

## GROWTH AND SELECTIVE ION TRANSPORT OF *LIMONIUM STOCKSII* PLUMBAGINACEA UNDER SALINE CONDITIONS

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### Abstract

*Limonium stocksii* is a perennial forb found on the Arabian Sea coast near Karachi, Pakistan. Plants were grown in plastic pots using sub-irrigation under natural conditions. Growth parameters and plant succulence were highest at 0 and 10 dS m<sup>-1</sup> salinity (both NaCl and seawater). An increase in growth medium salinity progressively decreased growth, but plants survived in up to 60 dS m<sup>-1</sup>. No significant difference was observed between NaCl and seawater treatments. Succulence did not change at low salinity (10 dS m<sup>-1</sup>), however, a further increase in salinity substantially decreased tissue water content. Plants accumulated high quantities of Na<sup>+</sup> and Cl<sup>-</sup> with the induction of salinity in the medium. The selective transport capacity of *L. stocksii* for Na<sup>+</sup> over other elements increased with an increase in salinity in both root and stem, however, roots displayed lower selective ion transport capacity compared to stem.

### Introduction

There is a wide spectrum of salt tolerance among higher plant species, and although many halophytes have been studied in great detail, the basic organismal and cellular mechanisms which clearly distinguish them are still obscure (Robinson *et al.*, 1997). Growth of some halophytes is generally stimulated by various levels of salinity (Walker, 1989; Drake & Ungar, 1989; Pfister, 1999; Gul & Khan, 1998; Khan *et al.*, 2000a, 2000b; Onkware, 2000; Pujol *et al.*, 2001). However, growth of some less tolerant halophytes decreases substantially with an increase in salinity (Jaenicke *et al.*, 1996; Köhl, 1997; Wang *et al.*, 1997; Fung *et al.*, 1998; Wu *et al.*, 1998; Lillebø *et al.*, 2003). Greenhouse experiments on subtropical halophytes from the Karachi coast indicated that species like *Arthrocnemum macrostachyum*, *Cressa cretica*, *Haloxylon stocksii* (*recurvum*) and *Suaeda fruticosa* could grow at high salinity and their growth was stimulated by low salinity (Khan & Aziz, 1998; Gul & Khan, 1998; Khan *et al.*, 2000a, 2000b). However, species like *Atriplex stocksii* (*griffithii*) could tolerate environments in upto only 400 to 500 mM NaCl (Khan *et al.*, 2000c).

Optimal growth of dicotyledonous halophytes may be associated with succulence of leaves and stem (Pfister, 1999), Na<sup>+</sup> exclusion at the root and ion accumulation and secretion through salt glands in leaves (Munns *et al.*, 1983; Flowers, 1986; Miyamoto *et al.*, 1996; Hester *et al.*, 2001). At the tissue level, relative amounts of Na<sup>+</sup> and K<sup>+</sup> appear to be important factors regulating growth of plants under saline conditions (Wang *et al.*, 1997; Pujol *et al.*, 2001). K<sup>+</sup> plays a key role in several physiological processes such as osmotic regulation, protein synthesis and enzyme activation (Wang *et al.*, 2002, 2004). The substitution of K<sup>+</sup> by Na<sup>+</sup> can lead to nutritional imbalance (Peng *et al.*, 2004). Many halophytes however, maintain a high ratio of Na: K in plant tissues (at least 5 to 10) and still exhibit growth promotion under saline conditions (Gorham *et al.*, 1980; Rozema, 1991). This is probably due to their ability to use Na<sup>+</sup> instead of K<sup>+</sup> in different metabolic

processes. Flowers (2004) reported that  $\text{Na}^+$  replaced  $\text{K}^+$  in regulating stomatal mechanism in the halophyte *Suaeda maritima*. Halophytes also differ in their ability to absorb nutrients selectively from soil solutions dominated by  $\text{Na}^+$  and  $\text{Cl}^-$  (Wang *et al.*, 2002) and in their capacity to transport and accumulate  $\text{Na}^+$  and  $\text{K}^+$  under saline condition (Wang *et al.*, 2002, 2004).

Intensive research programs to identify ornamental halophyte species suited to saline environment and/or irrigation with saline water are being developed in different parts of the world (Lieth, 1999) and some of these halophytic species including *Limonium* spp., are already grown commercially. Better utilization of such halophytic species depends on the knowledge of their degree of salt tolerance (Alarcon *et al.*, 1999; Hester *et al.*, 2001). Carter *et al.*, (2005) studied the effects of saline wastewater irrigation on *Limonium perezii* to develop more economically feasible floricultural techniques in California. Saline wastewaters similar to the San Joaquin Valley and Imperial/Coachella Valley were tested at different electrical conductivities. It was found that growth decreased as salinity increased, and salinized irrigation water changed leaf ion content. However, market quality flowers were produced when treatment waters were moderately saline (Carter *et al.*, 2005). *Limonium stocksii* (Boiss.) Kuntze is a good candidate for a coastal area ornamental plant. This perennial shrub is distributed in high coastal marshes as well as rocky grounds near the sea shores of Pakistan and India. This evergreen halophyte produces beautiful flowers twice a year (June and November) while facing high salinity, drought and temperature stress. After monsoon rains, *L. stocksii* recruits from seeds, whereas most other co-occurring species such as *Aeluropus lagopoides*, *Arthrocnemum macrostachyum*, *Atriplex stocksii*, *Suaeda fruticosa*, *Tamarix* spp., and *Urochondra setulosa* employ vegetative propagation (Khan, 2002). This study reports growth and selective transport of ions in *L. stocksii* under increasing seawater and NaCl at the mature vegetative phase of life cycle.

