment in terms of water availability (and soil chemistry, discussed later) and have access to the water in the capillary fringe when soil moisture is not available in the overlying sands. Both species have their highest root length density in the shallower soils (Fig. 1) but are reported to root to groundwater when it occurs within the depth range found in this study (Robinson, 1958; Rollins, Dylla, and Eckert, 1968; Harr and Price, 1972; Branson, Miller, and McQueen, 1976; Rickard and Warren, 1981). As at other locations, both species have massive tap roots at the study site, and we have found roots in soil cores from moist lacustrine clay layers just above the groundwater level. Woody *Sarcobatus* roots (> 4 mm diameter) in such cores were identified by color and a distinctive white starchy layer beneath the bark. Other woody roots found at depth could not positively be identified as *Chrysothamnus*, but no other shrubs occur at the sites where the deep holes were augered. Psychrometric measurements of soil water potential and neutron probe determinations of soil water content at this and other sites on the dunes indicate that, while moisture is available in the shallower soils early in the growing season, during July and August soil water potentials are −4.0 to −7.0 MPa or lower from the surface to 2 m depth (Muller, Richards, and Donovan, 1995). Soil moisture, however, is available in deeper soil layers (≥ −2.2 MPa at 2 m or deeper) or from groundwater throughout the growing season. In addition, preliminary determinations of the hydrogen isotopic composition of water in the stem xylem of both species in midsummer are not distinguishable from the isotopic composition of the groundwater at the site. All of this evidence, coupled with the high A and g of *Sarcobatus*, suggests that the low ψ_{pd} of that species is not indicative of limited water availability nor limited root access to moist soil layers.

The discrepancy of *Sarcobatus* ψ_{pd} and groundwater/soil moisture availability requires other explanations. One possibility is a low hydraulic conductivity of *Sarcobatus* deep roots during periods of low flow, such as at night. This would mean that the roots of *Sarcobatus*, which based on our xylem and seasonal leaf chemistry data are relatively high in salt, would not approach equilibrium as rapidly as *Chrysothamnus*. Recent analyses of the composite transport properties of tree root systems where flows were affected by osmotic rather than hydrostatic gradients have shown long half times of water flow equilibration and low hydraulic conductivities (Hallgren, Rüdinger, and Steudle, 1994; Steudle, 1994). Those experiments were done with well-watered roots subjected to external osmotica, so extension to the low xylem pressure potential conditions present in our study will require more detailed data on the xylem pressures, osmotic contents, and water fluxes and pathways in the roots of *Sarcobatus* under conditions similar to those we observed in the field, i.e., with shoot ψ_{pd} as low as −2.7 MPa.
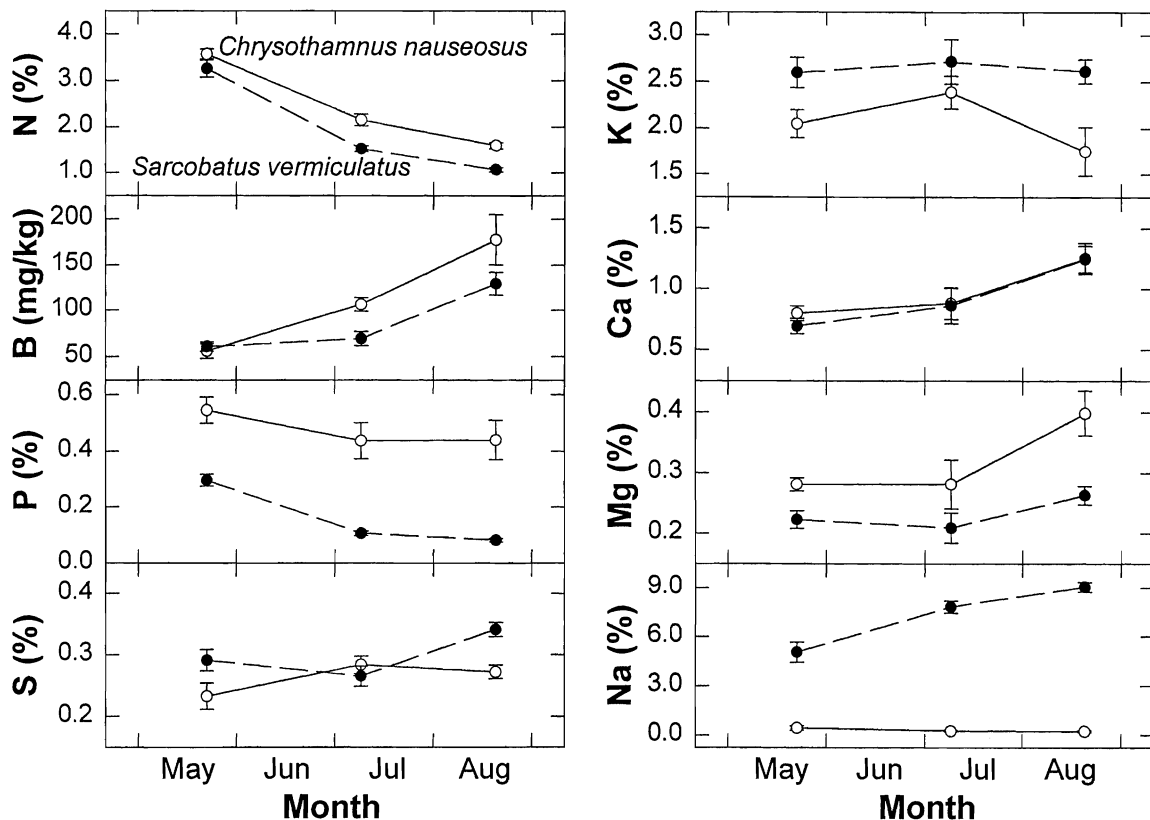
Fig. 3. Seasonal courses of leaf element contents for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* at Mono Lake, CA in 1994: nitrogen (N), boron (B), phosphorus (P), sulfur (S), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na); mean $\pm$ 1 SE, $N = 6$ (for statistics see Table 2). Total leaf ash content through the season is given in Table 1.

