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## EFFECT OF SALINITY AND PLANTING DENSITY ON PHYSIOLOGICAL RESPONSES OF *ALLENROLFEA OCCIDENTALIS*

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**ABSTRACT.**—Physiological responses of *Allenrolfea occidentalis* to salinity and seedling density were investigated. Effects of salinity (0, 200, 400, 600, 800, and 1000 mM NaCl) and 3 planting densities (2000, 4000, 6000 plants m<sup>-2</sup>) on the growth, survival, and ecophysiology of *A. occidentalis*, a stem succulent inland halophyte, were studied under controlled greenhouse conditions. Plants were grown in a sand culture using subirrigation. Dry mass of roots was highest at 600 mM NaCl at low density (2000 plants m<sup>-2</sup>), but declined as salinity increased. Tissue water content was highest at the 200 mM NaCl treatment and decreased with increased salinity. Water potential of the plants became more negative with increasing salinity due to the accumulation of NaCl in the leaves. Inorganic ions, especially Na<sup>+</sup> and Cl<sup>-</sup>, contributed substantially to dry mass. Na<sup>+</sup> and Cl<sup>-</sup> concentration in shoots and roots increased when NaCl level was increased while K<sup>+</sup>, Ca<sup>++</sup>, Mg<sup>++</sup>, SO<sub>4</sub><sup>--</sup>, and NO<sub>3</sub><sup>-</sup> contents decreased. Net photosynthesis increased at low salinity (200 mM), but photosynthesis at other salinities was not significantly different from the control. While *A. occidentalis* is very salt tolerant and photosynthesis functioned reasonably well at high salinities, extremely high salinity did decrease dry mass of roots and shoots.

*Key words:* salinity, planting density, *Allenrolfea occidentalis*, halophyte, salt tolerance, pickleweed.

Halophytes are plants that complete their life cycle at high salinities (Flowers et al. 1977), and their survival in salt marshes depends on salt tolerance at different stages of their life cycle (Adam 1990). Dry mass of halophytes usually decreases with increases in salinity (Ungar 1991), although growth of several halophytes is stimulated at some levels of salinity (Flowers and Yeo 1986, Munns et al. 1983, Khan and Aziz 1998). Nevertheless, high NaCl concentration is probably not essential for optimal growth of most halophytes. There are several halophytes that show optimal growth at NaCl concentrations of 400 mM or higher, e.g., *Cress crinitic* (425 mM NaCl; Khan and Aziz 1998), *Suaeda fruticosa* (400 mM NaCl), *Haloxylon recurvum* (400 mM NaCl), and several cold-desert halophytic species like *Salicornia rubra*, *S. utahensis*, *Suaeda moquinii*, and *Kochia scoparia* (600 mM NaCl; Khan et al. unpublished data).

Intraspecific competition may influence survival, growth, and fecundity of annual populations in saline habitats (Ungar 1991). However, the role of competition in perennial populations appears to be limiting in reference to new recruitment (Khan and Aziz 1998, Gul and Khan 1999). Most perennial halophytes

usually do not recruit through seeds, and ramets are competitively superior to genets at the recruitment phase of the life cycle (Gul and Khan 1999). In a saline habitat dominated by perennials, drought, temperature, and salinity stress synergistically cause death of seedlings and depress growth of adult plants. Mortality in perennial halophytes occurs at the seedling stage due to high salinity, temperature, or severe drought, while adult plants enter into a phase of dormancy to avoid death (Khan and Aziz 1998).

Osmotic active adjustment under saline conditions may be achieved by ion uptake, synthesis of osmotica, or both (Cheesman 1988, Popp 1995). Halophytes differ widely in the extent to which they accumulate ions and overall degree of salt tolerance (Glenn et al. 1996). Stem- and leaf-succulent chenopods are commonly known as salt accumulators and have high Na<sup>+</sup> and Cl<sup>-</sup> content (Breckle 1975, Albert and Popp 1977, Gorham et al. 1980, Neumann 1997, Khan and Aziz 1998). Halophytes have adapted to highly saline conditions by their ability to adjust osmotically to increasing salinity levels (Reihl and Ungar 1982, Clipson et al. 1985). Tolerance of photosynthetic systems to salinity is associated with

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the capacity of plant species to effectively compartmentalize ions in the vacuole, cytoplasm, and chloroplast (Reddy et al. 1997). Chlorophyll fluorescence, an analytical tool for investigating stress damage mechanisms, has been used for detecting tolerance to chilling, freezing, drought, and air pollution stress. It may prove equally useful for salinity tolerance screening (Mekkaoui et al. 1989, Monnieveux et al. 1990) or for detecting salt effects before visible damage occurs (West 1986).

