



## The effect of salinity on the growth, water status, and ion content of a leaf succulent perennial halophyte, *Suaeda fruticosa* (L.) Forssk

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*Suaeda fruticosa* (L.) Forssk plants grown in saline conditions (200 to 400 mol m<sup>-3</sup> NaCl) had greater fresh and dry weights than those grown in non-saline controls, and 600 to 1000 mol m<sup>-3</sup> NaCl inhibited growth. Gibberellic acid and kinetin both alleviated some of the inhibitory effects of salinity at 800 mol m<sup>-3</sup> NaCl on shoot growth of *S. fruticosa* while root growth was promoted by kinetin. Tissue water content increased in up to 200 mol m<sup>-3</sup> NaCl but decreased with a further increase in salinity. Water potential and osmotic potential of plants became more negative with an increase in salinity. Leaf Ca<sup>2+</sup>, Mg<sup>2+</sup>, and K<sup>+</sup> concentration decreased with increasing salinity, while both Na<sup>+</sup> and Cl<sup>-</sup> increased and reached 1391 and 1673 mmol kg<sup>-1</sup> dry weight, respectively. Total glycinebetaine content of shoots was highest at 600 to 1000 mol m<sup>-3</sup> NaCl.

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**Keywords:** gibberellic acid; glycinebetaine; halophyte; kinetin; salt tolerance; *Suaeda fruticosa*

### Introduction

Many arid and semi-arid regions in the world contain soils and water resources that are too saline for most of the common economic crops (Nerd & Pasternak, 1992). The utilization of halophytic plants in pasture and fodder production in saline soils is the only economic solution presently available (Yeo & Flowers, 1980). Some halophytes not only tolerate high levels of salinity but reach optimal levels of growth under saline conditions (Flowers *et al.*, 1977; Ungar, 1991). Growth stimulation by salinity has been reported in annual species of *Suaeda* but no data are available for the perennial salt desert species *Suaeda fruticosa* (L.) Forssk. (Williams & Ungar, 1972; Boucaud & Ungar, 1978; Ke-Fu *et al.*, 1995).

Laboratory investigations indicate that halophytes have adapted to saline habitats by their ability to adjust osmotically to increasing salinity levels (Flowers *et al.*, 1977; Karimi & Ungar, 1984; Clipson *et al.*, 1985). *Suaeda* spp. have been reported to accumulate glycinebetaine as an osmoticum in the cytoplasm when plants were exposed to increasing salinity (Storey & Wyn Jones, 1975; Gorham, 1995). It is hypothesized that plants

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partition  $\text{Na}^+$  and  $\text{Cl}^-$  in cell vacuoles and that glycinebetaine serves as a balancing osmoticum in the cytoplasm (Gorham, 1995)

Waterlogging and salinity are major environmental and economic problems in Pakistan and a number of other arid and semi-arid regions of the world. Use of native species to reclaim the saline areas would not only be economically beneficial but would also be ecologically relevant. Chaudhri *et al.* (1964) estimated from field studies that plantings of *S. fruticosa* could remove about  $2,646 \text{ kg ha}^{-1}$  of salt per year in salt desert habitats.

Little data are available concerning the effect of growth regulators on the growth response of halophytes under saline conditions (Ungar, 1991). One possible explanation for decreased growth with an increase in salinity is that the production of the growth promoters gibberellic acid and cytokinin is inhibited. One aim of this investigation was to determine the effect of exogenous applications of gibberellic acid and kinetin on the biomass yield of *S. fruticosa*. We also ascertain how *S. fruticosa* responds to different salinity levels in terms of growth, water status, and glycinebetaine and ion accumulation.

### Materials and methods

Seeds of *S. fruticosa* were collected during the fall of 1994 from salt flats situated on the Karachi University Campus in Karachi, Pakistan. Seeds were separated from the inflorescence and stored at  $4^\circ\text{C}$ . These seeds were brought to Ohio University, U.S.A., and growth studies started in May 1996. Seeds were surface sterilized using the fungicide phygon and germinated in sand in pots at a thermoperiod of  $25^\circ\text{C}: 35^\circ\text{C}$  (night:day) and a 12-h photoperiod.

Plants were grown in a growth chamber at a thermoperiod of  $25^\circ\text{C}: 35^\circ\text{C}$  (night: day), and a 12-h photoperiod ( $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ , 400–700 nm). Ten replicate pots for each of the six treatments, containing five seedlings each, were grown in a half-strength Hoagland and Arnon no. 2 nutrient solution containing 0, 200, 400, 600, 800, and  $1000 \text{ mol m}^{-3}$  NaCl in sand culture. Pots were subirrigated, and the water level was adjusted daily to correct for evaporation. Salt solutions were completely replaced once a week to avoid build-up of salinity in pots. At the initiation of the experiment, salinity concentrations were gradually increased by  $200 \text{ mol m}^{-3}$  at 2-day intervals to reach the maximum salinity levels of  $1000 \text{ mol m}^{-3}$  NaCl after 10 days. Gibberellic acid ( $1 \text{ mol m}^{-3}$  GA<sub>3</sub>) and kinetin ( $0.1 \text{ mol m}^{-3}$ ) solution were sprayed on the leaves twice a week 7 days after the desired salinity concentrations were reached.