A second possible cause of the large discrepancy between *Sarcobatus* ψ_{pd} and groundwater/soil moisture availability might be continued nighttime water leakage (i.e., hydraulic lift) by an extensive, active, shallow root system, which prevents the shrub from rapidly reaching an equilibrium with water availability in the deeper, wetter soil layers. Here the dry soil layers act as an external, linked capacitance that affects the rehydration times for the entire root/shoot system. Extended equilibration times were demonstrated experimentally in hydraulically lifting, nonphreatophytic *Artemisia tridentata* (Richards and Caldwell, 1987). Hydraulic lift, and thus active fine roots in shallow ($<$ 2 m depth), dry soil layers, have been demonstrated for *Sarcobatus* at a site $<$ 500 m from this study site (Muller, Richards, and Donovan, 1995). The effect of hydraulic lift on the nighttime recovery of xylem pressure potential will be dependent on the relative distribution and hydraulic properties of roots in shallow dry soil and deep moist soil. In *Sarcobatus* the proportion of roots in the deep soil is probably quite small, given the observed high root length density in the upper metre of soil, the extensive spread of major laterals that we have observed in field excavations ($>$7 m), and the difficulty that roots would face proliferating in the physically restrictive lacustrine clay layers above the groundwater. Although *Chrysothamnus* roots would face the same constraints near groundwater, the stable hydrogen isotope data from two Utah sites, one a sand dune site, suggest that *Chrysothamnus* shallow roots are not active in water

transport during midsummer (Flanagan, Ehleringer, and Marshall, 1992; Donovan and Ehleringer, 1994b). This would effectively eliminate shallow soil capacitance and allow much more rapid equilibration with the moist soil layers. Thus differences between the species in shallow root system developmental characteristics, such as phenology, suberization, and fine root shedding, which affect root system hydraulic properties, may contribute strongly to the species differences in water relations characteristics. With this hypothesis, both species would then have access to the groundwater, be able to maintain relatively high rates of daytime water use, as reflected by our *A* and *g* measurements, yet operate at quite different levels of water potential. The advantage for *Sarcobatus* to operate at much lower water potentials relates to its salinity tolerance, which requires large accumulations of osmotically active salts in the leaves.