*Allenrolfea occidentalis* (Wats.) Kuntze (Chenopodiaceae), a  $C_3$  plant common in the western U.S., is found in an environment where halomorphic soil induces extreme osmotic stress in concert with erratic and low precipitation during the growing season (Trent et al. 1997). During drought this species exhibits low photosynthesis, stomatal conductance, and transpiration in comparison to years with high moisture (Skougard and Brotherson 1979). *Allenrolfea occidentalis* is restricted to a few communities directly at the margin of playas where soils are often poorly drained and have high soil salinity (Hansen and Weber 1975).

Because little information is available on the growth and salt tolerance of *Allenrolfea occidentalis*, the objective of this study was to determine the physiological responses of *A. occidentalis* to salinity and seedling density. We hypothesized that increased salinity and seedling density would decrease the growth response of *A. occidentalis*.

#### MATERIALS AND METHODS

We collected *Allenrolfea occidentalis* seedlings from an inland salt playa located on the east of Goshen, in northwestern Utah (39:57:06N 111:54:03W, 4530 ft). Equal-sized seedlings (about 1 sq cm in size) were transplanted into 12.7-cm-diameter  $\times$  12.7-cm-tall plastic pots containing nutrient-free sand. We used 3 planting densities (low, 25 plants per pot, which was equal to the rate of 2000 plants  $m^{-2}$ ; medium, 50 plants per pot, equal to the rate of 4000 plants  $m^{-2}$ ; and high, 75 plants per pot, equal to the rate of 6000 plants  $m^{-2}$ ). Six salinity (0, 200, 400, 600, 800, and 1000 mM NaCl) treatments were used. Four replicate pots were used for each saline treatment group, and pots were placed in plastic trays containing half-strength Hoagland's nutrient solution. All pots were watered immediately

after planting. Seedlings were thinned by removing excess plants from the pots to produce 3 treatment densities equal to 2000, 4000, and 6000 plants  $m^{-2}$ . Plants were grown for 1 wk in a greenhouse by subirrigation by placing the pots in plastic trays containing half-strength Hoagland's solution; the 2nd wk different salinities were applied. Plants were subirrigated by placing the pots in plastic trays and adjusting the water level daily to correct for evaporation. Once weekly we completely replaced salt solutions to avoid buildup of salinity in pots. At the initiation of the experiment, we gradually increased salinity concentrations by 200 mM at 1-d intervals until the maximum salinity level of 1000 mM NaCl was obtained. Seedlings were grown in a greenhouse at a thermoperiod of 25°C:35°C (night:day) for a total of 90 d after final salinity concentrations were reached.

Dry mass of plant shoots and roots was measured 90 d after the highest salt concentration was reached. Dry mass of plants from an individual pot was determined after drying for 48 h in a forced-draft oven at 80°C. Ion concentration was determined by boiling 0.5 g of plant material in 25 mL of water for 2 h at 100°C using a dry-heat bath. This hot water extract was cooled and filtered using Whatman no. 2 filter paper. One mL of hot water extract was diluted with distilled water for ion analysis. Chloride, nitrate, and sulfate ion contents were measured with a DX-100 ion chromatograph. Cation contents,  $Na^+$ ,  $K^+$ ,  $Ca^{2+}$ , and  $Mg^{2+}$ , of plant organs were analyzed using a Perkin Elmer model 360 atomic absorption spectrophotometer.

Using an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE), we measured the net  $CO_2$  assimilation rate of 4 plants for each treatment. Level of stress in plants growing at different salinities was determined to be the amount of fluorescence measured from photosystem II with a Morgan CF-1000 chlorophyll fluorescence measurement system (PK. Morgan Instruments, Andover, MA). Stress is measured as a ratio of  $F_v$  (variable fluorescence) to  $F_m$  (maximum fluorescence). Water potential was measured at midday with a pressure chamber (PMS Instrument Co., Corvallis, OR). Results of growth, ion contents, net  $CO_2$  exchange rate, water potential, and stress were analyzed with a 3-way ANOVA to determine if significant differences were present among

means. A Bonferroni test determined whether significant ( $P < 0.05$ ) differences occurred between individual treatments (SPSS 1996).

### RESULTS

A 3-way ANOVA showed significant individual effects of plant density, salinity, plant part, and their interactions on dry mass of *A. occidentalis* plants. Interactions between density and salinity and among all factors were not significant. Dry mass of shoots at low density (2000 plants  $m^{-2}$ ) was not affected by low salinities (200 and 400 mM NaCl; Fig. 1). There was a significant ( $P < 0.001$ ) promotion in shoot growth at 600 mM NaCl (Fig. 1). Shoot growth at 1000 mM NaCl was not significantly different from the nonsaline control at medium density. At high seedling density (6000 plants  $m^{-2}$ ), there was no significant difference in shoots among various salinity treatments (Fig. 1). As density increased, shoot growth progressively decreased at all salinity treatments. Root growth at low density and 200 mM salinity was similar to 0 salinity (Fig. 2). Salinity  $\geq 600$  mM generally decreased dry mass of roots. At low salinity, dry mass de-

creased with increased density, but there was no density effect at higher salinities (Fig. 2).

