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Effects of Salinity on Growth, Water Relations and Ion Accumulation of the Subtropical Perennial Halophyte, *Atriplex griffithii* var. *stocksii*

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The effects of salinity on growth, water relations, glycinebetaine content, and ion accumulation in the perennial halophyte *Atriplex griffithii* var. *stocksii* were determined. The following questions were addressed: (1) What effect does salinity have on growth responses at different ages? (2) Is *A. griffithii* an ion accumulator? (3) Does *A. griffithii* accumulate glycinebetaine in response to salinity? *Atriplex griffithii* plants were grown in pots at 0, 90, 180 and 360 mM NaCl in sand culture in a plant growth chamber and plants were harvested after 30, 60 and 90 d. Plant total dry weight was significantly inhibited at 360 mM NaCl. Root growth showed a substantial promotion at 90 mM NaCl. The water potential and osmotic potential of shoots became more negative with increasing salinity and time of growth. The Na^+ and Cl^- content in both shoots and roots increased with increases in salinity. Increased treatment levels of NaCl induced decreases in Ca^+, K^+ and Mg^{2+} in plants. *Atriplex griffithii* accumulated a large quantity of ions, with the ash content reaching 39% of the dry weight in leaves. Inorganic ion accumulation is significant in osmotic adjustment and facilitates water uptake along a soil-plant gradient. Glycinebetaine concentration was low in roots, and in stems it increased with increases in salinity. Total amounts of glycinebetaine in leaves increased with increases in salinity, and its concentration increased substantially at 360 mM NaCl.

Key words: *Atriplex griffithii*, glycinebetaine, growth, ions, water relations.

INTRODUCTION

Halophytes face a two-fold problem: they must tolerate the high salt concentrations of their habitats, and they must absorb water from a soil solution that has a low water potential. To maintain water uptake and turgor under these conditions halophytes need to maintain a water potential that is more negative than that existing in the soil solution. It is advantageous if this is achieved mainly by accumulation of inorganic ions that can easily be taken up from the soil (Flowers *et al*., 1977).

Arid and semi-arid lands constitute approximately one-third of the world's land surface (Archibold, 1995). Competition among plants in these stressful environments favours those species that are able to become established, grow to maturity, and survive until they are able to reproduce. At each of these critical stages in the growth cycle, species with superior tolerance to salinity, drought and temperature extremes are the best competitors (Tiedemann *et al*., 1983). *Atriplex* shrubs have adaptations enabling them to tolerate the adverse effect of salts internally, or excrete salt from cells and tissues (McKell, 1994). As a result they have an advantage over plant species that lack strategies to deal with salt in the soil and are thus excellent competitors in saline environments.

In general, low salinity levels do not appear to have a deleterious effect on the growth of *Atriplex* spp. and may actually stimulate growth (Ashby and Beadle, 1957; Chatterton and McKell, 1969; Zid and Boukharis, 1977; Matoh *et al*., 1986). However, high salinity levels may cause a reduction in total growth of *Atriplex* spp., especially in leaf biomass (Greenway, 1968; Mozafar *et al*., 1970; Priebe and Jager, 1978; Richardson and McKell, 1980; Aslam *et al*., 1986; Uchiyama, 1987; Ungar, 1996).

Most halophytes utilize the controlled accumulation and sequestration of inorganic ions as the basic mechanism by which they adjust the osmotic potential of their internal tissues to the external salinity (Flowers and Yeo, 1986; Cheeseman, 1988). Halophytic species differ widely in the extent to which they accumulate ions and their overall degree of salt tolerance (Glenn and O'Leary, 1984; Glenn *et al*., 1996). In *Atriplex*, both K^+ and Na^+ are involved in the osmotic adjustment of the leaf tissue to low external water potential, which can be caused by low soil moisture or high soil salinity (Osmond *et al*., 1980). In general, K^+ is accumulated in response to low soil moisture, while Na^+ is accumulated under saline conditions (Glenn *et al*., 1996). Gorham (1995) pointed out that cells are able to increase salt levels in the vacuoles by intracellular compartmentalization of ions and thus avoid high levels in the cytoplasm. Another means of osmotic adjustment is the synthesis and concentration of non-toxic solutes in the cytoplasm. Species of Chenopodiaceae commonly accumulate glycinebetaine in the cytoplasm, which acts as an osmoprotectant and can offset the high salinity concentration in the vacuole (Wyn Jones and Storey, 1981).