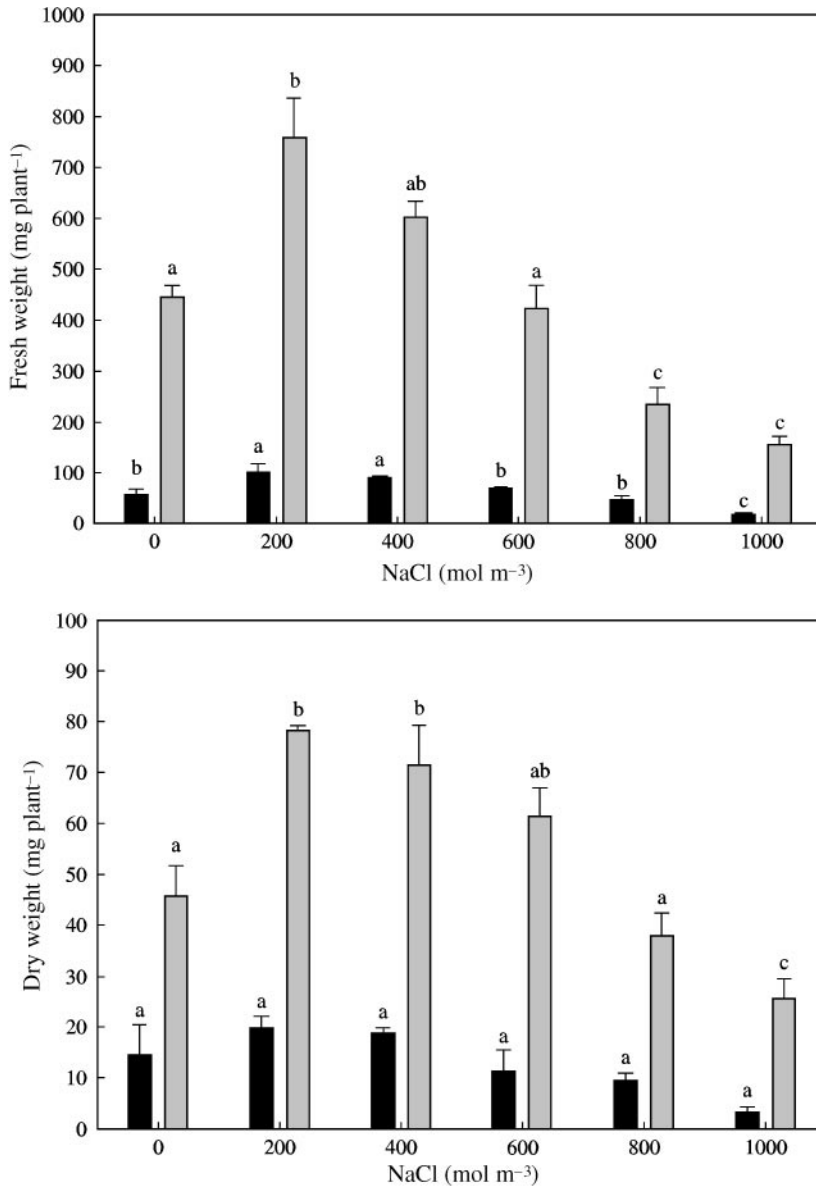
Fresh and dry weight of plant shoots and roots of a subsample of five plants from each treatment were measured at 90 days after the highest salt concentration was reached. Dry mass was determined after drying for 48 h in a forced-draft oven at  $60^\circ\text{C}$ . Organic content (ash-free dry weight) was determined after plants were treated in a muffle furnace at  $500^\circ\text{C}$  for 24 h. Plant water status was evaluated by shoot xylem pressure potentials measured with a pressure bomb on five shoots from each treatment. Osmotic potential was determined from a pressure volume curve.

For glycinebetaine and ion measurements, five replicates from the previous salinity experiment of 0.5 g fresh weight of plant material were boiled in 10 ml of water for 2 h at  $100^\circ\text{C}$  using a dry heat bath. This hot water extract was cooled and filtered using Whatman no. 42 filter paper, and then used directly to measure glycinebetaine in a Hewlett Packard HPLC model HP 1050 modular 3D LC system with a diode array detector (Khan *et al.*, 1997). 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  $\text{Na}^+$  and  $\text{K}^+$  concentrations of plant tissue were assayed by flame emission, and  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  concentrations were determined by atomic absorption spectrometry.

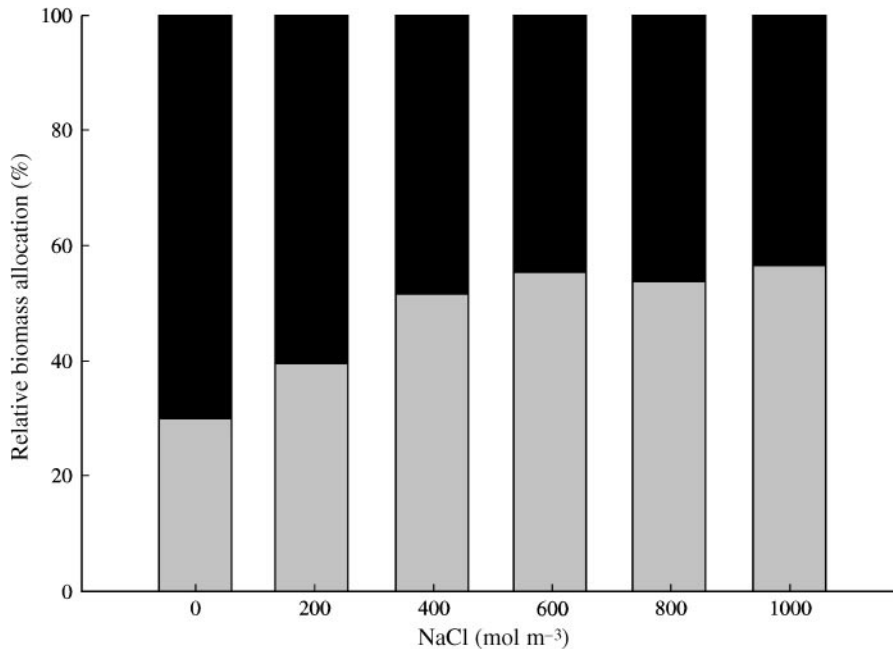
Results of growth, glycinebetaine and ion content, and water status of plants were analysed with a one-way ANOVA to determine if significant differences were present among means. A Bonferroni test was carried out to determine if significant ( $P < 0.05$ ) differences occurred between individual treatments (SPSS, 1996).