A 3-way ANOVA showed a significant individual effect of salinity ( $P < 0.05$ ) and shoots-roots ( $P < 0.001$ ), while density was not significant in affecting succulence. Interactions between density and plant part were significant. Shoot tissue water showed significant increase at 400 mM NaCl compared to 0 mM NaCl. At high densities (4000 and 6000 plants  $m^{-2}$ ) and all other salinities, the effect was not significant (Fig. 3). At low planting density, root succulence was higher except for 1000 mM NaCl, where at high density there was a substantial increase in succulence. A 3-way ANOVA showed a significant ( $P < 0.0001$ ) effect of various concentrations of NaCl on net photosynthesis, water potential, and  $F_v/F_m$  ratio. Net photosynthesis was higher at 200 mM NaCl and then significantly declined with increased salinity (Table 1). Water potential progressively decreased with increasing salinity, reaching  $-6.7$  MPa at 1000 mM NaCl. The  $F_v/F_m$  ratio declined with increasing salinity.

A 3-way ANOVA showed significant individual effects of shoots-roots, salinity, density, and their interaction in affecting ion content

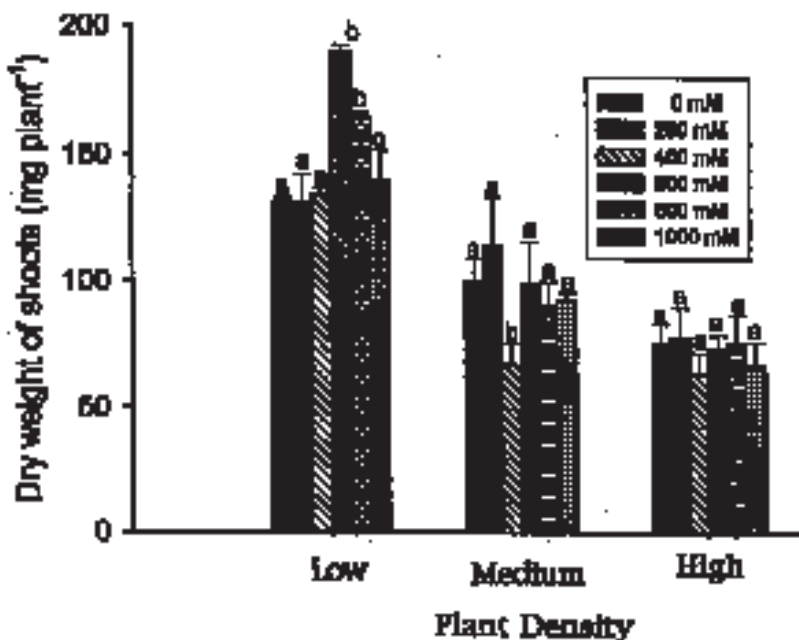


Fig. 1. Effect of NaCl (0, 200, 400, 600, 800, and 1000 mM) on dry mass of shoots of *Allenrolfea occidentalis* plants grown at low (2000  $m^{-2}$ ), medium (4000  $m^{-2}$ ), and high (6000  $m^{-2}$ ) plant density. Bar represents mean  $\pm$  s.e. Different letters above bars represent significant differences ( $P < 0.05$ ) among treatments.

