

WATER POTENTIAL AND IONIC EFFECTS ON GERMINATION AND SEEDLING GROWTH OF TWO COLD DESERT SHRUBS¹

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We tested expectations that two desert shrubs would differ in germination and seedling relative growth rate (RGR) responses to Na and Ψ_s stress. The study species, *Chrysothamnus nauseosus* ssp. *consimilis* and *Sarcobatus vermiculatus* (hereafter referred to by genus), differ in their distribution along salinity gradients, with *Chrysothamnus* inhabiting only less saline areas. In growth chamber studies, declining Ψ_s (-0.82 to -2.71 MPa) inhibited germination of both species, and *Chrysothamnus* was less tolerant of Ψ_s stress than *Sarcobatus*. Germination fell below 10% for *Chrysothamnus* at -1.64 MPa (NaCl and PEG), and for *Sarcobatus* at -2.4 MPa PEG. Neither species exhibited ion toxicity. There was substantial ion enhancement for *Sarcobatus* in lower Ψ_s , allowing for 40% germination in -2.71 MPa NaCl. For seedling RGR, species were not different at -0.29 or -0.82 MPa (0 and 100 mmol/L NaCl, respectively), but *Chrysothamnus* RGR declined substantially at -1.3 MPa (200 mmol/L NaCl). The greater stress tolerance of *Sarcobatus* was not associated with a lower RGR under nonsaline conditions. Species differences in seed and seedling Ψ_s stress tolerance probably contribute to the restricted distribution of *Chrysothamnus* to less saline areas. The Na uptake of *Sarcobatus* seedlings enhances its ability to deal with declining Ψ_s and establish in more saline areas.

Key words: *Chrysothamnus nauseosus*; plant distribution; relative growth rate; salinity; *Sarcobatus vermiculatus*; seed germination; stress tolerance.

Seed germination and seedling growth are critical life history stages often subject to high mortality rates. Seeds and seedlings may be less stress tolerant than adults or may be exposed to the more extreme environmental fluctuations at or near the soil surface. In either case, the ability to successfully negotiate this “regeneration niche” can be a strong determinant of species distributions in harsh environments. In coastal and inland saline habitats, salinity and water availability (flooding and/or drought) are the abiotic stresses thought to primarily limit species distributions (Waisel, 1972; Ungar, Benner, and McGraw, 1979; Snow and Vince, 1984; Ungar, 1991; Pennings and Callaway, 1992; Ball and Pidsley, 1995). There is contrasting evidence as to whether the differential germination and early growth responses to salinity contribute to species distributions and zonation in these habitats (Waisel, 1972; Rozema, 1975; Rabinowitz, 1978; Huiskes et al., 1985; Ungar, 1991). We investigated seed germination and seedling growth responses to salinity for two desert shrubs that are differentially distributed along a steep salinity gradient at Mono Lake, CA.

Increasing salinity generally reduces germination in glycophytes and to a lesser degree in halophytes (Hayward and Bernstein, 1958; Waisel, 1972; Ungar, 1991, 1996; Khan and Ungar, 1997). Two processes mediate

this reduction: osmotic effects due to declining soil solute potential (Ψ_s), creating a water stress for the plant, and ionic effects due to seed or seedling ion uptake and/or accumulation (Hayward and Bernstein, 1958; Waisel, 1972; Ungar, 1991). Under natural conditions, however, these basic effects additionally interact with soil moisture content (volume of water relative to soil). As soil moisture declines, soil total water potential (Ψ_w) declines due to both soil matric potential (Ψ_m) and covarying soil Ψ_s , which reflects increased concentration of solutes (Caldwell, 1974; Roundy, 1984; Hardegree and Emmerich, 1990). Thus it is a challenge to examine the interacting effects Ψ_s and Ψ_m may have on plant establishment in saline desert soils that routinely experience wide fluctuation in soil moisture at the surface.

Salinity-induced declines in germination are usually due to only osmotic (substrate Ψ_s) effects for halophytes, whereas glycophytes are more likely to exhibit additional ion toxicity (Hayward and Bernstein, 1958; Ungar and Hogan, 1970; Macke and Ungar, 1971; Cluff, Evans, and Young, 1983; Romo and Haferkamp, 1987; but see Hyder and Yasmin, 1972). Ionic effects may be distinguished from osmotic effects by comparing the effects of salt solutions and isotonic (equal Ψ_s) solutions of an inert osmotic medium such PEG (polyethylene glycol) that cannot penetrate into the cell wall. Inhibition of germination in PEG-treated seeds is attributed to osmotic effects, and any difference in germination of salt-treated relative to PEG-treated seeds is attributed to ionic effects. Although usually negative, ionic effects occasionally increase germination over the baseline Ψ_s (Macke and Ungar, 1971; Romo and Eddleman, 1985). In this case, ion uptake assists in making the seed or seedling Ψ_w more negative than soil Ψ_w , thus helping the plant to overcome the Ψ_s effects of the saline substrate (Eddleman and Romo,

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1987). The general lack of ion toxicity for halophytes has been alternatively confirmed by almost complete recovery of germination potential after salt-treated seeds are returned to fresh water (Ungar, 1996; Egan, Ungar, and Meekins, 1997).