### Results

A one-way ANOVA on the biomass production of *S. fruticosa* indicated that salinity significantly affected root fresh weight ( $F = 12.62$ ,  $p < 0.0001$ ), shoot dry weight



**Figure 1.** Effect of NaCl (0, 200, 400, 600, 800 and 1000 mol m<sup>-3</sup>) on the fresh and dry weight of *S. fruticosa* plants. Bars represent mean  $\pm$  S.E. Different letters above bars represent significant differences ( $p < 0.05$ ) among treatments. ■ Root; □ shoot.

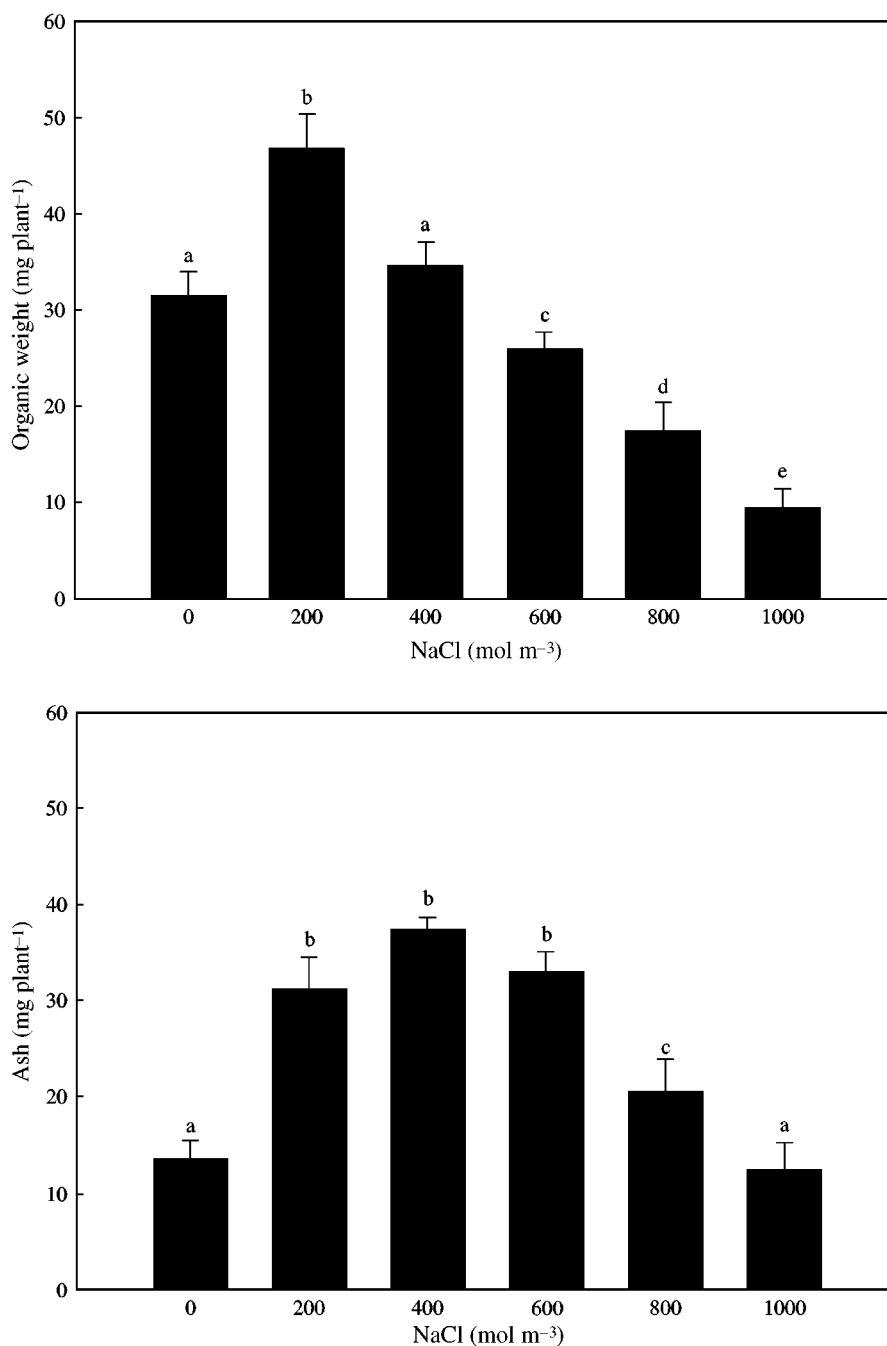


**Figure 2.** Effect of NaCl (0, 200, 400, 600, 800 and 1000 mol m<sup>-3</sup>) on relative biomass allocation in *S. fruticosa* shoots. ■ Organic; □ ash.

( $F = 6.54$ ,  $p < 0.001$ ) and shoot fresh weight ( $F = 26.38$ ,  $p < 0.0001$ ). Root dry weight was not significantly ( $F = 0.72$ ,  $p > 0.05$ ) affected by salinity. Shoot dry weight increased significantly in salinities of 200 and 400 mol m<sup>-3</sup> NaCl, but yields of shoots progressively declined with further increases in salinity (Fig. 1). In contrast, root fresh weight was not promoted at low salinity but was inhibited at higher salinity (Fig. 1). Ash made up about 30% of the total dry mass in non-saline control plants, and there was a significant increase ( $F = 46.38$ ,  $p < 0.0001$ ) in ash content with increasing salinity, reaching from 55 to 60% of the total dry mass (Fig. 2). Organic content (ash-free dry weight) of plants peaked in 200 mol m<sup>-3</sup> NaCl and progressively declined with increasing salinity (Fig. 3).