Many species of *Atriplex* are excellent livestock fodder because of their favourable crude protein content (McKell, 1994). *Atriplex griffithii* Moq. var. *stocksii* Boiss. occurs in

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both inland and coastal marshes and deserts around Karachi, Pakistan. Coastal species receive seasonal inundation, whereas inland populations either tap underground water sources or rely on monsoon rains that fall during July and August. Seeds germinate after monsoon rains and survival is high. Young seedlings and older plants that are dormant become active and produce new shoots. They produce seeds after about 90 d before becoming dormant again. This population of *A. griffithii* is usually found in areas with relatively low salinity.

Currently, little information is available on the salt tolerance of *Atriplex griffithii* Moq. var. *stocksii* Boiss. at different stages of growth (Khan and Rizvi, 1994). It has the potential to be used as a forage plant in degraded saline ecosystems of Pakistan. The present study addresses the following questions: (1) what effect does salinity have on growth responses at different ages? (2) is *A. griffithii* an ion accumulator? (3) does *A. griffithii* accumulate glycinebetaine in response to salinity?

MATERIALS AND METHODS

Seeds of *Atriplex griffithii* Moq. var. *stocksii* Boiss. were collected during autumn 1994 from salt flats situated on the Karachi University Campus in Karachi, Pakistan. These seeds were taken to Ohio University, Athens, Ohio, USA and growth studies began in May 1995.

Plants were grown in 10 cm diameter pots in a growth chamber at a thermoperiod of 25 °C/35 °C (night/day), and a 12 h photoperiod (300 μmol photons m^{-2} s^{-1}, 400–700 nm). Plants were initially grown in half-strength Hoagland and Arnon 2 solution to supply the macro- and micronutrients (Moore, 1960) until they reached about 7·5 cm in height. Pots were then thinned to 20 equal sized plants each. Two days after thinning, salt concentrations were gradually increased by 90 mM NaCl increments at 2 d intervals to reach the maximum salinity level of 360 mM NaCl after 8 d. Plants were grown in ten replicate pots in sand culture and watered with 0, 90, 180 and 360 mM NaCl. Pots were arranged in a completely random design within treatment trays and the position of the trays was changed weekly to avoid a position effect in the growth chamber. Pots were placed in trays with standing salt solution, and distilled water was added daily to correct for evaporation. Salt solutions were completely replaced once a week to maintain salinity levels in the pots.

Fresh and dry weight of plant shoots and roots were measured at 30 d intervals after the highest salt concentration was reached. Dry mass was determined after drying for 48 h in a forced-draft oven at 60 °C. To determine the relative growth rate (RGR), 15 plants were harvested immediately prior to beginning the salt treatments. Thereafter, successive harvests were taken after 30, 60 and 90 d with five plants per harvest. Dry mass at each harvest was used for calculating the RGR [relative growth rate = (ln mass2—ln mass1)/time]. Plant water status was evaluated by measuring shoot xylem pressure potentials with a pressure bomb apparatus (model 3005, Soil Moisture Equipment Corporation, Santa Barbara, California, USA) on five randomly chosen shoots from each treatment. Osmotic potentials were estimated from pressure volume curves using the bench dehydration method (Richardson and McKell, 1980).

Glycinebetaine and ion measurements were made on ten replicate 0·5 g samples of plant material that were boiled in 10 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. 42 filter paper, and then directly used to measure glycinebetaine, using a Hewlett Packard HPLC model HP 1050 modular 3D LC system with diode array detector. One ml of hot water extract was diluted with distilled water for ion analysis. Chloride ion content was measured with a Beckman specific ion electrode. Cation content of plant organs was analysed using a Perkin Elmer model 360 atomic absorption spectrophotometer. The Na^+ and K^+ concentrations of plant tissue were assayed by flame emission spectrophotometry and Ca^{2+} and Mg^{2+} concentrations by atomic absorption spectrophotometry. Tissue water content was determined by the difference between fresh weight and dry weight of the tissue.

Data for growth, ion content, glycinebetaine, and water relations were analysed using ANOVA (completely randomized) to determine if significant differences were present among means. A Bonferroni multiple range test was carried out to determine if significant ($P < 0·05$) differences occurred between individual treatments (SPSS, 1996).