The two possibilities that we have proposed to explain the discrepancy between *Sarcobatus* and soil water availability could certainly operate together, and could also be joined by a third possibility. It may be that shoot xylem pressure potentials in *Sarcobatus* do not reflect root xylem pressure potentials. This would require low axial hydraulic conductance in the taproot–stem system of *Sarcobatus*. This seems somewhat unlikely given the apparent capability of the system to sustain high water flux rates during the daytime, allowing relatively high *A* and *g*. The role of xylem cavitation and embolism repair
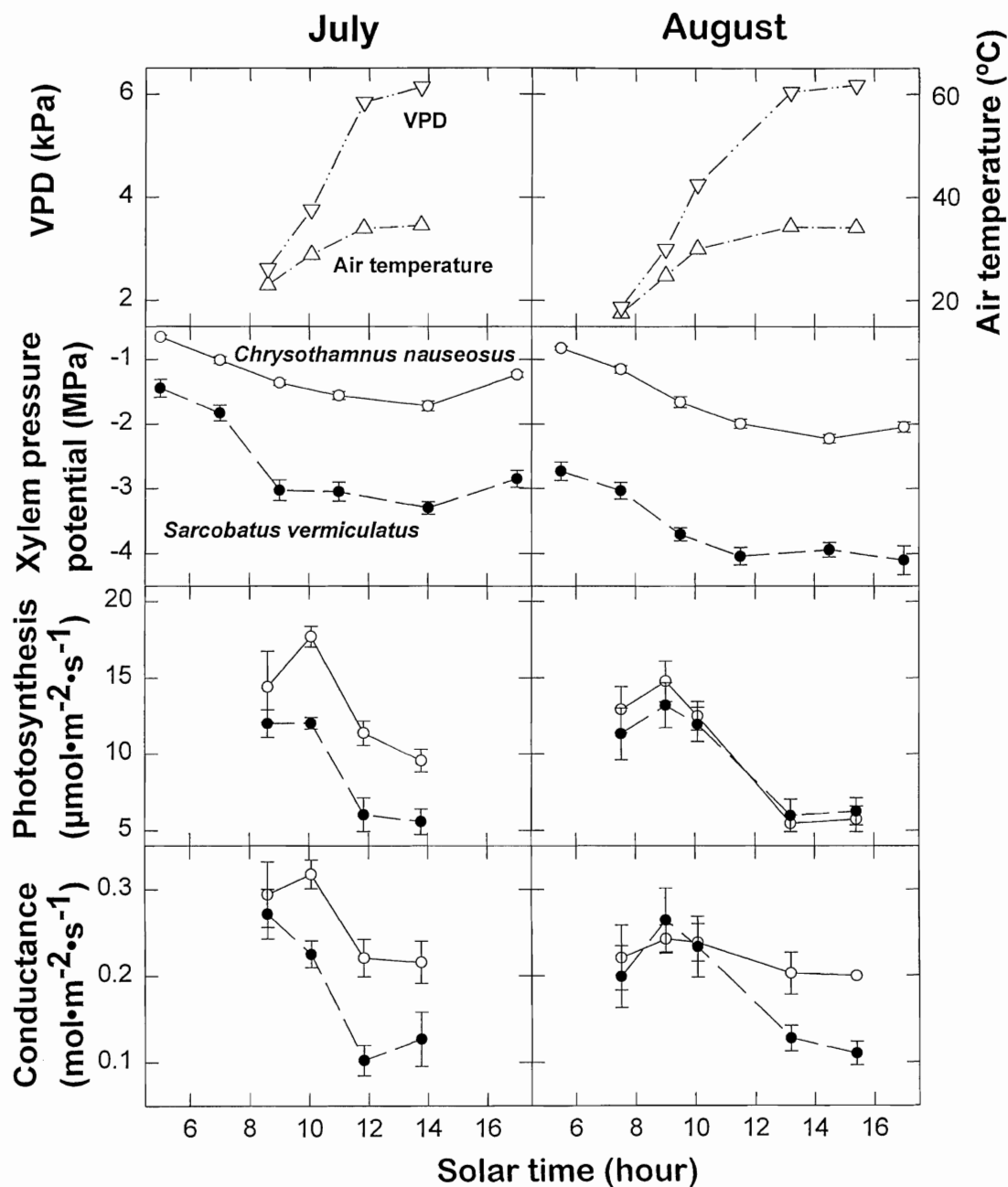
Fig. 4.   Diurnal xylem pressure potentials (ψ), rates of photosynthesis (*A*), and conductance (*g*) for *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* at Mono Lake, CA on 7 July and 17 August 1994. Leaf-to-air vapor pressure deficit (VPD) and air temperature at the time of measurement are also shown; mean ± 1 SE, *N* = 6 (for statistics see Table 2).