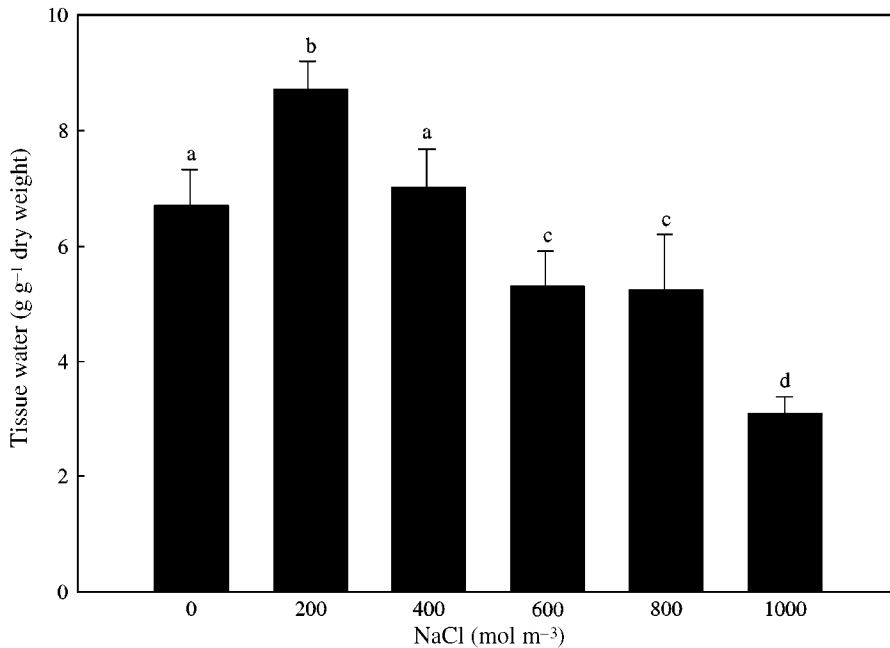
Salinity significantly affected tissue water content (succulence) of *S. fruticosa* shoots on a unit dry weight basis ( $F = 30.18$ ,  $p < 0.0001$ ). Tissue water (g g<sup>-1</sup> dry weight) increased slightly at low salinities, but declined at higher salinities (Fig. 4). A one-way ANOVA of the water status of *S. fruticosa* revealed that salinity significantly affected the water potential ( $F = 172.75$ ,  $p < 0.0001$ ) and osmotic potential ( $F = 141.8$ ,  $p < 0.0001$ ) of plant shoots. Water potential and osmotic potential of *S. fruticosa* plants became increasingly negative with an increase in media salinity (Fig. 5).

A one-way ANOVA of the ion content of *S. fruticosa* revealed that salinity significantly affected Ca<sup>2+</sup> ( $F = 5.06$ ,  $p < 0.01$ ), Cl<sup>-</sup> ( $F = 35.45$ ,  $p < 0.0001$ ), Mg<sup>+</sup> ( $F = 10.52$ ,  $p < 0.0001$ ), K<sup>+</sup> ( $F = 12.55$ ,  $p < 0.0001$ ) and Na<sup>+</sup> ( $F = 11.44$ ,  $p < 0.0001$ ) content of plants. Sodium and Cl<sup>-</sup> content increased in both shoots and roots with an increase in salinity, and this increase was greater in shoots in comparison to roots (Table 1). The Ca<sup>2+</sup>, Mg<sup>2+</sup>, and K<sup>+</sup> content of plants decreased with an increase in salinity, with the exception of Ca<sup>2+</sup> in roots and Mg<sup>2+</sup> in shoots which remained unchanged (Table 1).



**Figure 3.** Effect of NaCl (0, 200, 400, 600, 800 and 1000 mol m<sup>-3</sup>) on organic (ash-free dry weight) and ash weight of *Suaeda fruticosa* shoots. Bars represent mean  $\pm$  S.E. Different letters above bars represent significant differences ( $p < 0.05$ ) among treatments.

Salinity significantly affected the concentration of glycinebetaine (mol m<sup>-3</sup> tissue water) of *S. fruticosa* shoots ( $F = 2.90$ ,  $p < 0.05$ ), and total glycinebetaine (mmol kg<sup>-1</sup> dry weight) ( $F = 6.26$ ,  $p < 0.004$ ). The concentration of glycinebetaine on a tissue



**Figure 4.** Effect of NaCl (0, 200, 400, 600, 800 and 1000 mol m<sup>-3</sup>) on tissue water content of *S. fruticosa* shoots. Bars represent mean  $\pm$  S.E. Different letters above bars represent significant differences ( $p < 0.05$ ) among treatments.