Biotic factors can also play a role in determining species distributions in harsh habitats (Ungar, Benner, and McGraw, 1979; Bertness and Ellison, 1987; Ungar, 1992; Bertness and Hacker, 1994). Plant responses to abiotic and biotic factors may be related through relative growth rate (RGR). Adaptations to unproductive and adverse habitats (i.e., stress tolerance) often include an inherently low RGR (Grime and Hunt, 1975; Grime, 1979; Chapin, 1991; Chapin, Autumn, and Pugnaire, 1993; Ball and Pidsley, 1995). Because low RGR is also thought to be correlated with poor competitive ability, there may be an apparent trade-off between stress tolerance and competitive ability. The upper limits for the distribution of halophytic species along salinity gradients may be limited by competition with less stress-tolerant species (Snow and Vince, 1984; Kenkel et al., 1991). Thus, it is worthwhile to determine whether greater stress tolerance is associated with inherently lower maximum RGR under optimal conditions.

At Mono Lake, California, declines in the lake level have created a steep abiotic stress gradient by exposing former lakebed substrates. At the Mono Dunes Ecosystem Research Site, the end of the gradient farthest from shoreline consists of marginally saline sand dunes (Toft, 1995; Donovan, Richards, and Muller, 1996). This site supports a diverse plant community dominated by two shrubs: *Chrysothamnus nauseosus* (Palla.) Britt. ssp. *consimilis* (E. Greene) H. M. Hall & Clements (Asteraceae) and *Sarcobatus vermiculatus* (Hook.) Torrey (Chenopodiaceae). Soil salinity increases with proximity to the Mono Lake shoreline and more saline substrates are populated only by *Sarcobatus* and *Distichlis spicata* (Schaber, 1994; Donovan, Richards, and Schaber, 1997). Although *Chrysothamnus* is generally characterized as a Na-excluding glycophyte, the ssp. *consimilis* has been described as somewhat salt tolerant (Roundy, Young, and Evans, 1981). In contrast, *Sarcobatus* is a Na-accumulating halophyte that can survive in solutions up to 1 mol/L NaCl (McNulty, 1969; Glenn and O'Leary, 1984). Thus, species differences in salinity tolerance at various life history stages may drive differences in spatial distribution. Intermediate regions of the gradient, where *Chrysothamnus* does not occur, do receive high seed input and can support *Chrysothamnus* germination and growth when well watered (Schaber, 1994; Fort and Richards, 1998). This suggests that Na toxicity is not preventing *Chrysothamnus* recruitment in these soils. However, Na ion and Ψ_s effects at lower soil Ψ_w warrant further examination.

In this study, our first objective was to determine whether the study species differed in seed germination responses to declining Ψ_s generated by NaCl or PEG. We predicted that Ψ_s inhibition of germination would be greater for *Chrysothamnus* than for *Sarcobatus* and that NaCl would have both osmotic and ion toxicity effects on *Chrysothamnus* and osmotic and possibly ion enhancement effects on *Sarcobatus*. Our second objective was to determine whether the study species differed in

seedling RGR. We predicted that declines in seedling RGR in response to salinity would be greater for *Chrysothamnus* than for *Sarcobatus*, but that *Chrysothamnus* would have a higher RGR than *Sarcobatus* in nonsaline substrates.

MATERIALS AND METHODS

Seeds of *Chrysothamnus* and *Sarcobatus* mature and disperse by wind in the fall, and germination is most abundant in early spring when surface soil EC and pH are at a minimum due to snowmelt and spring rains (Schaber, 1994). At maturity, *Sarcobatus* seeds contain a fully formed chlorophyllous embryo, surrounded by a membranous pericarp (Eddleman, 1979). The embryo uncoils within hours of imbibition when the pericarp is weak or ruptured. The intact pericarp can inhibit germination, but under natural conditions it is probably breached during overwintering by freeze-thaw cycles and sand abrasion. *Sarcobatus* has a 30–60 d after-ripening period, and cold stratification is not required, but after cold stratification optimal germination temperatures are 20°–30°C (Eddleman, 1979). *Chrysothamnus* seeds have temperature-dependent dormancy that varies by population, with the temperature response generally appropriate to ensure early spring germination (Khan et al., 1987; Meyer, McArthur, and Jorgensen, 1989).

For our experiment, seeds of *Chrysothamnus* and *Sarcobatus* were collected in the fall of 1994 from the Mono Dunes Ecosystem Research Site, near Mono Lake, California, USA (38°5' N, 118°58' W), and stored at 4°C until use. The study was conducted in early 1996 using *Chrysothamnus* seeds (from six plants) that were visually checked for presence of an embryo, and *Sarcobatus* seeds (from eight plants) that were scarified by hand using sandpaper to rupture the pericarp and to check for presence of an embryo.