needs to be considered before this possibility is discounted (Tyree and Sperry, 1989).

As mentioned above, the differences in xylem pressure potentials between *Chrysothamnus* and *Sarcobatus* are accounted for, at least partially, by the species differences in leaf chemistry, with greater leaf ion content associated with more negative leaf osmotic potentials and xylem pressure potentials in *Sarcobatus*. Soil cores at the study site indicate fairly uniform soil chemistry consisting of low ion concentrations through both the aeolian sand and buried lacustrine clay substrates (EC ranges from 0.9 to 1.7 dS/m in saturated soil pastes of samples from 0 to 4

m depth). One exception to this uniformity is increased Na concentrations immediately under the *Sarcobatus* canopies (Schaber and Richards, 1995). At our study site, this Na (and B) enrichment is small, and lateral roots of *Sarcobatus* extend many metres beyond the canopy (J.H. Richards and L.A. Donovan, field excavations). The soils at the site are marginally saline because some Na is available in both the soil and groundwater, but cannot be considered saline as soil-saturated pastes from shrub interspace areas usually have EC values less than the technical saline soil guideline (1.5 dS/m; Richards, 1954). If the two shrub species are exposed to a similar belowground
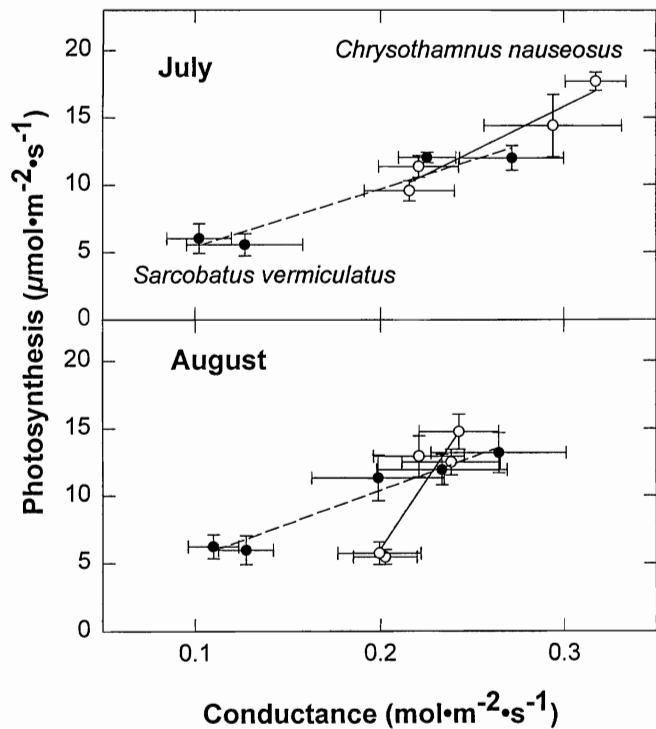
Fig. 5. Relationship of photosynthesis (A) to conductance (g) for Chrysothamnus nauseosus and Sarcobatus vermiculatus at Mono Lake, CA on 7 July and 17 August 1994; mean ± 1 SE, N = 6 (for regression statistics see text).