RESULTS

A two-way ANOVA showed a significant individual effect of salinity and time of harvest and their interaction in affecting the root and stem dry weight of *A. griffithii* (Table 1). Salinity and the interaction of salinity and time of harvest did not significantly affect leaf dry weight (Table 1). Total dry weight accumulation of plants was not inhibited at low salinities, but dry weight production was significantly inhibited at 360 mM NaCl (Fig. 1). Leaf dry weight did not show a significant effect of salinity in any of the harvests, whereas stem dry weight progressively declined with an increase in salinity. Root growth showed a substantial promotion in low salinity (90 mM NaCl) in the third harvest, and further increases in salinity caused a progressive decline

TABLE 1. *Results of a two-way analysis of variance of plant characteristics by salinity treatment* (*S*), *and time of harvest* (*T*)

Dependent variable	S	T	S × T
Root dry weight (mg)	4·7**	21·6***	3·3**
Stem dry weight (mg)	9·1***	43·6***	2·8**
Leaf dry weight (mg)	1·8 n.s.	47·9***	0·5 n.s.
Plant dry weight (mg)	8·9**	45·9***	3·1*
Osmotic potential (−MPa)	3·3*	0·5 n.s.	1·1 n.s.
Pressure potential (−MPa)	0·9 n.s.	0·9 n.s.	1·1 n.s.
Water potential (−MPa)	72·0***	21·3***	9·7***

Numbers represent *F* values: $*P < 0·01$; $**P < 0·001$; $***P < 0·0001$; n.s., non significant.