Germination study—Four replicates of 25 randomly selected seeds each were used for each treatment. Treatment factors were two species (SP), two osmotica (OS), and six water potentials (Ψ_s), applied in a randomized complete block design. Additionally, controls with no osmotica were included for each species in each block. Replicates consisted of 11-cm diameter covered petri dishes wrapped with Parafilm[®] and contained 40 g of sterilized river sand brought to field capacity with solution. Solutions consisted of one-fourth-strength modified No. 2 Hoagland's solution (Epstein, 1972) mixed with osmotica: NaCl or PEG (m.w. 8000). NaCl solutions were 100, 200, 300, 400, 500, or 600 mmol/L. Isotonic quantities of PEG were computed by the program of Michel and Radcliffe (1995). Soil Ψ_s (approximated by Ψ_w due to low Ψ_m) was then measured with individually calibrated thermocouple psychrometers (series 83, J. R. D. Merrill, Logan, Utah, USA) (Brown and Bartos, 1982). Final soil Ψ_s treatments were –0.29 MPa (Hoagland's solution only), –0.82, –1.30, –1.65, –2.04, –2.40 and –2.72 MPa. *T* test comparisons of measured Ψ_s confirmed that there were no significant differences for NaCl-enhanced sand and PEG-enhanced sand at each target Ψ_s .

Seeds were dusted with N-[(trichloromethyl)-thio]-4-cyclohexene-1,2-dicarboximide (Captan[®]) prior to incubation to control fungi. Seeds were incubated in a growth chamber at 25°C, which is within the range of optimal temperature for germination of both species (Romo and Eddleman, 1985; Khan et al., 1987) with a photoperiod of 14-h:10-h (light:dark). Although temperature does affect germination of these species, the temperature optima are broad and decreasing temperature does not change the basic shape of the germination response to salinity (Eddleman, 1979; Romo and Eddleman, 1985; Khan et al., 1987). Light was provided by compact fluorescent bulbs (15 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 400–700 nm). Germination was recorded daily through 20 d. *Chrysothamnus* seeds were considered germinated upon emergence of the radicle. *Sarcobatus* seeds were considered germinated when the embryos uncoiled and root hairs were evident. We were unable to test recovery of germination potential after returning salt-treated seeds to fresh water because

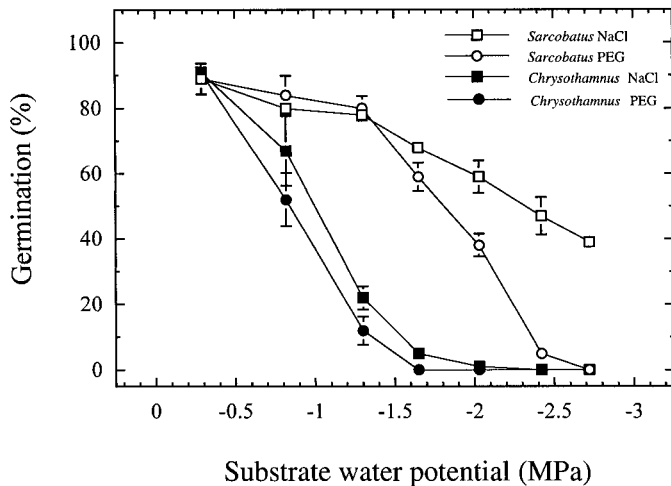


Fig. 1. Seed germination (mean \pm SE) of *Chrysothamnus* and *Sarcobatus* as a function of osmotica (NaCl or PEG) and substrate water potential.

of fungal infections on many of the ungerminated seeds by the end of the 20-d treatments.

Germination percentage values (Percentage of total number of seeds in each petri dish) on day 20 were arcsine transformed and analyzed in a three-way analysis of variance (ANOVA) procedure (PROC GLM; SAS, 1989). When a significant three-way interaction was found, further analyses were made using a two-way ANOVA.

RGR study—Seeds were germinated on moistened filter paper and subsequently transplanted to 3.8 cm diameter \times 19 cm long tube pots of washed river sand, \sim 72 h after radicle elongation. Plants were grown in a growth chamber at a thermoperiod of 25°C:15°C (day:night) and a 14-h photoperiod (700 μ mol·m⁻²·s⁻¹, 400–700 nm), and watered daily. The three treatments were 0, 100, and 200 mmol/L NaCl in one-fourth-strength modified Hoagland's solution. At field capacity, soils watered with these solutions had soil Ψ_w of -0.29 , -0.82 , and -1.30 MPa, respectively. Half-strength salinity treatments began on day 11 (after transplant), and full-strength salinity treatments followed on day 14.