TABLE 3. One-way analysis of variance comparisons between Chrysothamnus nauseosus and Sarcobatus vermiculatus for instantaneous WUE (water-use efficiency) and NUE (nitrogen-use efficiency) ($N = 6$) at Mono Lake, CA in 1994. For each variable: mean ± SE, F statistic and significance. $* P < 0.05$, $** P < 0.01$, $*** P < 0.001$, and NS is not significant.

	Chrysothamnus	Sarcobatus	F
Instantaneous WUE			
(A/E, mmol CO_2/mol H_2O)			
7 July	1.49 ± 0.04	1.44 ± 0.06	0.6NS
18 August	2.06 ± 0.13	1.73 ± 0.14	2.9NS
Instantaneous NUE			
(A/N, μmol $CO_2 \cdot mol\ N^{-1} \cdot s^{-1}$)			
7 July	57.0 ± 4.6	52.6 ± 5.6	0.7NS
18 August	64.3 ± 7.9	82.5 ± 9.8	0.2NS

son, 1980). Differences in membrane transport have been associated with differential root membrane selectivity for K and Na (Greenway and Munns, 1980; Osmond, Björkman, and Anderson, 1980; Reimann and Breckle, 1993). Sarcobatus has high leaf Na levels and molar ratios of K/Na <<1, which are characteristic of the Chenopodiaceae and halophytes from other dicotyledonous families. The lower leaf Na values and K/Na >1 for Chrysothamnus are more similar to values associated with nonhalophytes. These comparative Na contents and K/Na molar ratios hold for halophytes and nonhalophytes co-occurring in natural habitats in the Great Basin (Wiebe and Walter, 1972) as well as for those grown together experimentally in standard nutrient media with added NaCl, although addition of high concentrations of K to the substrate can increase K/Na ratios for both halophytes and nonhalophytes (Reimann and Breckle, 1993). Ca also plays a role in membrane integrity and ability to maintain ion selectivity for nonhalophytes (Cramer, Läuchli, and Epstein, 1986). In our study, leaf Ca was not significantly different for these species at any time during the growing season, but xylem Ca in August was much higher for Chrysothamnus than for Sarcobatus.

When Na is taken up by halophytes, it is generally sequestered in vacuoles in mature leaves, and balanced with cytoplasmic K and organic solutes, particularly glycinebetaine for many Chenopodiaceae (Flowers, Troke, and Yeo, 1977; Storey, Ahmad, and Wyn Jones, 1977; Gorham and Wyn Jones, 1983; but see Cheeseman, 1988). This increased leaf ion concentration can be used to maintain lower osmotic potentials and thus maintain water uptake (Atkinson et al., 1967; Flowers, Troke, and Yeo, 1977; Osmond, Björkman, and Anderson 1980; Glenn and O'Leary, 1984; Reimann and Breckle, 1993). Romo and Haferkamp (1989) concluded that Sarcobatus reduced osmotic potential in order to maintain turgor and high stomatal conductance, as compared to an adjacent nonhalophyte, Artemisia tridentata. In our study, large species differences in leaf chemistry, succulence, and water relations might be expected to lead to differences in gas exchange characteristics. However, Chrysothamnus and Sarcobatus showed similar diurnal gas exchange patterns, and the rates of photosynthesis and conductance were different only by an average of 1.5 times in July and were not different in August (Fig. 4). NUE and WUE also did not differ. This is surprising since greater ion

chemical environment, in addition to the similar water availability environment discussed above, then many differences in water relations and leaf chemistry may reflect differences in how the two species are dealing with the low ion concentrations in the sands, lacustrine clays, and groundwater.