## Materials and Methods

Seeds of *L. stocksii* were collected in February 2000, from the study site, which is a flat area in between Manora Creek and Hawks Bay, Karachi, Pakistan (24°52'-647'N and 66°53'-321'E). Seeds were separated from the inflorescence, surface sterilized using Clorox® (0.85 % Sodium hypochlorite) and stored dry at 4°C. Growth experiments were initiated in August 2000 in a greenhouse at the University of Karachi under ambient atmospheric conditions. Plants were grown from seed in 10 x 8 cm plastic pots with holes in the bottom and filled  $\frac{3}{4}$  full with sandy soil. Sandy soil was collected from the beach and washed 3 times to completely remove the salt. Plants were allowed to grow for 2 months until they attained a height of approximately 2 cm. Similar sized plants were thinned to 10 per pot. Half strength Hoagland and Arnon solution No. 2 (Moore, 1960) was provided to the plants treated with NaCl salinity while seawater treated plants were nourished by a nitrogen nutrition supplement. The N supplement was added to compensate for the differences in seawater (Popp & Polania, 1989). Pots (n=5) were sub-irrigated and the water level was adjusted daily to correct for evaporation. Each was grown in sand culture having NaCl and seawater solutions of 0, 10, 20, 30, 40, 50, and 60 dS  $\text{m}^{-1}$ . Salinities of the growth medium were selected after a preliminary test of salt tolerance. Salt solutions for both experiments were replaced once a week to avoid buildup of salinity in the pots. At the initiation of the experiment, salinity concentrations were

gradually increased by 10 dS m<sup>-1</sup> at 2 d intervals to reach the maximum salinity levels of 60 dS m<sup>-1</sup> after 12 d. The fresh and dry weight of roots, stems and leaves was determined. The length of roots and shoots were measured by harvesting plants 60 d after the highest salt concentration was reached. Plants were oven dried at 80°C for 48 h before dry weight was determined.

Plants were rinsed 3 times to remove salt from the plant surface, but not the tissue. Ion content of plant tissue was determined by placing 0.5 gram of plant tissue in 10 ml of water and boiling it in a screw-capped test-tube for 2 hours in a dry heat bath. The samples were diluted with 50 mM Potassium dihydrogen phosphate buffer adjusted to a pH of 4.6. Samples were filtered using a 0.45 µm filter membrane. Chloride ion was measured with a Beckman specific ion electrode. Cation content of root, shoot and leaves was analyzed using a Perkin Elmer model 360 atomic absorption spectrophotometer. The Na<sup>+</sup> and K<sup>+</sup> levels of plants were examined by flame emission spectrometry and Ca<sup>2+</sup> and Mg<sup>2+</sup> levels by atomic absorption spectrometry.

Values for selective transport capacity (ST<sub>n</sub>) by different plant parts (root/stem = ST1 and stem/leaf = St2) for Na<sup>+</sup> over K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup> and Cl<sup>-</sup> at different salinity levels were estimated by the formula "ST<sub>n</sub> = A / B," where A stands for ionic ratio in part A and B stands for ionic ratio in part B while *n* is the number of ST in various parts, *n* = 1, 2, 3... The bigger the ST value, the stronger part A controls Na<sup>+</sup> and promotes transport of other ions to part B, indicating a stronger selective transport capacity of part A (Wang *et al.*, 2002).

A completely randomized ANOVA analysis was used to test for significant differences within mean values for growth and ion relations. A Bonferroni test was carried out to check for differences within individual treatment means (Anon., 2002).

## Results

There were few significant differences which were observed between NaCl and seawater treatments on morphological attributes of *L. stocksii*. Growth changed little by salinity increments up to 20 dS m<sup>-1</sup> in both seawater and NaCl solutions. Further increases in salinity resulted in a decrease of stem length, as well as a decrease in the fresh and dry weights of roots, stems and leaves (Figs. 1, 2 and 3). Root length of *L. stocksii* remained unaffected by type and level of salinity treatment (Fig. 1). A two-way ANOVA indicated significant (*p*<0.0001) effects of salinity, plant parts (stems, roots and leaves) and their interaction on fresh weight. However, a non-significant interaction was observed for dry weight (Table 1). Fresh and dry weights of leaves was substantially higher than either stem or root and varied little in up to 20 dS m<sup>-1</sup>. Further increases in salinity caused significant inhibition with little difference between types of salinity treatments (Fig. 2 and 3). Both roots and stems exhibited no significant change in fresh and dry weight with increasing salinity of either NaCl or seawater (Figs. 2 and 3).

A two-way ANOVA indicated no significant difference in tissue water of any plant part with the type of salinity used in the experiment. Significant (*p*<0.0001) interactions between salinity and plant parts were observed in affecting tissue water of *L. stocksii* (Table 1). Leaf tissue water was considerably higher than stem and root. Tissue water content of both leaf and stem remained unaffected with increasing salinity. Root tissue water declined sharply above 10 dS m<sup>-1</sup> (Fig. 4).