The experiment used a split-split plot design with three factors (species, salinity, and harvest date). Plants were harvested on days 19, 24, 30, 36, 42, and 48 after transplant, using five replicates of each species in each salt treatment at each harvest date. Leaf area was measured and analyzed with a scanner and Delta-T Scan software (Delta-T Devices Ltd., Cambridge, UK). Roots were excavated using water to gently wash away the sand. Plants were dried at 70°C to determine total dry biomass (leaf, stems, and roots). For plants harvested on days 19 and 36, ground leaves were ashed at 500°C and the ash was dissolved in dilute acid (10% nitric and 30% hydrochloric acid). Leaf extracts were analyzed for Na, K, Ca, and Mg with an Inductively Coupled Plasma Emission Spectrometer (965, Thermo Jarrell Ash Corp., Franklin, Massachusetts, USA) at the University of Georgia Chemical Analysis Laboratory.

Relative growth rates (RGR, g·g⁻¹·d⁻¹) were analyzed using the method of Poorter and Lewis (1986). In this ANOVA analysis, ln-transformed plant biomass (dependent variable) is modeled as a function of harvest date. Significant interaction terms that include harvest date (HD) indicate differences in RGR. Graphs of RGR were made using a modification of the classical interval method that derives RGR values for nonadjacent dates (skipping one harvest) to minimize auto-correlation (Poorter, 1989). These RGR values were assigned to each harvest day in that interval and the resulting two to three RGR values for each harvest date were then averaged. This method smoothes out variation between harvests while retaining trends in RGR (Poorter, 1989).

TABLE 1. Results of two-way ANOVA for germination within *Chrysothamnus* or *Sarcobatus*. Seeds were exposed to six levels of water potentials, with water potential created by two different osmotica (NaCl and PEG). ns is not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Source	df	MS	F
<i>Chrysothamnus</i>	Block	3	0.0162	1.50ns
	Water potential (Ψ_s)	5	1.0100	93.40***
	Osmotica (OS)	1	0.1036	9.58**
	$\Psi_s \times OS$	5	0.0150	1.39ns
	Error	33	0.0108	
<i>Sarcobatus</i>	Block	3	0.0032	0.35ns
	Water potential (Ψ_s)	5	0.8857	97.54***
	Osmotica (OS)	1	0.6718	73.99***
	$\Psi_s \times OS$	5	0.1995	21.97***
	Error	33	0.0090	

RGR is the product of the LAR (leaf area ratio, m²/g) and NAR (net assimilation rate, g·m⁻²·d⁻¹). Instantaneous values of LAR were calculated using the equation of Hunt (1990, p. 16). Differences among instantaneous values of LAR for each harvest were examined by an ANOVA, and significant differences among means were evaluated using the Student-Newman-Keuls range test. Instantaneous NAR was calculated using the equation of Hunt (1990, p. 16), using non-adjacent intervals and averaging as was done for the RGR graphing. However, NAR values could not be statistically compared in this study design because (a) NAR values for each date were not independent of other dates and this ruled out the use of separate ANOVAs for each harvest, and (b) NAR cannot be represented by the slope of a line plotting two dependent variables (i.e., it is a compound growth rate parameter containing three variables [Hunt, 1990]), and this rules out the RGR ANOVA technique. The relationships between LAR and RGR and between NAR and RGR were analyzed with regressions.

RESULTS

Germination study—In the control treatment (-0.29 MPa, no NaCl or PEG), *Chrysothamnus* and *Sarcobatus* germination averaged 91.0 ± 1.2 and $89.0 \pm 3.1\%$, respectively, and did not differ significantly between the species (df = 1, $F = 0.10$, $P = 0.76$) (Fig. 1). For germination in the remaining six Ψ_s treatments, the results of a three-way ANOVA indicated that the main effects of species (SP), water potential (Ψ_s), and osmotica (OS) were all highly significant ($P < 0.001$). However, all of the interaction terms were also highly significant ($P < 0.001$), so it was necessary to perform further analyses within each species in order to elucidate the nature of the differences.

For *Chrysothamnus*, the main effects of Ψ_s and OS were significant, and interaction term of $\Psi_s \times OS$ was not significant (Table 1). Germination declined with decreasing Ψ_s in both NaCl and PEG and NaCl increased germination by a small percentage at Ψ_s as compared to PEG (Fig. 1). *Chrysothamnus* germination fell below 10% at -1.65 MPa for both NaCl and PEG. The few seeds that did germinate in NaCl at -1.65 MPa (5%) and -2.03 MPa (1%) looked sickly and did not proceed with radicle elongation.