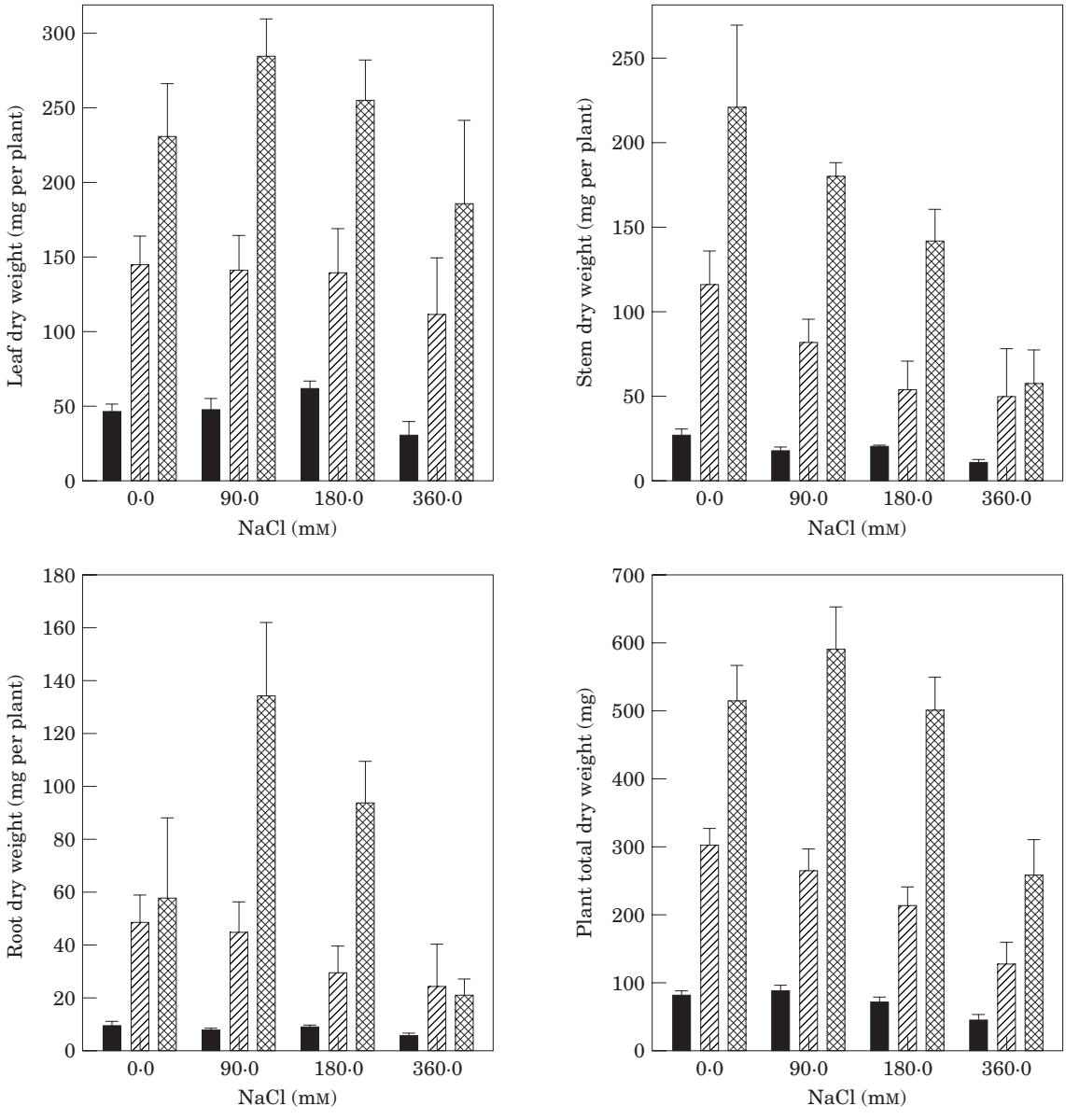

FIG. 1. Effect of NaCl (0, 90, 180 and 360 mM) on the leaf, stem, root and total plant dry weight in *Atriplex griffithii* Moq. var. *stocksii* Boiss. plants after 30 (■), 60 (▨), and 90 (▩) d. Bars represent mean ± s.e.; $n = 5$.

in growth (Fig. 1). The ash content of leaves was higher than that of stems and roots (Table 2). Ash content increased with increase in salinity in all plant parts. The maximum ash content was found in leaves (39% of the dry weight) followed by the stem (14% of the dry weight) and roots (8% of the dry weight).

The relative growth rate (RGR) of shoots was calculated at different times to determine the optimal growth stage. During the 0 to 30 d period the highest growth rate was observed in the low salinity treatment and the highest salinity substantially inhibited growth (Table 3). Highest growth rates were usually obtained during the 30 to 60 d period. Non-saline controls had the highest growth rate, whereas the salinity treatments were not significantly different from each other (Table 3). During the 60 to 90 d period the growth rate was very low in the non-saline control and salinity treatments were not significantly different from each other.

A three-way ANOVA showed a significant individual effect of harvest time, plant tissue, salinity and their interaction in affecting the water content of the shoot (with the exception of the interaction between plant tissue and salinity which was not significant; Table 4). Leaf tissue water content increased with the age of the plant in the non-saline control (Fig. 2). Increase in salinity had no significant effect on the water content after 30 and 60 d, but the water content of plants was significantly reduced at later stages of growth with increasing NaCl.

A two-way ANOVA showed a significant individual effect of salinity and time of harvest and their interaction in affecting water potential of *A. griffithii* (Table 1). Pressure potential did not change significantly over time and osmotic

TABLE 2. *Dry weight, ash-free dry weight, and ash weight in* Atriplex griffithii *harvested 90 d after highest salinity was reached*

Plant parts	NaCl (mM)	Dry weight (mg per plant)	Ash (% dry weight)	Ash-free dry weight (mg per plant)
Root	0	58 ± 9·5	2·4 ± 0·3	57 ± 8·6
	90	142 ± 11·2	2·2 ± 0·7	139 ± 10·1
	180	98 ± 7·5	2·2 ± 0·14	96 ± 8·3
	360	19 ± 2	7·9 ± 1·13	17 ± 1·6
Stem	0	220 ± 32	3·4 ± 0·63	212 ± 31·4
	90	170 ± 3·5	4·9 ± 0·58	162 ± 2·8
	180	143 ± 8·7	7·6 ± 0·17	132 ± 6·4
	360	46 ± 8·7	13·6 ± 1·14	40 ± 6·7
Leaf	0	149 ± 23	8·8 ± 0·14	136 ± 19·2
	90	270 ± 17	14·7 ± 0·27	230 ± 18·3
	180	248 ± 16	18·0 ± 0·98	203 ± 15·6
	360	170 ± 35	38·6 ± 3·4	104 ± 28·3

TABLE 3. *Relative growth rates (RGR) (mean ± s.e.) of* Atriplex griffithii *exposed to 4 levels of salinity (0, 90, 180 and 360 mM NaCl) in the external solution and harvested at 30, 60 and 90 d after the highest salinity was reached*

	RGR (g g^{-1} d^{-1}) for three time periods		
NaCl (mM)	30 d	60 d	90 d
0	0.035^{a} ± 0.002	0.043^{a} ± 0.001	0.018^{a} ± 0.006
90	0.038^{a} ± 0.003	0.036^{b} ± 0.03	0.026^{b} ± 0.003
180	0.030^{b} ± 0.0008	0.037^{b} ± 0.004	0.028^{b} ± 0.0009
360	0.015^{c} ± 0.002	0.034^{b} ± 0.002	0.024^{b} ± 0.003

Values in each column with the same superscript are not significantly different at $P < 0.05$, Bonferroni multiple range test.