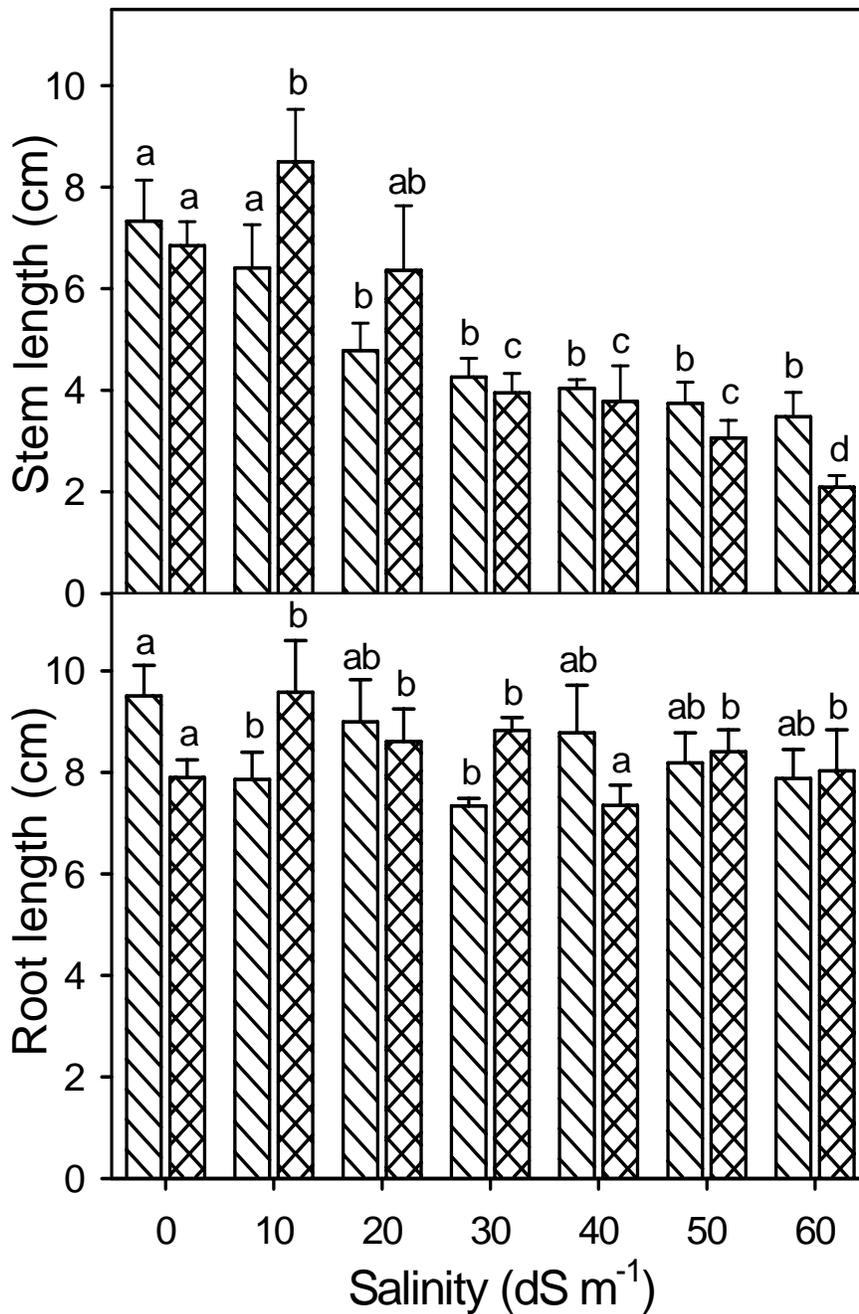


Fig. 1. Comparative effect of NaCl (▨) and seawater (▩) dilutions (0, 10, 20, 30, 40, 50 and 60 dS m<sup>-1</sup>) on stem and root length of *Limonium stocksii*. Bars (means ± S.E.) having same letters along increasing salinity are not significantly different ( $p > 0.05$ ) from each other.

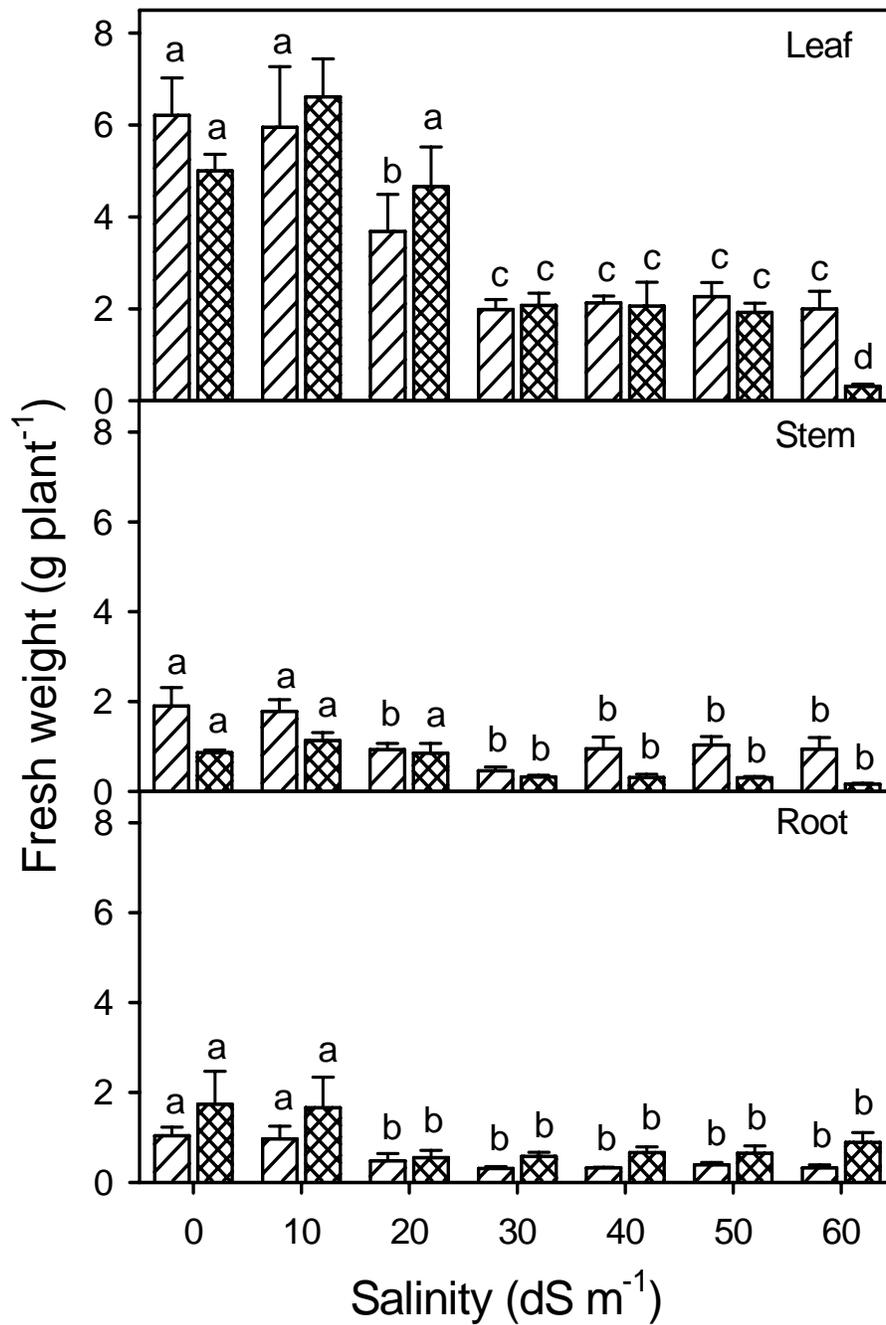


Fig. 2. Comparative effect of NaCl (▨) and seawater (▩) dilutions (0, 10, 20, 30, 40, 50 and 60 dS m<sup>-1</sup>) on fresh weight of leaf, stem and root of *Limonium stocksii*. Bars with same letters along salinity are similar ( $p > 0.05$ ) with each other. Bonferroni test.