For *Sarcobatus*, the main effects of Ψ_s and OS were significant, and, unlike *Chrysothamnus*, the interaction term of $\Psi_s \times OS$ was also highly significant (Table 1). Germination declined with Ψ_s in both NaCl and PEG, but

TABLE 2. Results of the split-split plot ANOVA using ln biomass as the dependent variable for *Chrysothamnus* and *Sarcobatus*. Differences in RGR are indicated by significant interaction terms including Harvest Date (HD) as a factor. Seedlings were exposed to three levels of salt concentrations for 48 d. ns is not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source	df	MS	F
Block	4	0.0113	0.07ns
Salinity (SL)	2	23.0705	148.46***
Mainplot error	8	0.1554	
Species (SP)	1	0.2543	0.94ns
SL × SP	2	4.2394	15.70***
Subplot error	12	0.2700	
Harvest (HD)	3	21.8570	200.90***
SL × HD	6	0.8409	7.73***
SP × HD	3	1.2669	11.65***
SL × SP × HD	6	0.5207	4.79***
Sub-subplot error	72	0.1088	

germination was greatly enhanced by the NaCl at lower Ψ_s , as compared to PEG (Fig. 1). *Sarcobatus* seeds were able to germinate in all treatments except -2.72 MPa PEG. Seeds that germinated in -2.42 MPa PEG (5%) were barely able to uncoil, looked sickly, and did not proceed with radicle elongation. *Sarcobatus* maintained the ability to germinate in solutions of lower Ψ_s than *Chrysothamnus*, regardless of whether the osmotica was NaCl or PEG.

RGR study—The split-split plot ANOVA for ln-transformed plant biomass (Table 2), which incorporated main effects of species (SP), salinity (SL), and harvest date (HD), used data from the first four harvests because *Chrysothamnus* seedlings did not survive the 200 mmol/L NaCl treatment after the fourth harvest. The significant second-order interaction in this analysis (SL × SP × HD) indicates that overall *Chrysothamnus* and *Sarcobatus* have different RGRs, but that the differential response to SL treatment needs to be taken into account to describe the species differences. RGR analysis of SP × HD for each salinity treatment indicated that the two species did not differ in RGR at 0 or 100 mmol/L NaCl (SP × HD not significant, Table 3), using data from all six harvests. At the 200 mmol/L NaCl, however, *Sarcobatus* did have a significantly higher RGR than *Chrysothamnus* (SP × HD significant, Table 3), using data from the first four harvests.

Additional split-plot analyses allow for intraspecific comparisons of RGR across salt treatments. For *Chrysothamnus*, RGR declined with increasing salinity (SL × HD significant, Table 4, Fig. 2). In contrast, RGR of *Sarcobatus* did not differ for the three salinities (SL × HD not significant, Table 4, Fig. 2). NAR roughly paralleled RGR for both species. NAR for *Chrysothamnus* at 0 mmol/L NaCl was ~900% (on average) higher than that for 200 mmol/L NaCl. For LAR, there were significant differences for *Chrysothamnus* on days 19, 36, and 48 and for *Sarcobatus* on days 30, 36, and 48. RGR was positively correlated with NAR (Fig. 3, $P < 0.001$) with r^2 values of 0.88 and 0.76 for *Chrysothamnus* and *Sarcobatus*, respectively. In contrast, RGR was not significantly correlated with LAR for either species.

TABLE 3. Results of split-plot ANOVA of ln biomass of *Chrysothamnus* and *Sarcobatus* for each NaCl concentration. Differences in RGR are indicated by significant interaction terms including Harvest Date (HD) as a factor. ns is not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Salinity	Source	df	MS	F
0 mmol/L (6 harvests)	Block	4	0.0357	0.77ns
	Species (SP)	1	8.5613	185.27***
	Mainplot error	4	0.0462	
	Harvest (HD)	5	18.0701	244.68***
	SP × HD	5	0.1569	2.12ns
	Subplot error	40	0.0739	
100 mmol/L (6 harvests)	Block	4	0.0216	0.07ns
	Species (SP)	1	0.7620	2.52ns
	Mainplot error	4	0.3022	
	Harvest (HD)	5	11.4354	57.81***
	SP × HD	5	0.3789	1.92ns
	Subplot error	40	0.1978	
200 mmol/L (4 harvests)	Block	4	0.1675	0.56ns
	Species (SP)	1	1.9423	6.48ns
	Mainplot error	4	0.2995	
	Harvest (HD)	3	3.1139	24.38***
	SP × HD	3	1.6127	12.63***
	Subplot error	24	0.1277	

For harvests on days 19 and 36 after planting (harvests 1 and 4), leaf tissue was assessed for ash content and Na, K, Ca, and Mg concentrations. Because leaves had to be combined to get enough tissue for analysis, and resulting replication was low, statistical comparisons were not appropriate, but comparisons of means and SE can be used to indicate trends. Leaf ash content was 9–26% for *Chrysothamnus* and 23–40% for *Sarcobatus* (Table 5). For both species, leaf ash content tended to increase with salinity treatment. Both species also tended to have increased leaf Na with increasing salinity, and a corresponding decrease in K, Ca, and Mg. Na accumulation tended to be greater in magnitude for *Sarcobatus* than for *Chrysothamnus*.