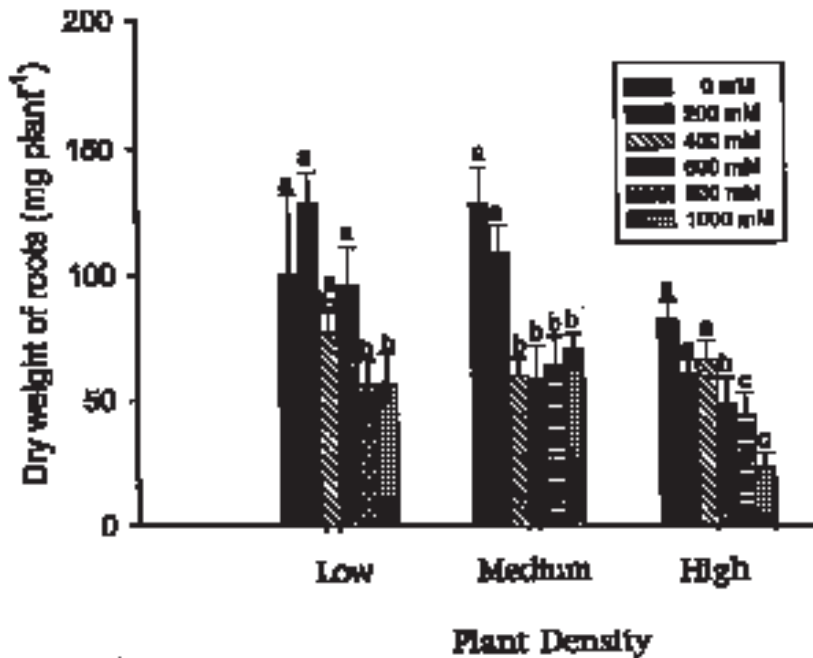


Fig. 2. Effect of NaCl (0, 200, 400, 600, 800, and 1000 mM) on dry mass of roots of *Allenrolfea occidentalis* plants grown at low (2000 m<sup>-2</sup>), medium (4000 m<sup>-2</sup>), and high (6000 m<sup>-2</sup>) plant density. Bar represents mean  $\pm$  s<sub>x</sub>. Different letters above bars represent significant differences ( $P < 0.05$ ) among treatments.

of *A. occidentalis*. Sodium content in shoots increased at lower salinity, but a further increase in salinity had no effect (Table 2). Change in density had little effect on shoot Na<sup>+</sup> concentration. Chloride concentration progressively increased with increases in salinity, but change in density had no effect (Table 2). Tissue concentrations of Ca<sup>-2</sup>, Mg<sup>-2</sup>, K<sup>+</sup>, NO<sub>3</sub><sup>-</sup>, and SO<sub>4</sub><sup>-2</sup> were very low in comparison to Na<sup>+</sup> and Cl<sup>-</sup>, and they decreased with increases in salinity (Table 2). Root ion concentrations followed a pattern similar to that of the shoot (Table 3).

#### DISCUSSION

*Allenrolfea occidentalis* showed optimal shoot growth at seawater salt concentration and higher (600–800 mM NaCl). Most halophytes show optimal growth in the presence of salt (Naidoo and Rughunanan 1990, Rozema 1991, Ayala and O'Leary 1995); however, most halophytic species are inhibited by high salt concentration, with none showing optimal growth at seawater concentration (Ungar 1991). Khan and Aziz (1998) reported that *Cressa*

*cretica* showed optimal growth at 425 mM NaCl, and there was no inhibition of growth at 850 mM NaCl. Great Basin Desert species collected from similar habitat, i.e., *Salicornia rubra*, *S. utahensis*, *Suaeda moquinii*, *Kochia scoparia*, and *Sarcobatus vermiculatus*, also showed optimal growth at or above seawater salinity (Khan, Gul, and Weber unpublished data). *Allenrolfea occidentalis* appears to be one of the most salt tolerant species reported.

Increased competition caused a progressive reduction in growth of *A. occidentalis*. High planting density decreased growth even at low salinities. At higher planting densities there was no significant difference in growth among various salinity treatments. Intraspecific competition may affect biomass production, reproduction, survival, and growth of halophytes in saline habitats (Badger and Ungar 1990, Ungar 1991, Federaro and Ungar 1997, Keiffer and Ungar 1997). Keiffer and Ungar (1997) reported that such species as *Salicornia europaea*, *Atriplex prostrata*, *Hordeum jubatum*, and *Spergularia marina* produce plants of similar biomass under all salinities when grown in higher density treatments. Keddy (1981)