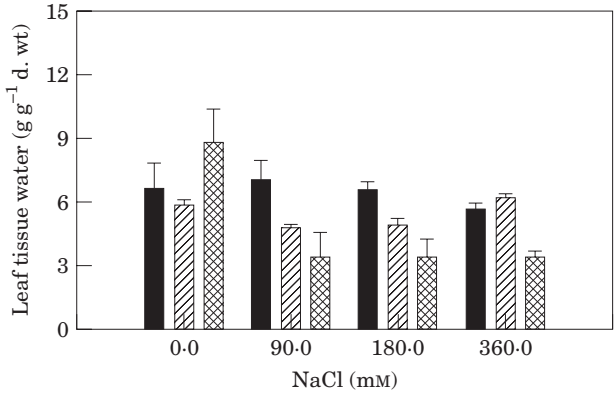

FIG. 2. Effect of NaCl (0, 90, 180 and 360 mM) on leaf tissue water (g g^{-1} d. wt) in *Atriplex griffithii* Moq. var. *stocksii* Boiss. plants after 30 (■), 60 (▨), and 90 (▩) d. Bars represent mean ± s.e.; $n = 5$.

potential became more negative. Both osmotic potential and water potential became more negative with increases in salinity, whereas pressure potential increased with increasing salinity (Fig. 3).

Total of cations (Na^+, K^+, Ca^{2+} and Mg^{2+}) and the anion (Cl^-) content increased with increases in salinity (Table 5). At all NaCl concentrations, the increase in total inorganic ions resulted from increased Na^+ and Cl^-, while Ca^{2+}, K^+ and Mg^{2+} concentrations decreased with an increase in salinity. These reductions were proportionally larger in the leaf compared to the root. In general, ion content increased from root to stem to leaf, and leaves had the highest Na^+ and Cl^- concentration (Table 5).

A three-way ANOVA showed significant individual effects of harvest time, plant tissue, salinity and their interaction in affecting glycinebetaine levels when expressed both on a dry weight as well as on a tissue water basis (Table 4). Glycinebetaine was only found in very small amounts in roots (data not shown). Stem tissue showed an increase in glycinebetaine concentration (mM l^{-1} tissue water) with an increase in salinity, and this increase was more pronounced

TABLE 4. *Results of a three-way ANOVA of plant characteristics by time of harvest (T), plant part (P), and salinity (S) treatments*

Independent variable	T	P	S	T × P	T × S	P × S	P × T × S
Tissue water (mg per plant)	57·3***	128·6***	4·6**	8·2***	2·2*	1·9 n.s.	2·6**
Betaine (mM l^{-1} tissue water)	7·1***	69·7***	9·2***	7·4***	2·4**	4·1***	3·7***
Betaine (mM kg^{-1} d. wt)	5·3**	201·7***	15·8***	4·0**	4·4***	7·4***	3·1**

Numbers represent F values: *$P < 0·01$; **$P < 0·001$; ***$P < 0·0001$; n.s., non significant.