TABLE 4. Results of split-plot ANOVA on ln biomass of *Chrysothamnus* and *Sarcobatus*. Differences in RGR are indicated by significant interaction terms including Harvest Date (HD) as a factor. ns is not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Source	df	MS	F
<i>Chrysothamnus</i> only (4 harvests)	Block	4	0.0730	0.61ns
	Salinity (SL)	2	22.6504	189.76***
	Mainplot error	8	0.1194	
	Harvest (HD)	3	6.6427	96.77***
	SL × HD	6	1.2672	18.46***
	Subplot error	36	0.0686	
<i>Sarcobatus</i> only (6 harvests)	Block	4	0.0878	0.57ns
	Salinity (SL)	2	9.7618	63.45***
	Mainplot error	8	0.1538	
	Harvest (HD)	5	22.6718	106.89***
	SL × HD	10	0.1831	0.86ns
	Subplot error	60	0.2121	

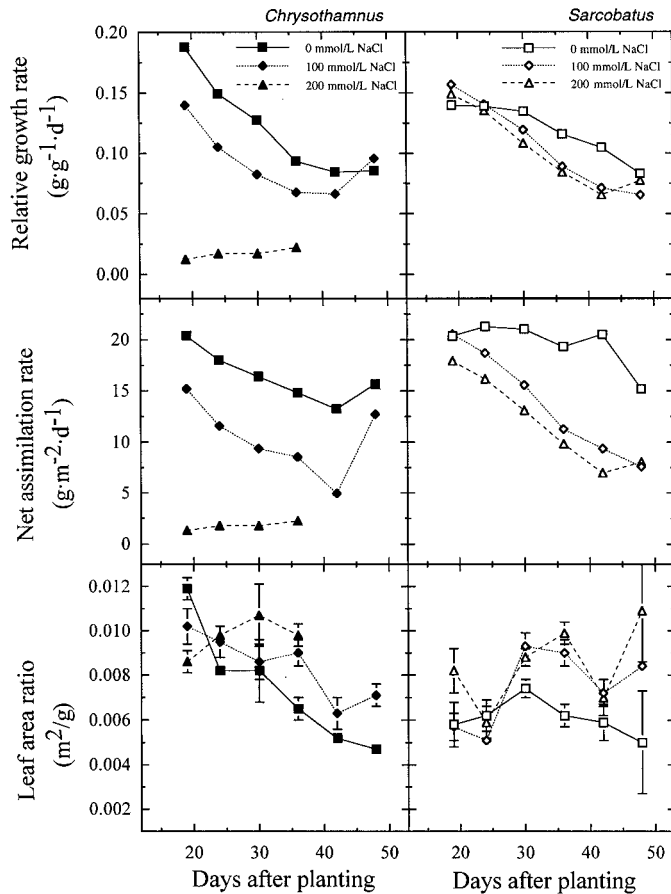


Fig. 2. Relative growth rate, net assimilation rate, and instantaneous leaf area ratio of *Chrysothamnus* and *Sarcobatus* seedlings in 0, 100, and 200 mmol/L NaCl (starting on day 14).

DISCUSSION

Our comparison of the seeds of *Chrysothamnus* (ssp. *consimilis*) and *Sarcobatus* from Mono Lake generally confirms the classification of the former as a nonhalophyte that is marginally salt tolerant, and the latter as a halophyte that is very salt tolerant (Roundy, Young, and Evans, 1981). We confirmed our prediction that seeds and seedlings of *Sarcobatus* would be more tolerant of salin-

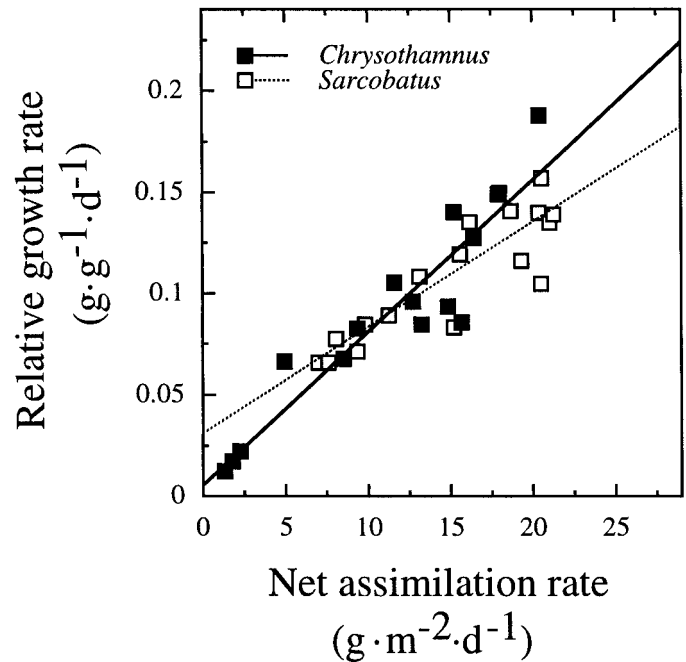


Fig. 3. Relationship between relative growth rate and net assimilation rate for *Chrysothamnus* ($N = 16$, $r^2 = 0.76$, $P < 0.01$) and *Sarcobatus* ($N = 18$ and $r^2 = 0.88$, $P < 0.01$).

ity stress than those of *Chrysothamnus*. However, the results did not support our prediction of ion toxicity for *Chrysothamnus* or of a higher seedling RGR for *Chrysothamnus* than for *Sarcobatus* under well-hydrated non-saline conditions.