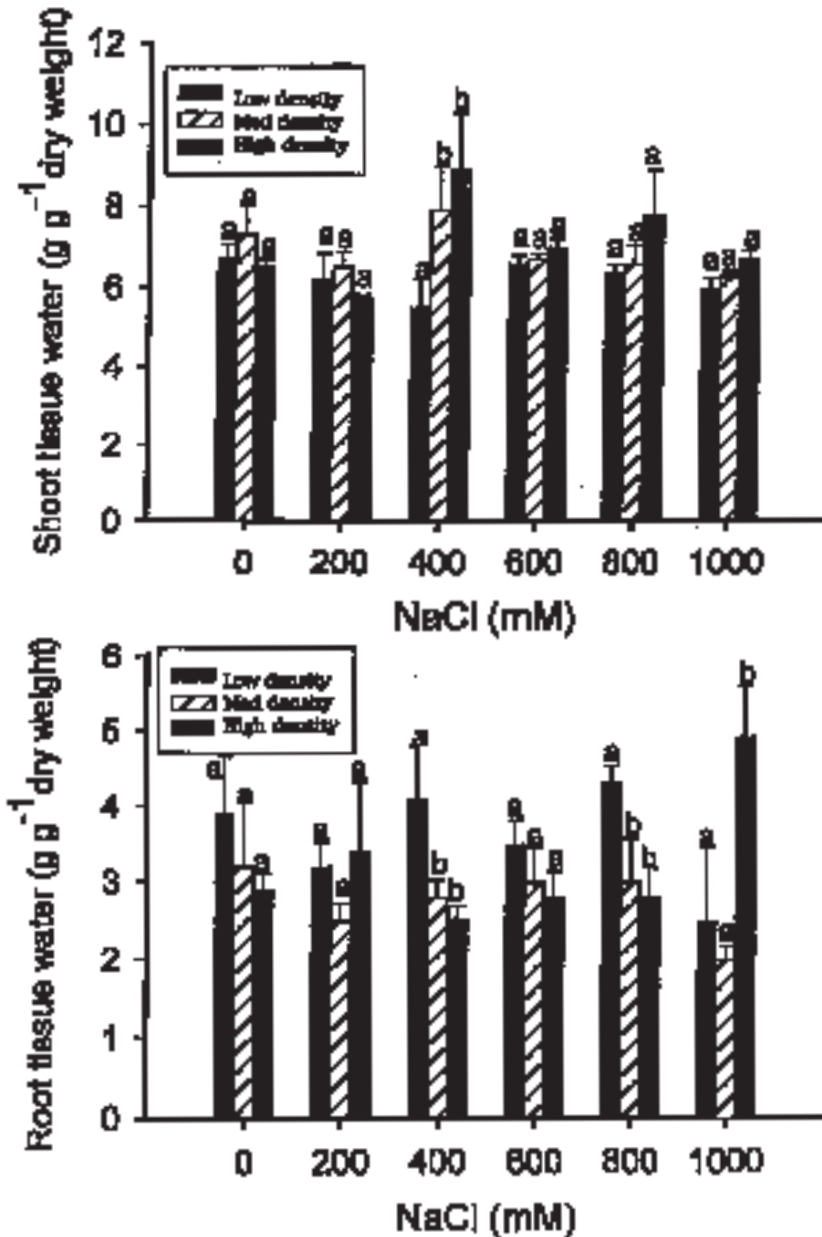


Fig. 3. Effect of NaCl (0, 200, 400, 600, 800, and 1000 mM) on shoot and root water content of *Allenrolfea occidentalis* plants grown at low (2000 m<sup>-2</sup>), medium (4000 m<sup>-2</sup>), and high (6000 m<sup>-2</sup>) plant density. Bar represents mean  $\pm$  s.e. Different letters above bars represent significant differences ( $P < 0.05$ ) among treatments.

reported the relative importance of density-dependent and density-independent effects can change along environmental gradients.

To avoid toxic effects of salt, halophytes have developed a number of mechanisms, including succulence, salt exclusion, and secretion (Ungar 1991). Succulence is thought

to contribute to salt regulation by increasing the vacuolar volume available for ion accumulation (Greenway and Munns 1980, Albert 1982, Ungar 1991). Salinity increased the water content of *Suaeda torreyana* (Glenn and O'Leary 1984), *Salsola kali* (Reimann and Breckle 1995), and *Arthrocnemum fruticosum* (Eddin

TABLE 1. Effect of salinity on net photosynthesis, midday water potential, and  $F_v/F_m$  ratio of *Allenrolfea occidentalis*.

NaCl (mM)	Net photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Water potential (-Mpa)	$F_v/F_m$ ratio
0	$9.8 \pm 0.6$	$-3.1 \pm 0.3$	$0.74 \pm 0.02$
200	$12.4 \pm 0.6$	$-3.4 \pm 0.3$	$0.68 \pm 0.02$
400	$7.3 \pm 0.7$	$-4.1 \pm 0.2$	$0.61 \pm 0.01$
600	$6.1 \pm 0.7$	$-4.4 \pm 0.6$	$0.71 \pm 0.04$
800	$7.7 \pm 1.1$	$-4.9 \pm 0.2$	$0.64 \pm 0.01$
1000	$7.4 \pm 0.4$	$-6.7 \pm 0.4$	$0.53 \pm 0.03$

and Doddema 1986), with this increase in succulence presumably being a result of salt accumulation. However, our results showed a significant increase in salt accumulation, but a significant reduction in succulence, at higher salinity and plant density. Roots showed a clear increase in water content over the entire salinity range, except at 1000 mM NaCl in low-density treatments. Species with succulent leaves (*Salicornia europaea*, *Allenrolfea occidentalis*, and *Batis maritima*) show a remarkable degree of dehydration when treated with high (720 mM NaCl) salinity (Glenn and O'Leary 1984). A progressive accumulation of salt with increase in salinity was found.