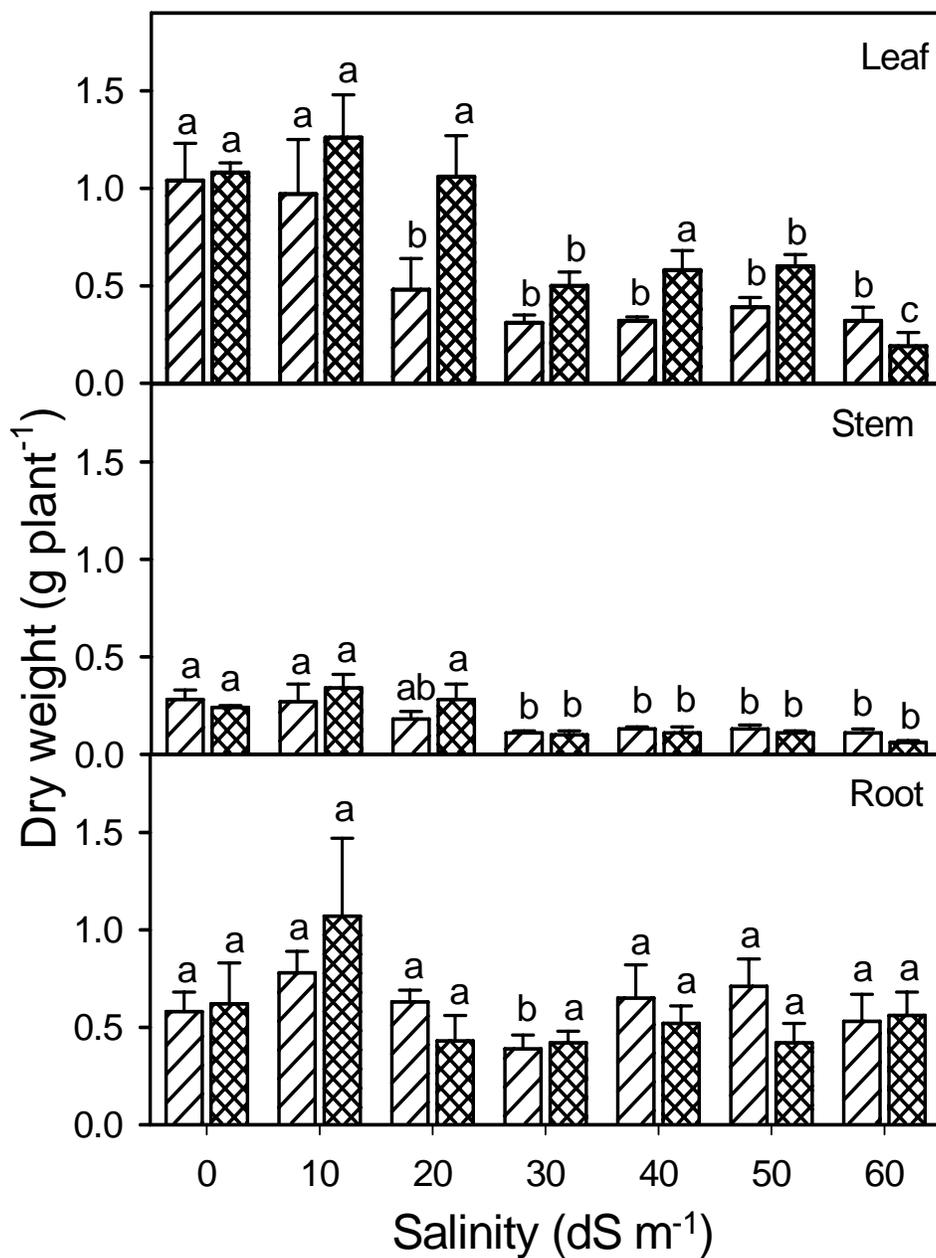


Fig. 3. Comparative effect of NaCl (▨) and seawater (▩) dilutions (0, 10, 20, 30, 40, 50 and 60 dS m<sup>-1</sup>) on dry weight of leaf, stem and root of *Limonium stocksii*. Bars (means ± S.E.) having same letters between different salinity treatments are not significantly different ( $p > 0.05$ ) from each other. Bonferroni test.