The Na concentrations of saturated soil pastes or groundwater provide minimum estimates of the concentrations to which the roots of the two species would be exposed. Based on a comparison of these soil and groundwater Na concentrations (soil solution 230–345 mg/L; groundwater 475 mg/L; see Results) and Na concentrations in xylem sap (142 and 22 mg/L, respectively; see Table 1), both species partially exclude Na prior to xylem transport. Chrysothamnus has much higher selectivity against sodium than Sarcobatus, as also reflected in leaf Na accumulations through the season (Fig. 3). The fact that field soil moisture content is generally much lower than that of saturated paste would increase estimates of Na concentration in the soil solution and thus increase the estimated extent of Na exclusion occurring in the field.

All plants take up some Na, and differences in leaf chemistry are the sum of differences in salinity of substrate, root uptake, transfer to the xylem and leaves, and leaf retention (Atkinson et al., 1967; Cheeseman, 1988; Wolf et al., 1990; Reimann and Breckle, 1993). Halophytes are distinguished from nonhalophytes by the extent to which they take up and tolerate larger amounts of Na in their leaves (Flowers, Troke, and Yeo, 1977; Greenway and Munns, 1980; Osmond, Björkman, and Ander-

content and more negative osmotic potentials for *Sarcobatus* might be expected to be associated with greater N investment in organic acids as cytoplasmic osmotica. These shrub species have similar patterns of gas exchange in July and August, despite the large underlying differences in water relations and leaf chemistry. Since both species maintain large green leaf areas through summer and have similarly open canopies, the similarities in gas exchange suggest that they can maintain comparable whole-plant carbon gain despite the large differences in water relations and salinity tolerance.

LITERATURE CITED

ATKINSON, M. R., G. P. FINDLAY, A. B. HOPE, M. G. PITMAN, H. D. W. SADDLER, AND K. R. WEST. 1967. Salt regulation in the mangroves *Rhizophora mucronata* Lam. and *Aegialitis annulata* R. Br. *Australian Journal of Biological Science* 20: 589–599.

BILLINGS, W. D. 1949. The shadscale vegetation zone of Nevada and eastern California in relation to climate and soils. *American Midland Naturalist* 42: 87–109.

———. 1951. Vegetational zonation in the Great Basin of western North America. *In* Comptes Rendus du Colloque sur les Bases Ecologique de la Regeneration de la Vegetation des Zones Arides, 101–122. International Union of Biological Sciences, Paris.

BRANSON, F. A., R. F. MILLER, AND I. S. MCQUEEN. 1976. Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. *Ecology* 57: 1104–1124.

CHEESEMAN, J. M. 1988. Mechanisms of salinity tolerance in plants. *Plant Physiology* 87: 547–550.

CLINE, J. F., AND W. H. RICKARD. 1974. Isotope uptake from halophyte-affected soil. *Northwest Science* 48: 235–238.

COMSTOCK, J. P., AND J. R. EHLERINGER. 1992. Plant adaptation in the Great Basin and Colorado Plateau. *Great Basin Naturalist* 52: 195–215.

CRAMER, G. R., A. LÄUCHLI, AND E. EPSTEIN. 1986. Effects of NaCl and CaCl$_2$ on ion activities in complex nutrient solutions and root growth of cotton. *Plant Physiology* 81: 792–797.

DAVIS, S. D., AND H. A. MOONEY. 1986. Water use patterns of four co-occurring chaparral shrubs. *Oecologia* 70: 172–177.

DETLING, J. K., AND L. G. KLIKHOFF. 1973. Physiological response to moisture stress as a factor in halophyte distribution. *American Midland Naturalist* 90: 307–318.