Increasing NaCl had a strong Ψ_s or osmotic effect that decreased germination of both species. This finding of highest germination at zero salinity is consistent with previous findings for *Sarcobatus* (Romo and Eddleman, 1985) and for *C. nauseosus* ssp. *viridulus* (Khan et al., 1987), which has alternatively been classified as a variety of ssp. *consimilis* (Anderson, 1986; Khan et al., 1987). Highest germination in the least saline substrate is the norm for most glycophytes and halophytes (see Introduction), and optimal germination in saline substrate (as compared to no salt) has only been found for a few extreme halophytes (Ungar, 1991).

TABLE 5. Leaf ash content (%) and elemental concentration of *Chrysothamnus* and *Sarcobatus* for each salinity treatment (SL), at harvest 1 (top half of table) and harvest 4 (bottom half of table).

Species	N	SL	% ash	Na (g/kg)	K (g/kg)	Mg (g/kg)	Ca (g/kg)
<i>Chrysothamnus</i>	3	0	17.9 ± 0.2	0.5 ± 0.3	50.8 ± 2.0	3.1 ± 0.7	12.7 ± 2.3
	3	100	13.3 ± 2.8	14.8 ± 2.1	22.6 ± 0.5	2.2 ± 0.4	5.5 ± 0.5
	3	200	24.2 ± 4.1	35.1 ± 7.9	22.6 ± 2.4	1.7 ± 0.1	5.0 ± 0.4
<i>Sarcobatus</i>	2	0	30.0 ± 3.6	1.5 ± 0.1	89.5 ± 5.9	5.1 ± 0.1	13.8 ± 0.7
	2	100	41.1 ± 0.1	60.6 ± 10.7	19.1 ± 6.4	2.1 ± 0.2	2.6 ± 0.7
	1	200	43.6	78.4	10.8	1.4	2.5
<i>Chrysothamnus</i>	3	0	8.6 ± 0.2	1.1 ± 0.9	28.3 ± 0.2	3.0 ± 0.4	13.0 ± 1.4
	3	100	16.3 ± 2.3	28.7 ± 1.5	11.8 ± 1.0	1.5 ± 0.3	3.6 ± 0.4
	3	200	26.1 ± 4.2	42.4 ± 9.9	16.7 ± 3.2	1.2 ± 0.1	2.3 ± 0.2
<i>Sarcobatus</i>	3	0	22.9 ± 2.6	5.2 ± 3.4	64.4 ± 11.5	5.7 ± 0.5	18.1 ± 2.8
	3	100	34.0 ± 1.4	59.6 ± 0.3	15.4 ± 1.3	1.8 ± 0.3	1.7 ± 0.1
	3	200	39.5 ± 2.9	71.1 ± 4.4	9.7 ± 2.4	1.0 ± 0.1	1.5 ± 0.3

A comparison of isotonic (same Ψ_s) substrates generated by PEG or NaCl demonstrated that neither study species exhibited ion toxicity, but both species exhibited significant ion enhancement. For *Chrysothamnus* the enhancement was relatively small and increased germination by only ~3–15% in the range of -0.82 to -1.65 MPa. For *Sarcobatus*, the ion enhancement effect was not apparent at less negative Ψ_s but increased dramatically with more negative Ψ_s . NaCl enhancement increased germination (relative to PEG) by 10% at -1.65 MPa and 40% at -2.72 MPa and allowed *Sarcobatus* germination to proceed at much lower Ψ_s . This magnitude of ion enhancement for *Sarcobatus* for Mono Lake populations is consistent with that found for other populations in Montana (Romo and Eddleman, 1985). The accumulation of Na by the imbibing embryo functions to promote a water potential gradient between the embryo and substrate, making germination conditions more favorable than possible on low Ψ_s substrates lacking Na (Romo and Eddleman, 1985; Eddleman and Romo, 1987). However, the trait of ion enhancement was not found for *Sarcobatus* populations from Oregon (Romo and Haferkamp, 1987), indicating substantial population differences (environmental and/or genetic) in this seed germination response. A substantial ion enhancement effect has also been found for NaCl and the halophyte *Puccinellia nuttalliana* at intermediate soil Ψ_w (-1.2 MPa) (Macke and Ungar, 1971), although in that case the NaCl enhancement of germination did not extend the lower limit of soil Ψ_w for successful germination.