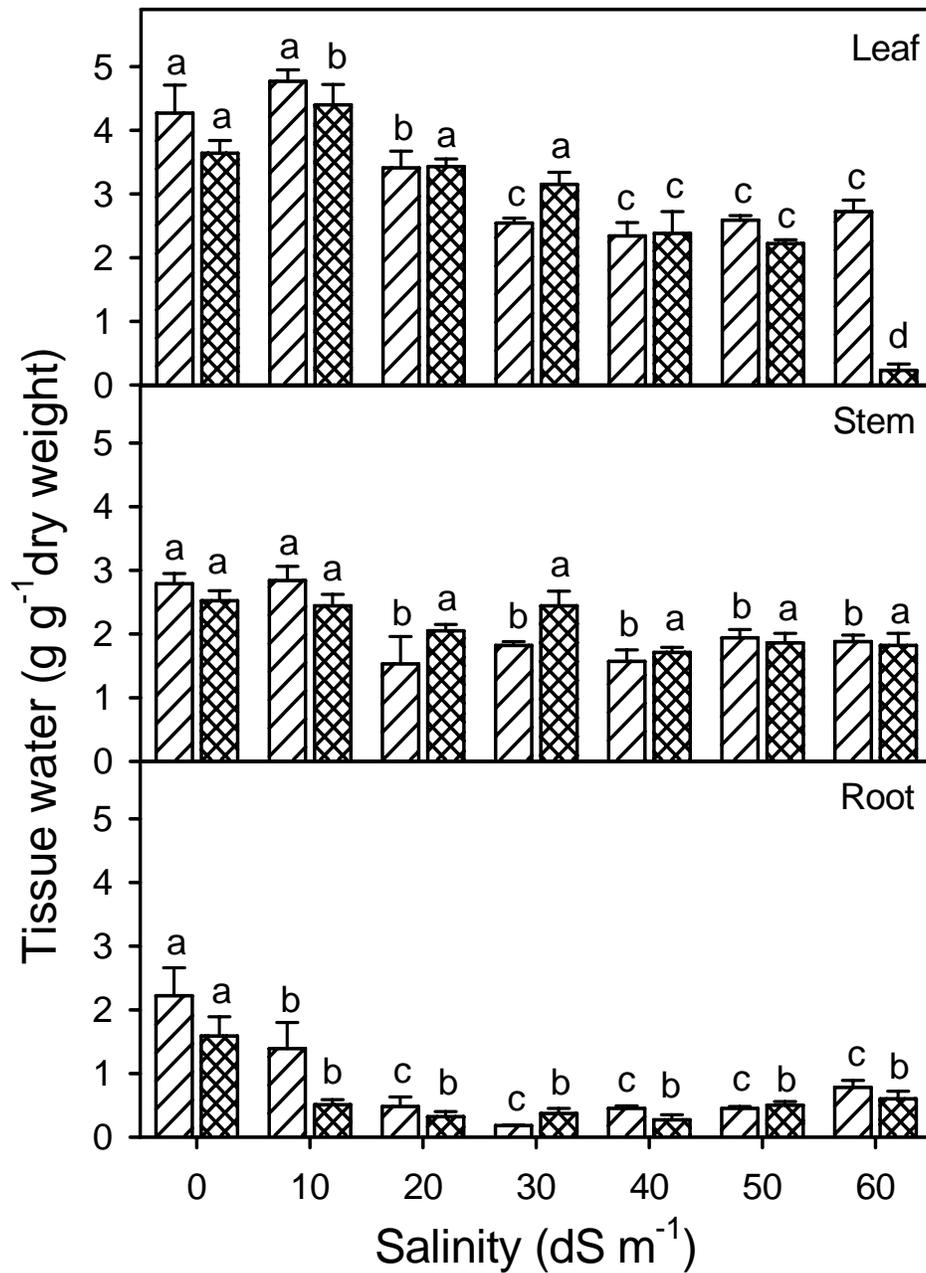


Fig. 4. Comparative effect of different NaCl (▨) and seawater (▩) dilutions (0, 10, 20, 30, 40, 50 and 60 dS m<sup>-1</sup>) on tissue water content of leaf, stem and root of *Limonium stocksii*. Bars (means ± S.E.) having same letters along increasing salinity are not significantly different ( $p > 0.05$ ) different from one another. Bonferroni test.

**Table 1. Results of two-way analysis of variance of characteristics by salinity (S) and plant part (P).**

Dependent variable	Salinity (S)	Plant part (P)	P x S
Fresh weight	19.425***	96.864***	8.034***
Dry weight	7.625 <sup>ns</sup>	34.105 <sup>ns</sup>	1.825*
Tissue water	34.91***	289.10***	17.79***

Numbers are F-values at \* $p < 0.01$ , \*\*\* $p < 0.0001$ , <sup>ns</sup> non-significant.

**Table 2. Results of two-way analysis of variance of different ions by salinity (S) and plant part (P).**

Dependent variable	Salinity (S)	Plant part (P)	P x S
Sodium	164.4***	80.7***	27.8***
Potassium	10.4 <sup>ns</sup>	56.8 <sup>ns</sup>	7.2 <sup>ns</sup>
Calcium	6.2***	24.3 <sup>ns</sup>	3.2**
Magnesium	4.8***	39.9 <sup>ns</sup>	4.3***
Chloride	7.937 <sup>ns</sup>	55.513 <sup>ns</sup>	5.788 <sup>ns</sup>

Numbers are F-values at \* $p < 0.01$ , \*\* $p < 0.001$ , \*\*\* $p < 0.0001$ , <sup>ns</sup> non-significant.

**Table 3. The ST1 (Root: Stem) and ST2 (Stem: Leaf) values of different ions in *Limonium stocksii* at various salinity levels.**

Salinity (dS m <sup>-1</sup> )	Na /K		Na /Ca		Na /Mg		Na /Cl	
	ST1	ST2	ST1	ST2	ST1	ST2	ST1	ST2
0	1.5	1.7	0.9	1.7	0.3	3.3	1.0	1.9
10	1.1	2.5	0.3	2.7	0.3	5.2	2.0	3.1
20	0.7	1.6	0.3	1.1	0.5	1.6	1.1	2.4
30	8.4	0.9	3.1	0.5	4.1	2.0	10.1	1.2
40	0.8	2.9	0.5	1.9	0.5	3.7	1.3	3.1
50	0.7	1.4	0.4	0.7	0.8	2.7	0.8	1.9
60	1.7	2.6	0.5	3.5	3.2	3.4	1.5	4.5

A two-way ANOVA indicated significant ( $p < 0.05$ ) effects of salinity (except for K<sup>+</sup> and Cl<sup>-</sup>) and plant parts (only for Na<sup>+</sup>) and their interaction (except for K<sup>+</sup> and Cl<sup>-</sup>) on ion content (Table 2). High ion accumulation was recorded at the highest salinity for all ions except Na<sup>+</sup>, which accumulated more in 40 dS m<sup>-1</sup> than 50 and 60 dS m<sup>-1</sup> (Fig. 5). Accumulation of Na<sup>+</sup> appeared highest in stems than in roots and leaves (Fig. 5). The selective transport capacity of *L. stocksii* for Na<sup>+</sup> over other elements increased with an increase in salinity in both roots and stems (Table 3). Selective transport capacity (ST2, stem/leaf) values of all the ionic ratios were greater than the ST1 (root/stem) values at all salinity levels (except for 30 dS m<sup>-1</sup>) indicating that the selective transport capacity of stems is higher than roots and leaves (Table 3).

## Discussion

Seawater and NaCl both equally affected different growth parameters of *L. stocksii*. Plants growing in 10 dS m<sup>-1</sup> salinity showed better growth in comparison to the non-saline control, however, this difference was not statistically significant. Species with high salinity tolerance show less morphological changes in the presence of low amounts of salt (Sánchez-Blanco *et al.*, 1991). Different *Limonium* species are reported to excrete salts