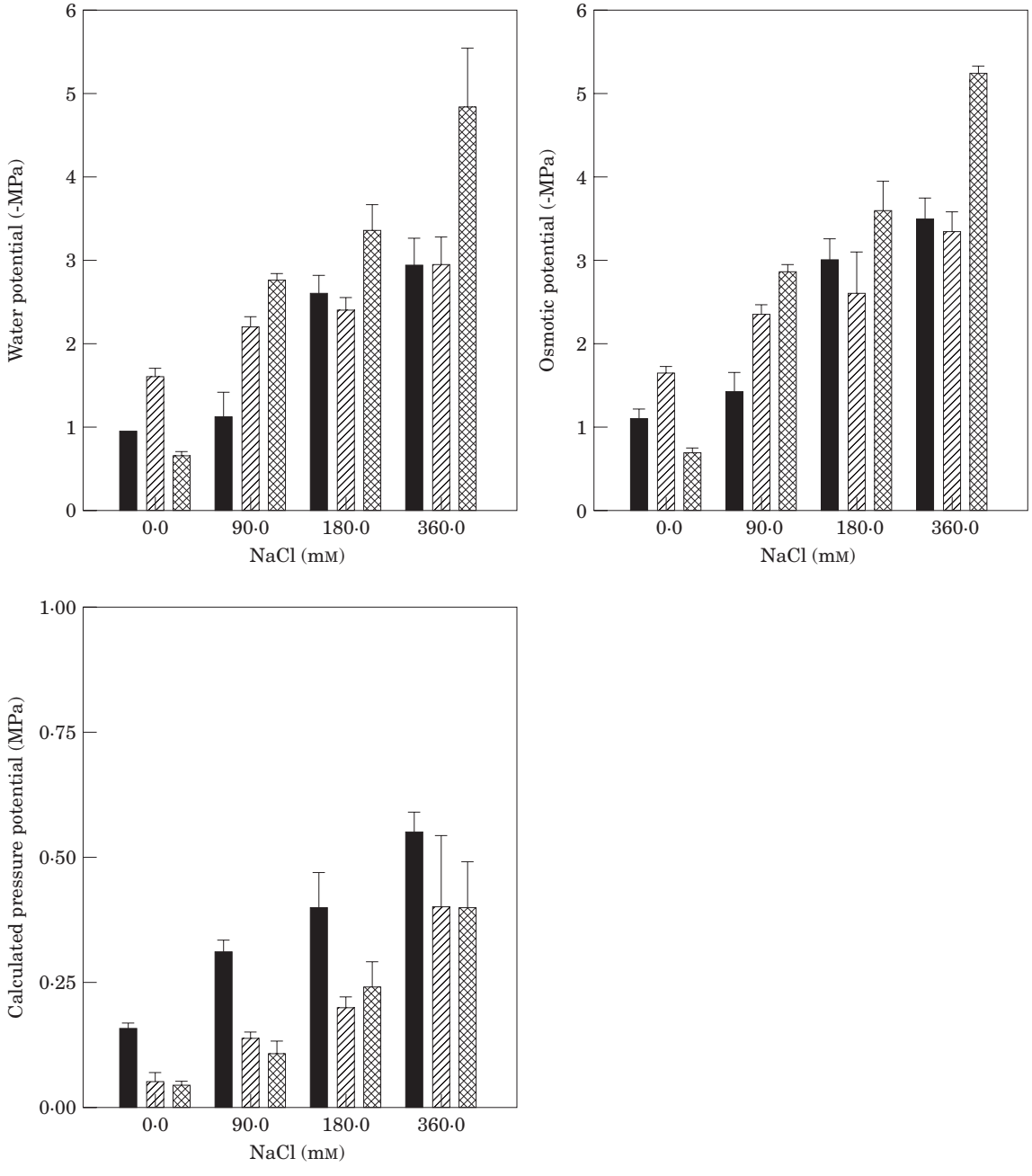

FIG. 3. Effect of NaCl (0, 90, 180 and 360 mM) on the water, osmotic, and pressure potential in *Atriplex griffithii* Moq. var. *stocksii* Boiss. plants after 30 (■), 60 (▨), and 90 (▩) d. Bars represent mean ± s.e.; $n = 5$.

in plants from the third harvest (Fig. 4). Concentrations (mM l^{-1} tissue water) of glycinebetaine among leaf harvests showed little change at the lower salinity, but at 360 mM NaCl there was a substantial increase in glycinebetaine concentration over time (Fig. 5).

DISCUSSION

Results of the present study indicate that *Atriplex griffithii* is a salt tolerant species during growth. Little inhibition in seedling growth was recorded in media containing up to 180 mM NaCl, but 360 mM NaCl was inhibitory to plant growth. Root growth was significantly promoted in the low salinity treatments. Halophytes such as *Atriplex* spp. show a stimulation of growth at NaCl concentrations that are inhibitory to the growth of non-halophytes (Osmond *et al.*, 1980). Ashby and Beadle (1957) showed that the growth of both *Atriplex inflata* F. Muell. and *A. nummularia* Lindl. was greater at 600 mM NaCl than in nutrient controls. *Atriplex* spp. vary in their degree of salt tolerance (Priebe and Jager, 1978). *Atriplex halimus* L. had the least decrease in dry mass production (40%) at 750 mM NaCl, whereas *A. calotheca* (Rafn.) Rafn. and Fries. (67%) and *A. nitens* Schkuhr (80%) had greater decreases but all three species

TABLE 5. *Ion concentrations (μmol g^{-1} dry weight) in* Atriplex griffithii *harvested 90 d after highest salinity was reached*