The study species differed in seedling RGR responses to decreasing Ψ_s induced by NaCl. *Sarcobatus* seedling RGR did not decline from 0 to 200 mmol/L NaCl, whereas *Chrysothamnus* seedling RGR declined substantially in response to 200 mmol/L NaCl. The 200 mmol/L NaCl treatment also induced mortality for *Chrysothamnus* so that there were no seedlings left to harvest after 2.5 wk. Our results for young seedlings (treatments initiated at 14 d) are consistent with those found for older seedlings of these species (treatments initiated at ~3 mo, Mono Lake seed source) for height growth and mortality responses to salinity (Richards, 1994). In that study, after a 5-wk salinity treatment, *Chrysothamnus* survival was 36 and 8% in 205 and 343 mmol/L NaCl, respectively, whereas *Sarcobatus* survival was 100% in all treatments up to 592 mmol/L NaCl (Richards, 1994).

Variation in RGR can be further explored by looking at its components of LAR and NAR. LAR is an index of the leafiness of the plant, i.e., ratio of photosynthetic surface area to respiratory mass. NAR can be interpreted as the combined physiological processes of photosynthetic carbon gain and carbon losses primarily from respiration (Poorter and Remkes, 1990). Our study showed that intraspecific variation in RGR was correlated with NAR and not LAR for each species. This intraspecific pattern is consistent with the findings for other species' responses to salinity (Jansen, Pot, and Lambers, 1986; Long and Baker, 1986; Ball, 1988; Cramer, Epstein, and Läuchli, 1990; Ball and Pidsley, 1995).

The species comparison of RGR under optimal conditions did not conform to our expectations. In the 0 mmol/L NaCl treatment, the seedling RGR of *Sarcobatus* was the same as that of the less salt-tolerant *Chrysotham-*

nus. This result has two potential implications. The first is on an evolutionary time scale: these data run contrary to the idea that species adaptation to stressful habitats comes at the cost of an inherently lower maximum growth rate under optimal conditions (Grime, 1979; Ball, 1988; Chapin, 1991; Chapin, Autumn, and Pugnaire, 1993; Ball and Pidsley, 1995). The second implication is on an ecological time scale: the lack of differences in maximum RGR under nonsaline conditions suggests that these species may not differ in competitive ability in nonsaline soils (Grime and Hunt, 1975; Grime, 1979; Ball, 1988; van Andel and Biere, 1989; Chapin, 1991). However, these implications need to be further explored using a wider range of water availability and salinity conditions and using more ontogenetic stages. For example, the RGRs in our study were higher by a factor of ten than those found by Brown (1997) for older (~5 mo) seedlings of these species in pot and field studies. In those studies, which were done under nonsaline conditions, *Chrysothamnus* did tend to have a higher RGR than *Sarcobatus*, although the study was not designed for a species comparison.

For the RGR experiment, elemental concentrations were based on small sample sizes for combined plants and thus should be interpreted with caution. However, they suggest that seedlings of both species took up Na and sequestered it in leaves, at the expense of other cations, and that effect was larger for *Sarcobatus* than for *Chrysothamnus*. The Na uptake was expected for *Sarcobatus* seedlings because mature plants of this species have extremely high Na concentration under field and experimental conditions (Glenn and O'Leary, 1984; Richards, 1994; Donovan, Richards, and Muller, 1996; Donovan, Richards, and Schaber, 1997). Both juvenile and mature plants accumulate leaf Na as part of their ability to actively osmotically adjust (Glenn and O'Leary, 1984; Romo and Haferkamp, 1989). Accumulation of leaf Na was not expected for *Chrysothamnus* seedlings since mature plants of these species do not have high leaf Na concentrations under field conditions (Donovan, Richards, and Muller, 1996). Seedling Na uptake promotes the water potential gradient between seedling and substrate and thus enhances the seedling ability to maintain turgor for growth.

Overall, osmotic and ionic effects of salinity on seeds and seedlings of *Chrysothamnus* and *Sarcobatus* could contribute to observed distribution patterns at Mono Lake, California. At the nonsaline end of the gradient, both species could do well in terms of germination and early seedling growth. At the extreme saline end of the gradient, where a salt crust often forms on the surface, only a halophyte species such *Sarcobatus* could germinate and grow. For the intermediate areas of the Mono Lake gradient, our results complement those of Schaber (1994). Although her results indicated no species-limiting differences in Na toxicity under well-watered conditions (but no Na leaching), our results additionally look at Na Ψ_s effects and ion enhancement when soil Ψ_w declines. In the field, surface soils are wettest in the spring, but rarely stay wet for extended periods of time. Seeds and seedlings at the surface would be subjected to drying cycles that would decrease the soil Ψ_w both due to decreasing Ψ_m and Ψ_s . Under moderately saline field con-

ditions, Ψ_w stress inhibition of *Chrysothamnus* germination and seedling growth would be exacerbated by the presence of Na. Faced with the same declining Ψ_w , *Sarcobatus* seeds and seedlings would take up Na ions and proceed with greater germination and growth than would have been possible in a drying soil without Na.

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