In dicotylenous halophytes, water relations and the ability to adjust osmotically are reported to be important determinants of the growth response to salinity (Flowers et al. 1977, Munns et al. 1983, Ayala and O'Leary 1995). Our results indicate that water potentials of plants reflect osmotic potentials of external solutions, especially at higher salinities. *Allenrolfea occidentalis* adjusted osmotically, maintaining a more negative water potential. Antlfinger and Dunn (1983) found that species growing in higher soil salinities had a lower xylem pressure potential than plants growing in less saline areas.

Growth inhibition under saline conditions is usually associated with dehydration at high salinity, which is due to increased water stress and the resultant loss of cell turgor because of inadequate tissue osmotic adjustment (Hellebust 1976, Ungar 1991). One major difference between plants grown at different salinities was photosynthetic response. In supraoptimal salinity conditions, plant growth was accompanied by reduced photosynthetic rates. In sub-optimal salinity conditions, similar growth reduction was accompanied by photosynthetic rates equal to or greater than those of plants

growing at optimal salinity. Differences in photosynthetic rates were not consistent with differences in growth (Ayala and O'Leary 1995). Our results indicate a small promotion of photosynthesis at low salinity, while all other treatments showed similar effect.

Changes in  $F_v/F_m$  were more evident when *A. occidentalis* was treated with 1000 mM NaCl. Low  $F_v/F_m$  values were found in the control and low-salinity treated plants, although lowest values logically appeared in higher salt treatments. Sharma and Hall (1998), Larcher et al. (1990), and Jimenze et al. (1997) also reported similar reduction in  $F_v/F_m$  values. At high salinity (1000 mM NaCl) *A. occidentalis* plants showed a slight decrease in mean  $F_v/F_m$  values, but this variation could not be attributed to salinity stress alone (Brugnoli and Lauteri 1990, 1991, Brugnoli and Björkman 1992).

A tendency to accumulate NaCl has been reported for many other halophytes and is associated with salt tolerance (Storey and Wyn Jones 1977, Greenway and Munns 1980, Glenn and O'Leary 1984, Naidoo and Rughunanan 1990, Nerd and Pasternak 1992, Khan and Aziz 1998). Total concentration of inorganic ions in *A. occidentalis* plants increased with salinity; this increase is due primarily to an increase in the concentration of  $\text{Na}^+$  and  $\text{Cl}^-$ . These 2 ions also contributed substantially to the dry mass content of plants. At all salinities *A. occidentalis* maintained  $\text{Na}^+$  concentrations higher than external solutions. *Allenrolfea occidentalis* plants grew poorly in the absence of NaCl; optimum growth occurred at 180–540 mM NaCl and was inhibited by 40% at 720 mM NaCl compared with 320 mM NaCl, similar to that for *Atriplex canescens* (Glenn and O'Leary 1984). In shoots and roots of *A. occidentalis*, increasing salinity significantly reduced potassium content. Sodium

TABLE 2. Effect of salinity on the concentration of cations and anions in shoots of *Allenroffea occidentalis* at low (L), medium (M), and high (H) densities. Values represent means  $\pm s_{\bar{x}}$ . Means in same column followed by the same letter are not significantly different ( $P < 0.05$ ) according to Bonferroni test.