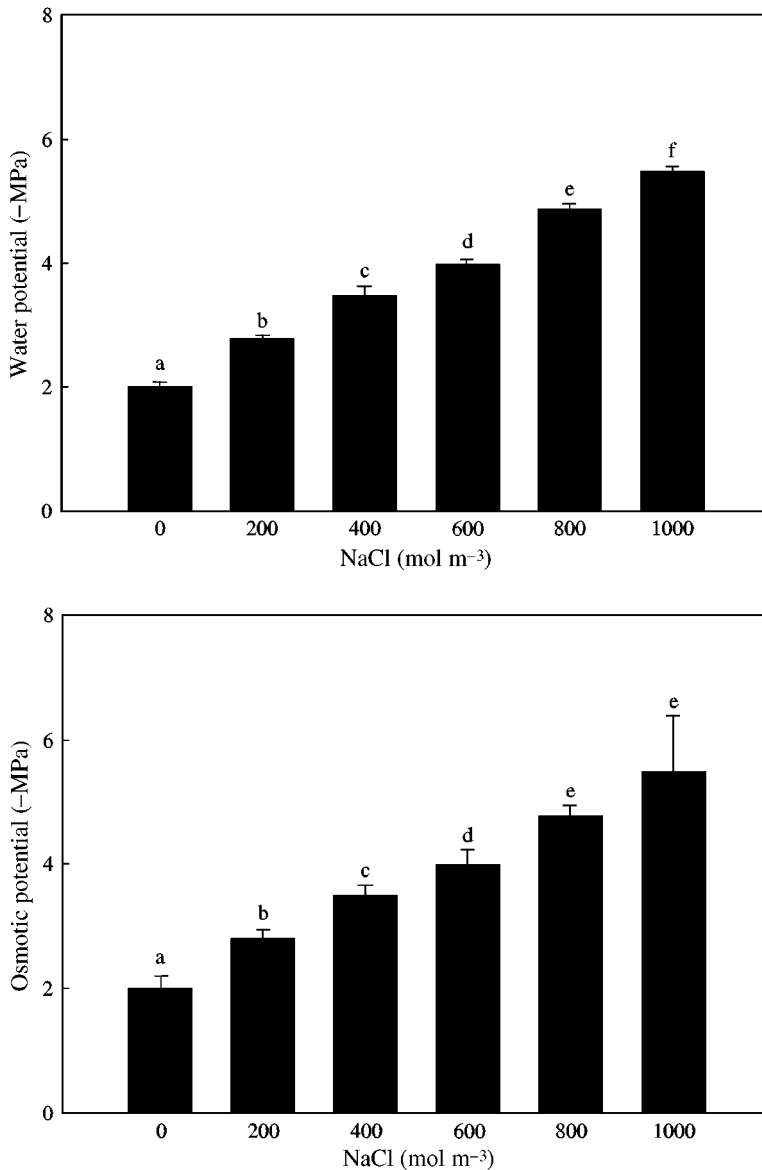
water basis did not change significantly between 0 to 400 mol m<sup>-3</sup> NaCl but increased at 600 mol m<sup>-3</sup> and higher salinities (Table 2).

A one-way ANOVA of the growth regulator effects on shoot growth of *S. fruticosa* plants grown under saline conditions revealed that gibberellic acid ( $F = 7.45$ ,  $p < 0.05$ ), and kinetin ( $F = 6.02$ ,  $p < 0.01$ ) significantly alleviated the effect of salinity (800 mol m<sup>-3</sup>, NaCl) on shoot growth, while only kinetin ( $F = 23.5$ ,  $p < 0.001$ ) alleviated salinity effects on root growth (Fig. 6).

## Discussion

*Suaeda fruticosa* shoot biomass production was significantly stimulated at 200 mol m<sup>-3</sup> NaCl, which differs from the results of Mahmood *et al.* (1996), where no salt stimulation was found. Similar results have been reported for other halophytes which have optimal growth in the presence of salt (Naidoo & Raghunan, 1990; Ayala & O'Leary, 1995). The ash content of plants increased from 30% in controls to about 60% in 1000 mol m<sup>-3</sup> NaCl and the organic content of plants was significantly reduced. Other halophytes are also reported to have high ash contents, mainly, as in the case of *S. fruticosa*, because of an accumulation of Na<sup>+</sup> and Cl<sup>-</sup> (Robinson & Downton, 1985; Naidoo & Raghunan, 1990; Ungar, 1991).

Trends in plant water content paralleled those of fresh weight, increasing significantly in low salinity and then declining with increased salinity. Water content of shoots increased in the 200 mol m<sup>-3</sup> NaCl treatment, but at higher salinities the water content progressively decreased. Measurements of plant water status indicated that *S. fruticosa* plants adjusted their water potential and osmotic potential to more negative levels as salinity increased. In dicotyledenous halophytes, water relations and the ability to adjust



**Figure 5.** Effect of NaCl (0, 200, 400, 600, 800 and 1000 mol m<sup>-3</sup>) on the water potential and osmotic potential of *S. fruticosa* shoots. Bars represent mean  $\pm$  S.E. Different letters above bars represent significant differences among treatments.

osmotically are important determinants of the growth response (Flowers *et al.*, 1977; Munns *et al.*, 1983). It would appear that the growth response at moderate salinities may be largely the consequence of an increased uptake of solutes that are required to induce cell expansion, since this maintains the pressure potential in plant tissues. At high salinities, growth reduction might either be caused by a reduced ability to adjust osmotically as a result of saturation of the solute uptake system, or because of excessive demand on the energy requirements of such systems (Munns *et al.*, 1983; Gale & Zeroni, 1984). Other factors, such as nutrient deficiencies, may also play an important role (Marschner, 1995).

**Table 1.** The effect of salinity on the concentration of ions (tissue water basis) in shoots and roots of *S. fruticosa*. Values represent means  $\pm$  standard error ( $n = 5$ ). Means in the same column followed by the same letter are not significantly different ( $p > 0.05$ )