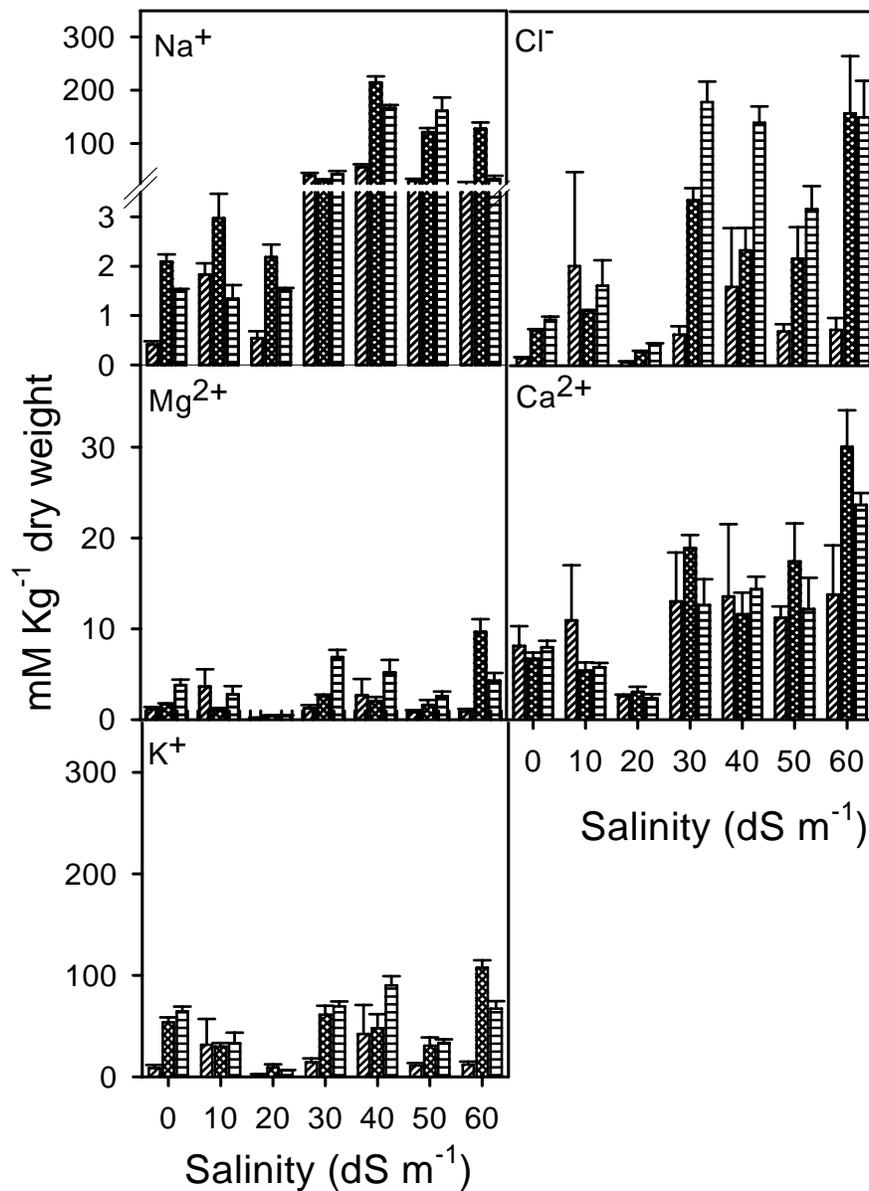


Fig. 5. Ion content of root (▨), stem (▤) and leaf (▥) of *Limonium stocksii* grown in various levels of saline medium. Bars represent means ( $\pm$  Standard Error).

directly via salt glands (Batanouny *et al.*, 1992; Alarcon *et al.*, 1999). Ungar (1991) suggested that the salt stimulated dry mass production in some halophytes acts as a dilution factor mechanism even though the level of succulence decreases. Little variation in dry weights of stems and roots of *L. stocksii* with increasing salinity and low water content in both parts supports this view. Similar results were obtained for *L. latifolium* cv.

*avignon* and a hybrid *L. beltaard* and it was suggested that low dry weight reduction with regard to control involves a higher tolerance to saline stress (Alarcon *et al.*, 1999).

*Limonium stocksii* could survive at 60 dS m<sup>-1</sup>, a concentration equal to full strength seawater. When compared to the salt tolerance of few co-occurring species such as *Arthrocnemum macrostachyum* (1000 dS m<sup>-1</sup>, Khan *et al.*, 2005), *Suaeda fruticosa* (1000 dS m<sup>-1</sup>, Khan *et al.*, 2000b), *Aeluropus lagopoides* (50 dS m<sup>-1</sup>, Gulzar *et al.*, 2003a) and *Urochondra setulosa* (50 dS m<sup>-1</sup>, Gulzar *et al.*, 2003b), *L. stocksii* appears to be moderately salt tolerant and could be grouped with miohalophytes (Greenway & Munns, 1980).

There are two main negative effects of high salt concentrations that influence plant growth and development: water deficit (Munns & Termaat, 1986) and ion toxicity associated with excessive Cl<sup>-</sup> and Na<sup>+</sup> (Niu *et al.*, 1995) leading to Ca<sup>2+</sup> and K<sup>+</sup> deficiency (Cramer *et al.*, 1987) and to nutrient imbalances (Marshner, 1995; El-Hamdaoui *et al.*, 2003). However plants differ greatly in their responses to salinity (Hasegawa *et al.*, 2000). Many halophytes accumulate and sequester Na<sup>+</sup> and K<sup>+</sup> balanced by Cl<sup>-</sup> as the basic mechanism to adjust the osmotic potential of their internal tissue to the external salinity (Flowers & Yeo, 1986; Cheeseman, 1988). Therefore a high Na<sup>+</sup>:K<sup>+</sup> ratio in plant tissue may favor growth. *Limonium stocksii* accumulated a large amount of ions, and their concentration increased with an increase in salinity in different parts of the plant. An increase in Na<sup>+</sup> and Cl<sup>-</sup> caused a decrease in their antagonistic solute i.e., K<sup>+</sup>. Dicotyledonous halophytes have the ability to maintain a high Na<sup>+</sup>: K<sup>+</sup> ratio by storing most of the Na<sup>+</sup> in their vacuole and thus require little K<sup>+</sup> for cytosolic metabolism (Flowers & Yeo, 1988; Glenn *et al.*, 1999). Ion accumulation was highest in stem and lowest in roots. Low ion content of roots in comparison to leaves and stems were also obtained for *Agriophyllum squarrosum*, *Artemisia sphaerocephala*, *Caragana korshinskii*, *Corispermum mongolicum* and *Zygophyllum xanthoxylum* (Wang *et al.*, 2004). Wang *et al.*, (2002) suggested that plants having salt glands in their aerial organs exhibit weak selective transport capacity in their roots with majority of Na<sup>+</sup> transporting through the stem and then leaves and finally secreted by salt glands as NaCl. Conversely, Tester & Davenport (2003) reported that roots tend to maintain fairly constant levels of NaCl over time and can regulate NaCl levels by export to the shoot. Generally, ion accumulation (except for Mg<sup>2+</sup>) and their selective transport to the upper parts increased with an increase in salinity. The highest concentration of all ions was observed in the stem at seawater concentrations indicating that its osmotic adjustment was through ion accumulation. This response has also been considered a mechanism of salt tolerance where the roots avoid the toxic effects of ions by transporting them toward upper parts and thus maintain their growth (Misra *et al.*, 1996, Alarcon *et al.*, 1999), while shoots may accumulate high concentrations of NaCl as an osmoticum (Flowers & Yeo, 1986; Glenn *et al.*, 1999). Munns (2002) suggested that salt tolerant plants may have a low rate of Na<sup>+</sup> and Cl<sup>-</sup> transport to leaves and have the ability to compartmentalize these ions in vacuoles to prevent their buildup in cytoplasm or cell walls and thus avoid salt toxicity.