Plant part	NaCl (mM)	Na	K	Cl	Mg	Ca
Root	0	$519^{a} \pm 96$	$60^{a} \pm 3$	$119^{a} \pm 18$	$141^{a} \pm 10$	$60^{a} \pm 2$
	90	$550^{a} \pm 31$	$40^{a} \pm 2$	$138^{a} \pm 17$	$91^{b} \pm 10$	$20^{b} \pm 7$
	180	$598^{a} \pm 31$	$23^{a} \pm 0{\cdot}6$	$131^{a} \pm 8$	$77^{b} \pm 9$	$16^{b} \pm 2$
	360	$2942^{b} \pm 253$	$12^{a} \pm 2$	$212^{b} \pm 4$	$127^{c} \pm 27$	$11^{ab} \pm 7$
Stem	0	$45^{a} \pm 41$	$69^{a} \pm 10$	$315^{a} \pm 70$	$209^{a} \pm 28$	$123^{a} \pm 16$
	90	$1225^{b} \pm 74$	$42^{b} \pm 9$	$378^{a} \pm 63$	$150^{b} \pm 6$	$48^{b} \pm 15$
	180	$2359^{c} \pm 41$	$32^{b} \pm 11$	$385^{a} \pm 137$	$125^{b} \pm 49$	$88^{b} \pm 25$
	360	$4114^{d} \pm 374$	$12^{c} \pm 0{\cdot}11$	$1022^{b} \pm 459{\cdot}8$	$102^{b} \pm 43$	$53^{b} \pm 26$
Leaf	0	$970^{a} \pm 510$	$311^{a} \pm 24$	$756^{a} \pm 124$	$627^{a} \pm 200$	$292^{a} \pm 3$
	90	$2613^{b} \pm 407$	$144^{b} \pm 20$	$1830^{b} \pm 147$	$352^{b} \pm 63$	$191^{b} \pm 55$
	180	$3244^{c} \pm 382$	$145^{b} \pm 13$	$2467^{c} \pm 152$	$210^{b} \pm 62$	$178^{b} \pm 58$
	360	$6151^{d} \pm 678$	$61^{a} \pm 5$	$6590^{d} \pm 324$	$169^{b} \pm 27$	$105^{c} \pm 44$

Values in each column with the same superscript are not significantly different at $P < 0{\cdot}05$, Bonferroni test.

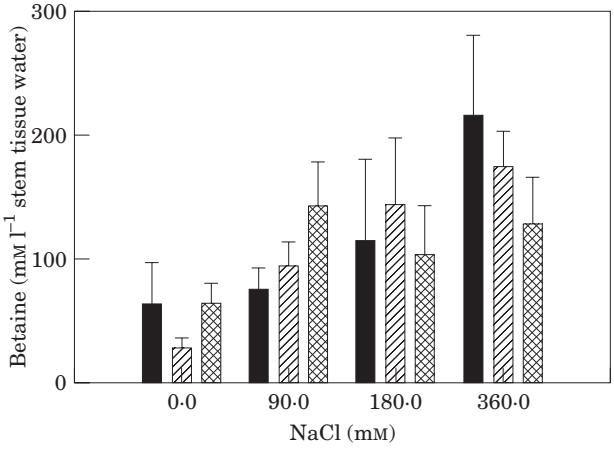

FIG. 4. Effect of NaCl (0, 90, 180 and 360 mM) on glycinebetaine content of stem in *Atriplex griffithii* Moq. var. *stocksii* Boiss. plants after 30 (■), 60 (▨), and 90 (▩) d. Bars represent mean ± s.e.; $n = 5$.

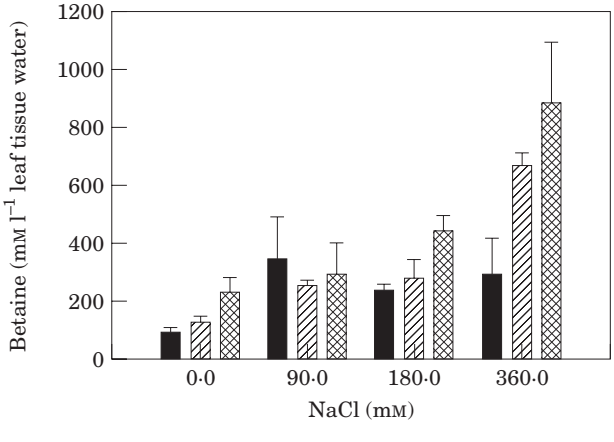

FIG. 5. Effect of NaCl (0, 90, 180 and 360 mM) on glycinebetaine content of leaf in *Atriplex griffithii* Moq. var. *stocksii* Boiss. plants after 30 (■), 60 (▨), and 90 (▩) d. Bars represent mean ± s.e.; $n = 5$.

were able to survive in this salt treatment (Priebe and Jager, 1978). Storey and Wyn Jones (1979) determined that *A. spongiosa* F. Muell. was able to grow in medium containing over 600 mM NaCl, with dry mass production decreasing by 50% at 800 mM NaCl.