NaCl (mol m <sup>-3</sup> )	Tissue ion concentration (mol m <sup>-3</sup> tissue water)									
	Na <sup>+</sup>		K <sup>+</sup>		Ca <sup>2+</sup>		Mg <sup>2+</sup>		Cl <sup>-</sup>	
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
0	370 <sup>a</sup> $\pm$ 11	388 <sup>a</sup> $\pm$ 125	113 <sup>a</sup> $\pm$ 16	83 <sup>a</sup> $\pm$ 24	65 <sup>a</sup> $\pm$ 22	56 <sup>a</sup> $\pm$ 9	16 <sup>a</sup> $\pm$ 3	33 <sup>a</sup> $\pm$ 12	204 <sup>a</sup> $\pm$ 38	267 <sup>a</sup> $\pm$ 112
200	615 <sup>b</sup> $\pm$ 82	486 <sup>a</sup> $\pm$ 141	61 <sup>b</sup> $\pm$ 11	56 <sup>b</sup> $\pm$ 14	72 <sup>a</sup> $\pm$ 12	64 <sup>a</sup> $\pm$ 6	18 <sup>a</sup> $\pm$ 4	18 <sup>b</sup> $\pm$ 4	502 <sup>b</sup> $\pm$ 85	578 <sup>b</sup> $\pm$ 9
400	585 <sup>b</sup> $\pm$ 87	675 <sup>b</sup> $\pm$ 74	39 <sup>c</sup> $\pm$ 1	22 <sup>c</sup> $\pm$ 11	64 <sup>a</sup> $\pm$ 10	58 <sup>a</sup> $\pm$ 4	15 <sup>a</sup> $\pm$ 1	15 <sup>b</sup> $\pm$ 1	647 <sup>b</sup> $\pm$ 89	548 <sup>b</sup> $\pm$ 89
600	713 <sup>b</sup> $\pm$ 25	683 <sup>b</sup> $\pm$ 90	41 <sup>c</sup> $\pm$ 7	100 <sup>ad</sup> $\pm$ 64	44 <sup>b</sup> $\pm$ 7	54 <sup>a</sup> $\pm$ 4	20 <sup>a</sup> $\pm$ 2	16 <sup>b</sup> $\pm$ 3	793 <sup>bc</sup> $\pm$ 77	667 <sup>bc</sup> $\pm$ 57
800	900 <sup>c</sup> $\pm$ 74	746 <sup>b</sup> $\pm$ 45	30 <sup>c</sup> $\pm$ 2	48 <sup>bc</sup> $\pm$ 24	41 <sup>b</sup> $\pm$ 5	46 <sup>a</sup> $\pm$ 8	20 <sup>a</sup> $\pm$ 2	17 <sup>b</sup> $\pm$ 4	781 <sup>bc</sup> $\pm$ 121	680 <sup>bc</sup> $\pm$ 85
1000	1391 <sup>d</sup> $\pm$ 142	863 <sup>b</sup> $\pm$ 110	25 <sup>c</sup> $\pm$ 3	30 <sup>bc</sup> $\pm$ 6	48 <sup>b</sup> $\pm$ 3	34 <sup>a</sup> $\pm$ 3	23 <sup>a</sup> $\pm$ 7	20 <sup>b</sup> $\pm$ 6	1673 <sup>d</sup> $\pm$ 65	984 <sup>d</sup> $\pm$ 64



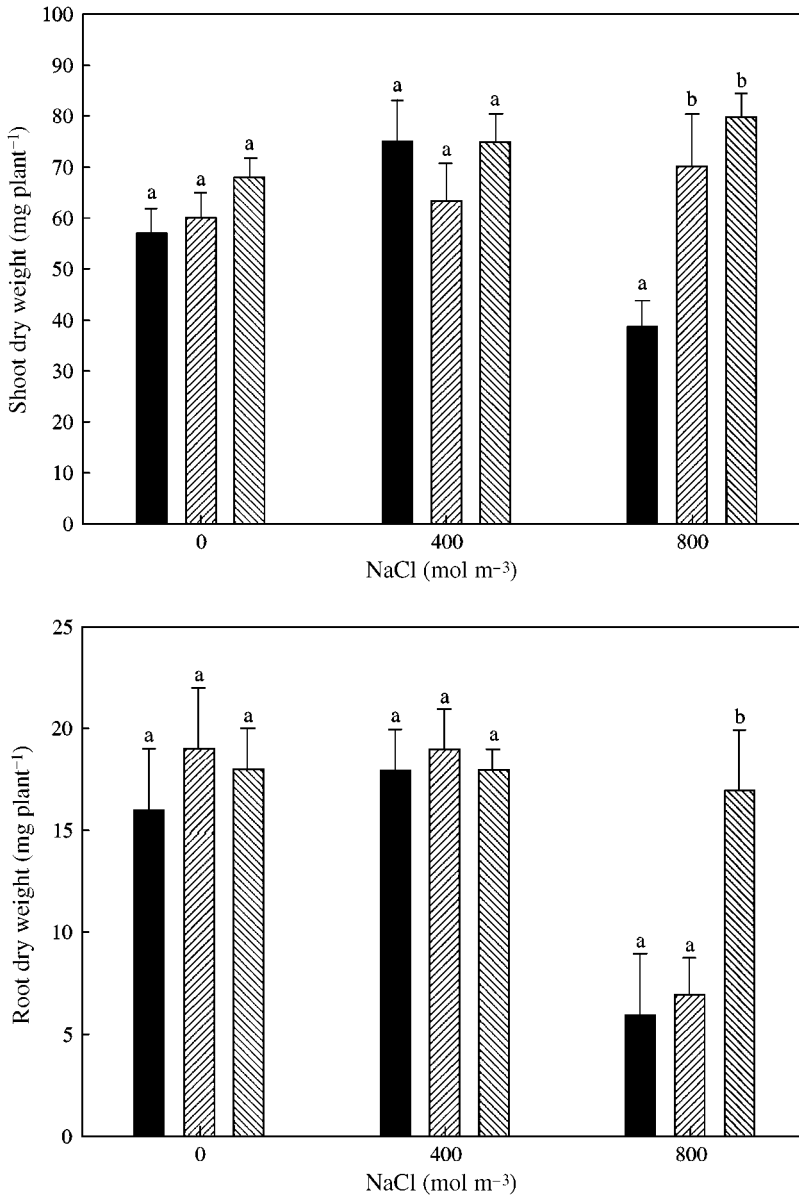
**Table 2.** The effects of salinity on the glycinebetaine content in the shoot of *S. fruticosa*. Values represent mean  $\pm$  standard error (n = 5). Means in the same row followed by the same letter are not significantly different (p > 0.05)