DONOVAN, L. A., AND J. R. EHLERINGER. 1994a. Carbon isotope discrimination, water-use efficiency, growth, and mortality in a natural shrub population. *Oecologia* 100: 347–354.

———, AND ———. 1994b. Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology* 8: 289–297.

EDDLEMAN, L. E., AND J. T. ROMO. 1987. Sodium relations in seeds and seedlings of *Sarcobatus vermiculatus*. *Soil Science* 143: 120–123.

FIELD, C., J. MERINO, AND H. A. MOONEY. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. *Oecologia* 60: 384–389.

FIREMAN, M., AND H. E. HAYWARD. 1952. Indicator significance of some shrubs in the Escalante desert, Utah. *Botanical Gazette* 114: 143–155.

FLANAGAN, L. B., J. R. EHLERINGER, AND J. D. MARSHALL. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant, Cell and Environment* 15: 831–836.

FLOWERS, T. J., P. F. TROKE, AND A. R. YEO. 1977. The mechanism of salt tolerance in halophytes. *Annual Review of Plant Physiology* 28: 89–121.

FORT, K. P., AND J. H. RICHARDS. 1995. Seed dispersal onto recently exposed playa at Mono Lake, CA. *Bulletin of the Ecological Society of America* 76: 84 (Abstract).

GATES, D. H., L. A. STODDART, AND C. W. COOK. 1956. Soil as a factor influencing plant distribution on salt-deserts of Utah. *Ecological Monographs* 26: 155–175.

GLENN, E. P., AND J. W. O'LEARY. 1984. Relationship between salt

accumulation and water content of dicotyledonous halophytes. *Plant, Cell and Environment* 7: 253–261.

GORHAM, J., AND R. G. WYN JONES. 1983. Solute distribution in *Suaeda maritima. Planta* 157: 344–349.

GREENWAY, H., AND R. MUNNS. 1980. Mechanisms of salt tolerance in nonhalophytes. *Annual Review of Plant Physiology* 31: 149–190.

GUREVITCH, J., AND S. T. CHESTER, JR. 1986. Analysis of repeated experiments. *Ecology* 67: 251–255.

HALLGREN, S. W., M. RÜDINGER, AND E. STEUDLE. 1994. Root hydraulic properties of spruce measured with the pressure probe. *Plant and Soil* 167: 91–98.

HARR, R. D., AND K. R. PRICE. 1972. Evapotranspiration from a greasewood-cheatgrass community. *Water Resources Research* 8: 1199–1203.

HINCKLEY, T. M., J. P. LASSOIE, AND S. W. RUNNING. 1978. Temporal and spatial variations in the water status of forest trees. Forest Science Monograph 20, Society of American Foresters, Bethesda, MD.

MCNULTY, I. 1969. The effect of salt concentration on growth and metabolism of a succulent halophyte. *In* C. C. Hoff and M.L. Piedesel [eds.], Physiological systems in semi-arid environments, 255–262. New Mexico University Press, Albuquerque, NM.

MULLER, M. W., J. H. RICHARDS, AND L. A. DONOVAN. 1995. Soil water availability to *Sarcobatus vermiculatus* along a successional gradient at Mono Lake, CA. *Bulletin of the Ecological Society of America* 76: 192 (Abstract).

OSMOND, C. B., O. BJÖRKMAN, AND D. J. ANDERSON. 1980. Physiological processes in plant ecology: toward a synthesis with *Atriplex*. Springer-Verlag, Berlin.

POTVIN, C., M. J. LECHOWICZ, AND S. TARDIF. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71: 1389–1400.

REIMANN, C., AND S.-W. BRECKLE. 1993. Sodium relations in Chenopodiaceae: a comparative approach. *Plant, Cell and Environment* 16: 323–328.

RICHARDS, J. H., AND M. M. CALDWELL. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73: 486–489.

RICHARDS, L. A. 1954. Diagnosis and improvement of saline and alkali soils. United States Department of Agriculture Handbook Number 60. Washington, DC.