NaCl (mM)	Na <sup>+</sup> (mM)		K <sup>+</sup> (mM)		Ca <sup>2+</sup> (mM)		Mg <sup>2+</sup> (mM)		Cl <sup>-</sup> (mM)		SO <sub>4</sub> (mM)		NO <sub>3</sub> (mM)						
	L	M	L	M	L	M	L	M	L	M	L	M	L	M					
0	1270 <sup>b</sup> ±86.2	1671 ±486	52 <sup>a</sup> ±6	38 <sup>a</sup> ±12	48 <sup>a</sup> ±4	78 <sup>b</sup> ±6	109 <sup>a</sup> ±24	44 <sup>a</sup> ±6	395 <sup>a</sup> ±10	267 <sup>a</sup> ±25	360 <sup>a</sup> ±7	1616 <sup>a</sup> ±213	2121 <sup>a</sup> ±105	1845 <sup>a</sup> ±340	280 <sup>a</sup> ±13	722 <sup>a</sup> ±170	331 <sup>a</sup> ±15	50 <sup>a</sup> ±5	46 <sup>a</sup> ±16
200	4434 <sup>b</sup> ±153	4859 ±88	42 <sup>a</sup> ±3	22 <sup>a</sup> ±4	40 <sup>a</sup> ±2	145 <sup>b</sup> ±68	61 <sup>b</sup> ±2	49 <sup>a</sup> ±8	394 <sup>a</sup> ±24	175 <sup>b</sup> ±32	340 <sup>a</sup> ±8	6290 <sup>b</sup> ±640	1088 <sup>b</sup> ±174	9742 <sup>b</sup> ±662	338 <sup>b</sup> ±80	426 <sup>b</sup> ±93	334 <sup>a</sup> ±44	178 <sup>b</sup> ±14	29 <sup>a</sup> ±18
400	5218 <sup>c</sup> ±274	5303 ±99	28 <sup>a</sup> ±12	27 <sup>a</sup> ±5	28 <sup>a</sup> ±1	85 <sup>a</sup> ±17	81 <sup>b</sup> ±19	117 <sup>b</sup> ±34	339 <sup>a</sup> ±15	154 <sup>b</sup> ±3	306 <sup>a</sup> ±10	6833 <sup>c</sup> ±874	1472 ±577	11130 <sup>c</sup> ±147	263 <sup>a</sup> ±28	275 <sup>c</sup> ±71	337 <sup>a</sup> ±77	87 <sup>a</sup> ±7	28 <sup>a</sup> ±9
600	5272 <sup>c</sup> ±29	5655 ±109	30 <sup>a</sup> ±4	26 <sup>a</sup> ±3	25 <sup>a</sup> ±2	56 <sup>a</sup> ±6	96 <sup>b</sup> ±6	46 <sup>a</sup> ±7	304 <sup>a</sup> ±9	160 <sup>b</sup> ±4	281 <sup>a</sup> ±5	7161 <sup>d</sup> ±137	1619 <sup>c</sup> ±343	11337 <sup>c</sup> ±834	133 <sup>c</sup> ±11	212 <sup>c</sup> ±16	262 <sup>b</sup> ±76	83 <sup>a</sup> ±26	25 <sup>a</sup> ±6
800	5284 <sup>c</sup> ±66	5464 ±165	31 <sup>a</sup> ±3	24 <sup>a</sup> ±5	23 <sup>a</sup> ±5	26 <sup>a</sup> ±1	39 <sup>b</sup> ±14	23 <sup>a</sup> ±7	276 <sup>b</sup> ±13	148 <sup>b</sup> ±21	269 <sup>a</sup> ±7	8881 <sup>c</sup> ±776	4029 <sup>d</sup> ±170	12061 <sup>d</sup> ±1811	136 <sup>c</sup> ±34	181 <sup>d</sup> ±18	171 <sup>c</sup> ±8	41 <sup>c</sup> ±16	27 <sup>a</sup> ±14
1000	5392 <sup>c</sup> ±224	5742 ±272	35 <sup>a</sup> ±4	23 <sup>a</sup> ±12	22 <sup>a</sup> ±4	25 <sup>a</sup> ±5	34 <sup>b</sup> ±16	13 <sup>a</sup> ±8	257 <sup>b</sup> ±11	138 <sup>b</sup> ±23	217 <sup>a</sup> ±8	8685 <sup>c</sup> ±343	6096 <sup>c</sup> ±497	12437 <sup>e</sup> ±2192	146 <sup>d</sup> ±29	137 <sup>d</sup> ±17	152 <sup>c</sup> ±29	25 <sup>c</sup> ±8	17 <sup>a</sup> ±6

TABLE 3. Effect of salinity on the concentration of cations and anions in roots of *Allenrolfea occidentalis* at low (L), medium (M), and high (H) densities. Values represent Means  $\pm$  s.e. Means in the same column followed by the same letter are not significantly different ( $P < 0.05$ ) according to Bonferroni test.