Glycinebetaine Content	NaCl (mol m <sup>-3</sup> )					
	0	200	400	600	800	1000
Glycinebetaine (mol m <sup>-3</sup> tissue water)	110 <sup>a</sup> $\pm$ 23	123 <sup>a</sup> $\pm$ 18	140 <sup>a</sup> $\pm$ 19	220 <sup>b</sup> $\pm$ 18	215 <sup>b</sup> $\pm$ 21	218 <sup>b</sup> $\pm$ 23
Glycinebetaine (mmol kg <sup>-1</sup> dw)	670 <sup>a</sup> $\pm$ 50	1100 <sup>b</sup> $\pm$ 20	994 <sup>b</sup> $\pm$ 30	1156 <sup>b</sup> $\pm$ 46	900 <sup>b</sup> $\pm$ 67	650 <sup>a</sup> $\pm$ 50

The accumulation of salt in vacuoles is particularly evident in some dicotyledenous halophytes, such as *Salicornia bigelovii* Torr. (Ayala & O'Leary, 1995) and *S. maritima* (Harvey *et al.*, 1981) that have succulent stems or leaves composed of enlarged cells in which the vacuoles occupy most of the volume. In such plants, the Na<sup>+</sup> and Cl<sup>-</sup> concentrations in plant tissues may exceed 1000 mM, and compatible osmotica (e.g. glycinebetaine) are accumulated in the cytoplasm to prevent dehydration of the cytoplasm (Gorham, 1995). Marcum & Murdoch (1992) suggested that 200 to 300 mM of organic osmotica in the cytoplasm is sufficient for osmotic adjustment at higher salinities. *Suaeda fruticosa* produces about 200 mM glycinebetaine, which is theoretically sufficient to balance the high salt accumulation in vacuoles. The decrease in total glycinebetaine at 1000 mol m<sup>-3</sup> NaCl may be related to the reduced tissue water content at this salinity.

It is hypothesized that increased medium salinity could restrict the synthesis of plant growth promoters such as cytokinins and increase the production of inhibitors such as abscisic acid (Prisco & O'Leary, 1972; Khan *et al.*, 1976; Ungar, 1991). Shoot growth of *S. fruticosa* was stimulated in the 800 mol m<sup>-3</sup> NaCl treatment by the application of both GA<sub>3</sub> and kinetin, and root growth was promoted by kinetin, but control plants and those growing at lower salinities were not promoted by either kinetin or GA<sub>3</sub>. Exogenous application of both kinetin and GA<sub>3</sub> stimulated the growth of the halophyte *S. maritima* var. *macrocarpa* at all salinity levels up to 360 mol m<sup>-3</sup> NaCl (Boucaud & Ungar, 1976). It has been reported that GA<sub>3</sub> application significantly stimulated growth of halophytes treated with NaCl (Ungar, 1978; Wochok & Sluis, 1980; Ke-Fu *et al.*, 1986), but the stimulatory effect of growth regulators at very high salinities (800 mol m<sup>-3</sup> NaCl) has not been reported previously in the literature.

The mechanism of salt tolerance in *S. fruticosa* could involve striking a delicate balance between ion accumulation, osmotic adjustment, production of osmotica (glycinebetaine), maintenance of pressure potential, and growth. At higher salinities, a significant reduction in growth occurs because of the plant's inability to adjust osmotically, and specific ion toxicities may have caused a significant reduction in growth. The balance of growth regulators could be changed at high salinities and this effect could be partially alleviated by application of exogenous growth promoter substances. This investigation indicates that *S. fruticosa* growth is salt-stimulated and that its ash content can increase to 60% of the total plant dry weight. Based on the model suggested for field plants by Chaudhri *et al.* (1964), *S. fruticosa* plants growing in a highly saline environment could remove about 2646 kg ha<sup>-1</sup> NaCl from the soil each year. Thus, given that *S. fruticosa* is a salt accumulating halophyte, it could be used successfully to reclaim highly salinized areas in semi-arid and arid regions of the world.



**Figure 6.** Effect of GA<sub>3</sub> and kinetin on the alleviation of NaCl (0, 400 and 800 mol m<sup>-3</sup>) induced growth inhibition of *S. fruticosa* plants. Bars represent mean  $\pm$  S.E. Different letters above bars represent significant differences ( $p < 0.05$ ) in the growth regulator response at a given salinity level. ■ Control; ▨ GA<sub>3</sub>; ▩ Kinetin.

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### References

- Ayala, F. & O'Leary, J.W. (1995). Growth and physiology of *Salicornia bigelovii* Torr. at suboptimal salinity. *International Journal of Plant Science*, **156**: 197–205.