Deleterious effects of salinity are thought to result from low water potentials, ion toxicities, nutrient deficiencies, or a combination of these factors. Nutrient deficiencies can occur in plants when high concentrations of Na^+ in the soil reduce the amounts of available K^+, Mg^{2+} and Ca^{2+} (Epstein, 1972) or when Na^+ displaces membrane-bound Ca^{2+} (Cramer *et al.*, 1985). In addition, Na^+ may have a direct toxic effect, such as when it interferes with the function of potassium as a cofactor in various reactions. Many of the deleterious effects of Na^+, however, seem to be related to the structural and functional integrity of membranes (Kurth *et al.*, 1986). Our results indicated that Na^+ and Cl^- content in shoots and roots increased with salinity. The Ca^{2+} and Mg^{2+} contents were reduced in shoots of *A. griffithii* plants grown at high salinity agreeing with results found for other halophytes (Flowers, 1972; Glenn and O'Leary, 1984; McNulty, 1985; Naidoo and Rughunanan, 1990; Ayala and O'Leary, 1995). Greenway *et al.* (1966) reported that growth of *Atriplex nummularia* was optimal at 100 to 200 mM NaCl. Leaf Na^+ content increased from 0·9 to 5·0 mmol g^{-1} d. wt and Cl^- increased from 0·4 to 3·6 mmol g^{-1} in treatments with 1 and 300 mM NaCl. Potassium content of the leaves decreased over this NaCl range from 1·8 to 0·6 mol g^{-1} d. wt. At optimal growth conditions plants accumulated from 4·1 to 6·4 mmol Na^+ g^{-1} and 2·0 to 3·0 mmol Cl g^{-1} d. wt of leaf material. Greenway (1968) reported that Na^+ increased and K^+ content decreased in leaves when *A. nummularia* was exposed to salinities ranging from 0 to 1% NaCl. Plants grown in 2% NaCl had 63% of the blade Na^+ content concentrated in salt hairs (0·360 mg Na^+ cm^{-2} leaf area), while controls contained 49% of the blade Na^+ content in salt hairs (0·065 mg Na^+ cm^{-2}) (Uchiyama, 1987). Anderson *et al.* (1977) showed that the tissue ion concentration of *A. hastata* var. *salina* increased as external NaCl concentration increased, but more Na^+ was

taken up than Cl^-. They concluded that endogenous organic substances and a hydrogen efflux pump balanced the excess Na^+ accumulated by *A. hastata* L. Ash content in leaves of *A. griffithii* was highest (39% of dry weight) at 360 mM NaCl. Since these data indicate that *A. griffithii* is an ion accumulator, it should be considered as a species that might be used to phytoremediate degraded saline lands.

Halophytes are characterized by their capacity to adjust tissue water potential to a level that is more negative than that of the soil water potential of the habitat in which they are growing (Ungar, 1991). Growth and survival of halophytes is dependent on the high levels of ion accumulation in its tissues for the maintenance of turgor and osmotic adjustment (Flowers *et al*., 1977). Water potential and osmotic potential in *A. griffithii* became increasingly more negative with the corresponding increase in media salinity, indicating that *A. griffithii* osmotically adjusts in response to increases in salinity. These results agree with those of Karimi and Ungar (1984), who demonstrated a high correlation ($r = 0{\cdot}87$) between leaf water potential and media salinity levels in *A. prostrata*.

Atriplex griffithii leaves accumulated increasing concentrations of glycinebetaine with increases in medium salinity. Halophytes are distinguished by their capacity to produce high concentrations of compatible osmotica, and in several *Atriplex* spp. the quaternary ammonium compound glycinebetaine is present in high concentrations (Storey and Wyn Jones, 1979). The glycinebetaine concentration in leaves of *A. spongiosa* is directly correlated with the NaCl concentration of the leaf sap. Glycinebetaine concentration in *Atriplex barclayana* Hall and Clements leaves rose slightly when culture salinity was raised to 100 mM NaCl and then remained constant up to a NaCl level of 400 mM (Nerd and Pasternak, 1992). Our data for *A. griffithii* showed a progressive increase in glycinebetaine with increasing salinity, which is in agreement with results for *A. spongiosa* and *A. halimus* L. (Wyn Jones *et al*., 1977; Wyn Jones, 1984).

In summary our results show that *A. griffithii* is a moderately salt tolerant halophyte, which accumulates large amounts of ions (40% of dry weight) to achieve a negative water potential gradient so that water uptake is not disrupted. *Atriplex griffithii* plants also accumulate glycinebetaine as an osmoprotectant or to achieve osmotic balance in the cytoplasm.

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