Results from this study indicate that *L. stocksii* is a moderately salt tolerant halophyte that could grow in salt concentrations above seawater. Growth of *L. stocksii* was equally affected both by NaCl and seawater. Roots of *L. stocksii* showed no effect of increasing salinity due to their low selective transport values. Plants accumulated a greater amount of K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup> and Cl<sup>-</sup> than Na<sup>+</sup> at lower salinities while a high concentration of Na<sup>+</sup> and Cl<sup>-</sup> was observed with increased in salinities. These results were similar to Carter *et al.*, (2005), who found that as salinity increased in *L. perezii*, leaf Cl<sup>-</sup>,

Mg<sup>2+</sup>, Na<sup>2+</sup> and S increased. However, with increasing salinity leaf Ca<sup>2+</sup>, K<sup>+</sup> and P decreased. There was also a decrease in stem length. An increase in salinity in *L. perezii* lead to a decrease in survival and seedling emergence (Carter *et al.*, 2005).

The high selective transport value in the stem indicates that *L. stocksii* preferentially protects its photosynthetic and reproductive organs so as to survive and reproduce in saline environments. *Limonium stocksii* has good economic potential as an ornamental plant that could be cultivated using either brackish water or seawater along the sea coast.

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### References

- Alarcon, J.J., M. A. Morales, A. Torrecillas and M.J. Sanchez-Blango. 1999. Growth, water relations and accumulation of organic and inorganic solutes in the halophytes *Limonium latifolium* cv. *avignon* and its interspecific hybrid *Limonium caspia* X *Limonium latifolium* cv. *betlaard* during salt stress. *J. Plant Physiol.*, 154: 795-801.
- Anonymous. 2002. *SPSS: SPSS 11 for Windows update*. SPSS Inc. Chicago, Illinois.
- Batanouny, K.H., A.A. Hassan and G. M. Fahmy. 1992. Eco-physiological study on halophytes in arid and semi-arid zones. II. The salt-secreting *Limonium delicatulum* (Gir.) Ktze. *Flora*, 186: 105-116.
- Carter, C.T., C.M. Grieve and J.A. Poss. 2005. Salinity effects on emergence, survival, and ion accumulation of *Limonium perezii*. *J. Plant Nutr.*, 28: 1243-1257.
- Cheesman, J.M. 1988. Mechanisms of salinity tolerance in plants. *Plant Physiol.*, 87: 547-550.
- Cramer, G.R., J. Lynch, A. Lauchli and E. Epstein. 1987. Influx of Na<sup>+</sup>, K<sup>+</sup> and Ca<sup>2+</sup> into roots of salt-stressed cotton seedlings. Effects of supplemental Ca<sup>2+</sup>. *Plant Physiol.*, 83: 510-516.
- Drake, D.R. and I.A. Ungar. 1989. Effect of salinity, nitrogen and population density on the survival, growth and reproduction of *Atriplex triangularis* (Chenopodiaceae). *Amer. J. Bot.*, 76: 1125-1135.
- El-Hamdaoui, A., M. Redondo-Nieto, B. Torralba, R. Rivilla I. Bonilla and L. Bolanos. 2003. Influence of boron and calcium on the tolerance to salinity of nitrogen-fixing pea plants. *Plant Soil*, 251: 93-103.
- Flowers, T.J. and A.R. Yeo. 1986. Ion relations of plants under drought and salinity. *Aust. J. Plant Physiol.*, 13: 75-91.
- Flowers, T.J. and A.R. Yeo. 1988. Ion relations of salt tolerance. In: *Solute transport in plant cells and tissues*. (Eds.): D. Baker & J. Halls. pp. 392-416. Harlow, Longman, NY.
- Flowers, T.J. 2004. Improving crop salt tolerance. *J. Exp. Bot.*, 55: 307-319.
- Fung, L.E., S. Wang, A. Altman and A. Hütterman. 1998. Effect of NaCl on growth, photosynthesis, ion and water relations of four poplar genotypes. *Forest Ecol. Manag.*, 107: 135-146.
- Glenn, E.P., J.J. Brown and E. Blumwald. 1999. Salt tolerance and crop potential of halophytes. *Crit. Rev. Plant Sci.*, 18: 227-255.
- Gorham, J., L.L. Hughes and R.G. Wyn Jones. 1980. Chemical composition of salt marsh plants from Yns Mon (Anglesey), the concept of physiotypes. *Plant Cell & Environ.*, 3: 309-318.
- Greenway, H. and R. Munns. 1980. Mechanisms of salt tolerance in non-halophytes. *Ann. Rev. Plant Physiol.*, 31: 149-190.