RICKARD, W. H. 1964. Demise of sagebrush through soil changes. *BioScience* 14: 43–44.

———. 1965. Sodium and potassium accumulation by greasewood and hopsage leaves. *Botanical Gazette* 126: 116–119.

———, J. F. CLINE, AND R. O. GILBERT. 1973. Soil beneath shrub halophytes and its influence upon growth of cheatgrass. *Northwest Science* 47: 213–217.

———, AND J. L. WARREN. 1981. Response of steppe shrubs to the 1977 drought. *Northwest Science* 55: 108–112.

ROBERTSON, J. H. 1983. Greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.). *Phytologia* 54: 309–324.

ROBINSON, T. W. 1958. Phreatophytes. United States Geological Survey Water-Supply Paper Number 1423. Washington, DC.

ROLLINS, M. B., A. S. DYLLA, AND R. E. ECKERT, JR. 1968. Soil problems in reseeding a greasewood-rabbitbrush range site. *Journal of Soil and Water Conservation* 23: 138–140.

ROMO, J. T., AND M. R. HAFERKAMP. 1989. Water relations of *Artemisia tridentata* ssp. *wyomingensis* and *Sarcobatus vermiculatus* in the steppe of southeastern Oregon. *American Midland Naturalist* 121: 155–164.

ROUNDY, B. A., J. A. YOUNG, AND R. A. EVANS. 1981. Phenology of salt rabbitbrush (*Chrysothamnus nauseosus* ssp. *consimilis*) and greasewood (*Sarcobatus vermiculatus*). *Weed Science* 29: 448–454.

SAH, R. N., AND R. O. MILLER. 1992. Spontaneous reaction for acid dissolution of biological tissues in closed vessels. *Analytical Chemistry* 64: 230–233.

SAS. 1989. SAS/STAT user's guide, Version 6, 4th ed., vols. 1 and 2. SAS Institute, Cary, NC.

SCHABER, E. J., AND J. H. RICHARDS. 1995. Nutrient and toxic ion constraints to shrub establishment on sand dunes at Mono Lake, CA. *Bulletin of the Ecological Society of America* 76: 237 (Abstract).

SHANTZ, H. L., AND R. L. PIEMEISEL. 1940. Types of vegetation in Escalante Valley, Utah, as indicators of soil conditions. United

States Department of Agriculture Technical Bulletin Number 713. Washington, DC.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman, New York, NY.

STOREY, R., N. AHMAD, AND R. G. WYN JONES. 1977. Taxonomic and ecological aspects of the distribution of glycinebetaine and related compounds in plants. *Oecologia* 27: 319–332.

STEUDLE, E. 1994. Water transport across roots. *Plant and Soil* 167: 79–90.

TOFT, C. A. 1995. A 10-year demographic study of rabbitbrush (*Chrysothamnus nauseosus*): growth, survival and water limitation. *Oecologia* 101: 1–12.

TYREE, M. T., AND J. S. SPERRY. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology* 40: 19–38.

VON ENDE, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. *In* S. M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments, 113–137. Chapman & Hall, New York, NY.

WALLACE A., E. M. ROMNEY, AND V. Q. HALE. 1973. Sodium relations in desert plants. 1. Cation contents of some plant species from the Mojave and Great Basin deserts. *Soil Science* 115: 284–287.

WEST, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. *In* M. G. Barbour and W. D. Billings [eds.], North American terrestrial vegetation, 213–230. Cambridge University Press, New York, NY.

WIEBE, H. H., AND H. WALTER. 1972. Mineral ion composition of halophytic species from northern Utah. *American Midland Naturalist.* 87: 241–245.

WOLF, O., R. MUNNS, M. L. TONNET, AND W. D. JESCHKE. 1990. Concentrations and transport of solutes in xylem and phloem along the leaf axis of NaCl-treated *Hordeum vulgare*. *Journal of Experimental Botany* 41: 1133–1141.