- Boucaud, J. & Ungar, I.A. (1976). Influence of hormonal treatments on the growth of two halophytic species of *Suaeda*. *American Journal of Botany*, **63**: 694–699.
- Boucaud, J. & Ungar, I.A. (1978). Halophile et resistance au sel dans le genre *Suaeda* Forssk. *Bulletin de la Société Botanique de France, Actualites Botanique*, **3–4**: 23–35.
- Chaudhri I.I., S.B.H., Nagri, N. & Mallik, I.A. (1964). Investigation on the role of *Suaeda fruticosa* in the reclamation of saline and alkaline soils of West Pakistan. *Plant and Soil*, **21**: 1–7.
- Clipson, N.J.W., Tomos, A.D., Flowers, T.J. & Wyn Jones R.G. (1985). Salt tolerance in the halophyte *Suaeda maritima* L. Dum. The maintenance of turgor pressure and water-potential gradients in plants growing at different salinities. *Planta*, **165**: 392–396.
- Flowers, T.J., Troke, P.F. & Yeo, A.R. (1977). The mechanism of salt tolerance in halophytes. *Annual Review of Plant Physiology*, **28**: 89–121.
- Gale, J. & Zeroni M. (1984). Cultivation of plants in brackish water incontrolled environmental agriculture. In: Staples, R.C. & Toenniessen, G.R. (Eds), *Salinity Tolerance in Plants*, pp. 363–380. New York: John Wiley and Sons. 443 pp.
- Gorham, J. (1995). Mechanism of salt tolerance of halophytes. In: Choukr-Allah R., Malcolm, C.V. & Hamdy, A. (Eds). *Halophytes and Biosaline Agriculture*, pp. 31–53. New York: Marcel Dekker, Inc. 400 pp.
- Harvey, D.M.R., Hall, J.L., Flowers, T.J. & Kent, B. (1981). Qualitative ion localisation within *Suaeda maritima* leaf mesophyll cells. *Planta*, **151**: 555–560.
- Karimi, S.H. & Ungar, I.A. (1984). The effect of salinity on the ion content and water relations of *Atriplex triangularis*. In: Tiedemann, A.R., McArthur, E.D., Stutz, H.C., Stevens, R. & Johnson, K.L. (Eds), *Proceeding of the Symposium on the Biology of Atriplex and Related Chenopods*, pp. 124–130. General Technical Report INT-172, Ogden, Utah: Forest service, U.S. Department of Agriculture. 309 pp.
- Ke-Fu, Z., Li, M. & Jia-yao, L. (1986). Reduction by GA<sub>3</sub> of NaCl-induced inhibition of growth and development in *Suaeda ussuriensis*. *Australian Journal of Plant Physiology*, **13**: 547–551.
- Ke-Fu, Z., Hai, F. & Harris P.J.C. (1995). The physiological basis of growth inhibition of halophytes by potassium. In: Khan, M.A. & Ungar, I.A. (Eds) *Biology of Salt Tolerant Plants*, pp. 221–227. Karachi: Department of Botany, University of Karachi, Pakistan. 419 pp.
- Khan, M.I., Khan, M.A. & Khizar, T. (1976). Plant growth regulators from species differing in salt tolerance as affected by soil salinity. *Plant and Soil*, **45**: 267–271.
- Khan, M.A., Ungar, I.A., Showalter, A.M. & Dewald, H. (1997). NaCl - induced accumulation of glycinebetaine in four subtropical halophytes from Pakistan. *Physiologia Plantarum*, **102**: 487–492.
- Mahmood, K., Malik, K.A., Lodhi, M.A.K. & Sheikh, K.H. (1996). Seed germination and salinity tolerance in plant species growing on saline wetlands. *Biologia Plantarum*, **38**: 309–315.
- Marcum, K.B. & Murdoch, C.L. (1992). Salt tolerance of the coastal salt marsh grass, *Sporobolus virginicus* (L.) Kunth. *New Phytologist*, **120**: 281–288.
- Marschner, H. (1995). *Mineral Nutrition of Higher Plants*. London: Academic Press. 889 pp.
- Munns, R., Greenway, H. & Kirst, G.O. (1983). Halotolerant eukayrotes. In: Lange, O.L., Nobel, P.S., Osmond, C.B. & Ziegler, H. (Eds), *Encyclopaedia of Plant Physiology, Vol. 12 C: Physiological plant ecology III*. pp. 59–135. Berlin: Springer. 799 pp.
- Naidoo, G.R. & Rughunanan, R. (1990). Salt tolerance in the succulent halophyte, *Sarcocornia natalensis*. *Journal of Experimental Botany*, **41**: 497–502.
- Nerd, A. & Pasternak, D. (1992). Growth, ion accumulation, and nitrogen fractioning in *Atriplex barclayana* grown at various salinities. *Journal of Range Management*, **45**: 164–166.
- Prisco, J.T. & O'Leary, J.W. (1972). Enhancement of intact bean leaf senescence by NaCl salinity. *Physiologia Plantarum*, **27**: 95–100.
- Robinson, S.P. & Downton, W.J.S. (1985). Potassium, sodium and chloride ion concentrations in leaves and solated chloroplasts of the halophyte *Suaeda australis* R. Br. *Australian Journal of Plant Physiology*, **12**: 471–479.
- Storey, R. & Wyn Jones, R.G. (1975). Betaine and choline levels in plants and their relationship to NaCl stress. *Plant Science Letters*, **4**: 161–168.
- SPSS Inc. (1996). *SPSS 7.0 for Windows 95*. U.S.A. SPSS Inc.
- Ungar, I.A. (1978). The effects of salinity and hormonal treatments on the growth and ion uptake of *Salicornia europaea*. *Bulletin de la Société Botanique de France, Actualites Botanique*, **3–4**: 95–104.
- Ungar, I.A. (1991). *Ecophysiology of Vascular Halophytes*. Boca Raton: CRC Press. 209 pp.

- Williams, M.D. & Ungar, I.A. (1972). The effect of environmental parameters on the germination, growth, and development of *Suaeda depressa* (Pursh) Wats. *American Journal of Botany*, **59**: 912-918.
- Wochok, Z.S. & Sluis, C.J. (1980). Gibberellic acid promotes *Atriplex* shoot multiplication and elongation. *Plant Science Letters*, **17**: 363-369.
- Yeo, A.R. & Flowers, T.J. (1980). Salt tolerance in the halophyte *Suaeda maritima* L. Dum: Evaluation of the effect of salinity upon growth. *Journal of Experimental Botany*, **31**: 1171-1183.