- Gul, B. and M.A. Khan. 1998. Population characteristics of the coastal halophyte *Arthrocnemum macrostachyum*. *Pak. J. Bot.*, 30: 189-197.
- Gulzar, S., Khan. M.A. and I.A. Ungar. 2003a. Effect of salinity on growth, ionic content and plant-water status of *Aeluropus lagopoides*. *Comm. Soil Sci. Plan An.*, 34: 1657-1668.
- Gulzar, S., M.A. Khan and I.A. Ungar. 2003b. Salt tolerance of a coastal salt marsh grass. *Comm. Soil Sci. Plan An.*, 34: 2595-2605.
- Hasegawa, P.M., R.A. Bressan, J.K. Zhu and H.J. Bohnert. 2000. Plant cellular and molecular responses to high salinity. *Annu. Rev. Plant Phys.*, 51: 463-499.
- Hester, M.W., I.A. Mendelssohn and K.L. McKee. 2001. Species and population variation to salinity stress in *Panicum hemitomon*, *Spartina patens* and *Spartina alterniflora*: morphological and physiological constraints. *Environ. Exp. Bot.*, 46: 277-297.
- Jaenicke, H., S.L. Herma and W.R. Ullrich. 1996. Growth, ion distribution, potassium and nitrate uptake of *Leucaena leucocephala* and effect of NaCl. *Plant Physiol. Bioch.*, 34: 743-751.
- Khan, M.A. 2002. Halophyte seed germination: Success and Pitfalls. In: *International symposium on optimum resource utilization in salt affected ecosystems in arid and semi arid regions*. (Eds.): A.M. Hegazi, H.M. El-Shaer, S. El-Demerdashe, R.A. Guirgis, A.A. Metwally, F.A. Hasan & H.E. Khashaba. Desert Research Center, Cairo, pp. 346-358.
- Khan, M.A. and S. Aziz. 1998. Some aspects of salinity, density and nutrient effects of *Cressa cretica*. *J. Plant Nutr.*, 21: 769-784.
- Khan, M.A., I.A. Ungar and A.M. Showalter. 2000a. Effects of Sodium chloride treatments on growth and ion accumulation of the halophyte *Haloxylon recurvum*. *Comm. Soil Sci. Plan. An.*, 31: 2763-2774.
- Khan, M.A., I.A. Ungar and A.M. Showalter. 2000b. The effect of salinity on the growth, water status and ion content of a leaf succulent perennial halophyte, *Suaeda fruticosa* (L.) Forssk. *J. Arid Environ.*, 45: 73-84.
- Khan, M.A., I.A. Ungar and A.M. Showalter. 2000c. Effect of salinity on growth, water relation and ion accumulation of the subtropical perennial halophyte, *Atriplex griffithii* var. *stocksii*. *Ann. Bot-London.*, 85: 225-232.
- Khan, M.A., I.A. Ungar and A.M. Showalter. 2005. Salt stimulation and tolerance in inter-tidal stem-succulent halophyte. *J. Plant Nutr.*, 28: 1365-1374.
- Köhl, K.I. 1997. NaCl homeostasis as a factor for survival of the evergreen halophyte *Armeria maritima* (Mill.) Willd., under salt stress in winter. *Plant Cell & Environ.*, 20: 1253-1263.
- Lieth, H. 1999. Development of crops and other useful plants from halophytes. In: *Halophyte uses in different climates I. Ecological and Ecophysiological studies*. (Eds.): H. Lieth, M. Moschenko, M. Lohmann, H.-W. Koyro and A. Hamdy. Backhuys Publishers, Leiden. pp. 1-17.
- Lillebø, A.I., A.P. Migue, M.N. João and C.M. João. 2003. Salinity as the major factor affecting *Scirpus maritimus* annual dynamics. Evidence from the field data and green house experiment. *Aquat. Bot.*, 77: 111-120.
- Marschner, H. 1995. *Mineral Nutrition of Higher Plants*. Academic Press Limited, London, UK.
- Misra, A.N., B. Murmu, P. Singh and M. Misra. 1996. Growth and proline accumulation in mungbean seedlings as affected by Sodium chloride. *Biol. Plantarum*, 38: 531-536.
- Miyamoto, S., E.P. Glenn and M.W. Olsen. 1996. Growth, water use and salt uptake of four halophytes irrigated with highly saline water. *J. Arid Environ.*, 32: 141-159.
- Moore, R.H. 1960. *Laboratory guide for elementary plant physiology*. Burgess Publishing Company, Minneapolis.
- Munns, R. 2002. Comparative physiology of salt and water stress. *Plant Cell & Environ.*, 25: 239-250.
- Munns, R. and A. Termaat. 1986. Whole-plant responses to salinity. *Aust. J. Plant Physiol.*, 13: 143-160.
- Munns, R., H. Greenway and G.O. Kirst. 1983. Halotolerant eukaryotes. In: *Physiological plant ecology II*. (Eds.): O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. pp 59-135. *Encyclopedia of plant physiology*, New Series 12C. Springer-Verlag, Berlin.

- Niu, X., R.A. Bressan, P.M. Hasegawa and J.M. Pardo. 1995. Ion homeostasis in NaCl stress environment. *Plant Physiol.*, 109: 735-742.
- Onkware, A.O. 2000. Effect of soil salinity on plant distribution and production at Lobura delta lake, Bogoria National Reserves, Kenya. *Austral Ecol.*, 25: 140.
- Peng, Y.H., Y.F. Zhu, Y.Q. Mao, S.M. Wang, W.A. Su and Z.C. Tang. 2004. Alkali grass resist salt stress through high [K<sup>+</sup>] and an endodermis barrier to Na<sup>+</sup>. *J. Exp. Bot.*, 55: 939-949.
- Pfister, R.W. 1999. *Limits to growth of Salicornia bigelovii Torr. at sub-optimal salinity. Ph. D. Thesis. University of Arizona, Tucson, Arizona.*
- Popp, M. and J. Polania. 1989. Compatible solutes in different organs of mangrove trees. *Ann. For. Sci.*, 46: 842-844.
- Pujol, J.A., J.F. Calvo and L. Ramirez-Diaz. 2001. Seed germination, growth and osmotic adjustment in response to NaCl in a rare succulent halophyte from southeastern Spain. *Wetlands*, 21: 256-267.
- Robinson, M.F., A.A. Very, D. Sanders and T.A. Mansfield. 1997. How can stomata contribute to salt tolerance? *Ann. Bot.*, 80: 387-393.
- Rozema, J. 1991. Growth, water and ion relationships of halophytic monocotyledonae and dicotyledonae: A unified concept. *Aquat. Bot.*, 38: 17-33.
- Sánchez-Blanco, M.J., M.C. Bolarin., J.J. Alarcón and A. Torrecillas. 1991. Salinity effects on *Lycopersicon esculentum* and its wild salt tolerant relative species *L. pennelli*. *Physiol. Plantarum*, 83: 269-274.
- Tester, M. and R. Davenport. 2003. Na<sup>+</sup> tolerance and Na<sup>+</sup> transport in higher plants. *Ann. Bot.*, 91: 503-527.
- Ungar, I.A. 1991. *Ecophysiology of Vascular Halophytes*. CRC Press, Boca Raton, Florida.
- Walker, R.R. 1989. Growth, photosynthesis and distribution of chloride, sodium and potassium ions in salt-affected quandong (*Santalum acuminatum*). *Aust J. Plant Physiol.*, 16: 365-377.
- Wang, L.W., A.M. Showalter and I.A. Ungar. 1997. Effect of growth, ion content and cell wall chemistry in *Atriplex prostrata* (Chenopodiaceae). *Am. J. Bot.*, 84: 1247-1255.
- Wang, S., W. Changgui, W. Yanrong, H. Chen, Z. Zhou, H. Fu and R.E. Sosebee. 2004. The characteristics of Na<sup>+</sup>, K<sup>+</sup> and free proline distribution in several drought resistant plants of the Alxa Desert, China. *J. Arid Environ.*, 56: 525-539.
- Wang, S.M., W.J. Zheng, J.Z. Ren and C.L. Zhang. 2002. Selectivity of various types of salt-resistant plants for K<sup>+</sup> over Na<sup>+</sup>. *J. Arid Environ.*, 52: 457-472.
- Wu, J., M. Denise, D.M. Seliskar and J.L. Gallger. 1998. Stress tolerance in marsh plant *Spartina patens*: Impact of NaCl on growth and root plasma membrane lipid composition. *Physiol. Plant.*, 102: 307-317.

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