NaCl (mM)	Na <sup>+</sup> (mM)		K <sup>+</sup> (mM)		Ca <sup>2+</sup> (mM)		Mg <sup>2+</sup> (mM)		Cl <sup>-</sup> (mM)		SO <sub>4</sub> (mM)		NO <sub>3</sub> (mM)					
	L	M	L	M	L	M	L	M	L	M	L	M	L	M				
0	1630 <sup>b</sup> ±402	2084 <sup>a</sup> ±166	22 <sup>a</sup> ±6	51 <sup>a</sup> ±4	26 <sup>a</sup> ±3	107 <sup>a</sup> ±13	222 <sup>a</sup> ±78	112 <sup>a</sup> ±15	179 <sup>a</sup> ±21	356 <sup>a</sup> ±24	226 <sup>a</sup> ±24	1732 <sup>a</sup> ±113	1899 <sup>a</sup> ±238	844 <sup>a</sup> ±26	277 <sup>a</sup> ±55	764 <sup>a</sup> ±22	39 <sup>a</sup> ±12	98 <sup>a</sup> ±20
	4900 <sup>b</sup> ±176	4996 <sup>b</sup> ±93	21 <sup>a</sup> ±2	36 <sup>a</sup> ±2	20 <sup>a</sup> ±4	99 <sup>a</sup> ±9	158 <sup>b</sup> ±6	104 <sup>a</sup> ±8	174 <sup>a</sup> ±19	344 <sup>a</sup> ±6	195 <sup>a</sup> ±8	1783 <sup>a</sup> ±100	6204 <sup>b</sup> ±183	648 <sup>b</sup> ±69	269 <sup>a</sup> ±13	739 <sup>a</sup> ±23	43 <sup>a</sup> ±18	57 <sup>a</sup> ±9
400	5318 <sup>c</sup> ±213	5557 <sup>c</sup> ±196	18 <sup>a</sup> ±4	33 <sup>a</sup> ±2	18 <sup>a</sup> ±1	63 <sup>ab</sup> ±4	87 <sup>c</sup> ±8	95 <sup>a</sup> ±12	150 <sup>a</sup> ±13	352 <sup>a</sup> ±15	186 <sup>a</sup> ±13	1837 <sup>a</sup> ±175	9237 <sup>a</sup> ±169	499 <sup>c</sup> ±9	281 <sup>a</sup> ±7	596 <sup>b</sup> ±17	34 <sup>a</sup> ±12	56 <sup>a</sup> ±10
	5460 <sup>c</sup> ±81	5580 <sup>c</sup> ±221	16 <sup>a</sup> ±1	31 <sup>a</sup> ±2	18 <sup>a</sup> ±2	46 <sup>b</sup> ±6	81 <sup>c</sup> ±2	69 <sup>b</sup> ±9	131 <sup>a</sup> ±14	343 <sup>a</sup> ±12	185 <sup>a</sup> ±8	1886 <sup>a</sup> ±124	12189 <sup>d</sup> ±782	431 <sup>c</sup> ±11	262 <sup>a</sup> ±12	470 <sup>c</sup> ±18	30 <sup>a</sup> ±6	30 <sup>ab</sup> ±2
800	5501 <sup>c</sup> ±352	5598 <sup>c</sup> ±140	16 <sup>a</sup> ±3	26 <sup>a</sup> ±1	17 <sup>a</sup> ±2	45 <sup>b</sup> ±5	73 <sup>c</sup> ±2	66 <sup>b</sup> ±12	116 <sup>b</sup> ±17	306 <sup>a</sup> ±13	174 <sup>a</sup> ±7	2990 <sup>b</sup> ±726	13864 <sup>c</sup> ±976	304 <sup>d</sup> ±13	251 <sup>a</sup> ±18	305 <sup>d</sup> ±10	28 <sup>a</sup> ±12	21 <sup>b</sup> ±1
	5676 <sup>c</sup> ±332	5738 <sup>c</sup> ±84	14 <sup>a</sup> ±2	24 <sup>a</sup> ±0.9	16 <sup>a</sup> ±2	39 <sup>b</sup> ±8	45 <sup>c</sup> ±5	43 <sup>b</sup> ±9	96 <sup>b</sup> ±3	283 <sup>a</sup> ±11	150 <sup>a</sup> ±11	6963 <sup>c</sup> ±486	13789 <sup>c</sup> ±744	205 <sup>d</sup> ±19	211 <sup>a</sup> ±9	142 <sup>d</sup> ±18	24 <sup>a</sup> ±8	19 <sup>b</sup> ±5



content rose steeply with increasing substrate salinity. This pattern of  $K^+$ - $Na^+$  balance is typical for relatively salt tolerant species such as *Suaeda maritima*, *Atriplex hortensis*, and *A. prostrata* (Flowers 1975, Jeshke and Stelter 1983, Karimi and Ungar 1984). Chloride concentration also increased with salinity, and this pattern is consistent with other perennial halophytes such as *Cressa cretica*, *Suaeda fruticosa*, *Atriplex griffithii*, *Haloxylon recurvum*, and *Halopyrum mucronatum* (Khan and Aziz 1998).

*Allenrolfea occidentalis* was found to complete its life cycle in 1000 mM NaCl and showed significant growth promotion in moderate salinity (600 mM NaCl) in low-density plantings. Density did not significantly affect growth. The mechanism for salt tolerance in this species could involve striking a delicate balance between ion accumulation, osmotic adjustment, maintenance of water potential, and growth. At salinities above 800 mM NaCl, this balance is perhaps disturbed. *Allenrolfea occidentalis* is one of the most salt tolerant and salt accumulating halophytes and could thus be used successfully to reclaim highly salinized areas in arid and semiarid regions of the world.

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