JOURNAL OF PLANT NUTRITION, 22(1), 191–204 (1999)

Effects of Salinity on Growth, Ion Content, and Osmotic Relations in *Halopyrum mucronatum* (L.) Stapf.

M. Ajmal Khan,[1] Irwin A. Ungar, and Allan M. Showalter

Department of Environmental and Plant Biology, Molecular and Cellular Biology Program, Ohio University, Athens, OH 45701-2979

ABSTRACT

Halopyrum mucronatum (L.) Stapf. is a perennial grass found on the coastal dunes of Karachi, Pakistan. *Halopyrum mucronatum* plants were grown in 0, 90, 180, and 360 mol m^{-3} NaCl in a sand culture using a sub-irrigation method. Fresh and dry weight of roots and shoots peaked at 90 mol m^{-3} NaCl. A further increase in salinity inhibited plant growth, ultimately resulting in plant death at 360 mol m^{-3} NaCl. The relative growth rate of plants was highest between 60 and 90 days after final salinity concentrations were reached. Maximum succulence was noted in 90 mol m^{-3} NaCl. Water potential and osmotic potential of plants became more negative with an increase in salinity, while plants lost turgor with increasing salinity. Time of harvest did not have any significant effect on the water relations of plants. Sodium (Na) and chloride (Cl) content of plants increased with an increase in salinity, while calcium (Ca), magnesium (Mg), and potassium (K) content decreased. Glycinebetaine content of shoots increased significantly only at the highest salinity (360 mol m^{-3} NaCl).

[1]Present address: Department of Botany, University of Karachi, Karachi 75270, Pakistan.

Copyright © 1999 by Marcel Dekker, Inc. www.dekker.com

INTRODUCTION

Halopyrum mucronatum (L.) Stapf. is a dominant grass species of the dune vegetation along the coast from Egypt to Mozambique, through Arabia to Pakistan, India and Sri Lanka (Jafri, 1966). It dominates sand dunes bordering the lower marsh of the Arabian Sea coast of Karachi, Pakistan. This species shows luxuriant growth with individuals attaining a height of 100 cm when inundated daily with seawater, as opposed to populations exposed to only monthly inundation with seawater where individuals attain a height of only 35 to 45 cm (Khan, unpublished data). *Halopyrum mucronatum* flowers twice a year, from April to May and September through November. A large number of seeds germinate after monsoon rains, but few of these seeds are recruited into the population. Although recruitment from seeds is infrequent, it is much greater than for other neighboring perennial halophytes [*Suaeda fruticosa* (L.) Forssk., *Haloxylon recurvum* Bunge ex Boiss., *Cressa cretica* L., *Aeluropus lagopoides* (L.) Trin. Ex Thw., and *Arthrocnemum indicum* (Willd.) Moq.]. *Halopyrum* also reproduces vegetatively by means of an extensive underground network of stolons (Noor and Khan, 1995).

Soil salinity imposes a major constraint on plant growth and survival in arid and maritime regions. Coastal areas that are not inundated daily with seawater have a rapid salinity build up due to the high rate of evapotranspiration. Relatively little is known about the response of the grasses to salinity (Marcum and Murdoch, 1990, 1994; Younger and Lunt, 1967; Ramakrishnan and Nagpal, 1973; Dudeck et al., 1993) and almost no information exists for *Halopyrum mucronatum*. Mahmood et al. (1996) found that grasses collected from saline areas of Faisalabad, Pakistan vary in their salt tolerance. *Sporobolus arabicus* Boiss. was the most tolerant grass in comparison to *Cynodon dactylon* (L.) Pers, *Polypogon monspeliensis* (L.) Desf., and *Desmostachya bipinnata* (L.) Stapf. *Sporobolus arabicus* could survive in up to 30 dS m^{-1} (350 mol m^{-3} NaCl) salinity, and this response could be attributed to the greater accumulation of Na in tissues in comparison to other species (Mahmood et al., 1996). Turfgrass species studied varied in the tolerance to salinity, ranging from a low of 170 mol m^{-3} NaCl [*Eremochloa ophiuroides* (Munro) Hack.] to higher than 400 mol m^{-3} NaCl [*Zoysia matrella* (L.) Merr.] (Marcum and Murdoch, 1990, 1994). Shoot and root ion concentrations were higher in the more salt tolerant species (Marcum and Murdoch, 1990, 1994). Gorham (1995) indicated that by intracellular compartmentalization cells are able to accumulate salts in vacuoles and thus avoid higher levels in the cytoplasm. Levels of glycinebetaine increased with increases in salinity in the shoots of most grasses studied (Marcum and Murdoch, 1994; Marcum, 1995). Osmotic adjustment under increased salinity occurred concurrently with an increase in shoot Na and Cl content, a decrease in shoot K content, and a decrease in shoot succulence (Marcum and Murdoch, 1990, 1994). Osmotic adjustment and maintenance of positive turgor under salt stress occurred in *Paspalum vaginatum* Swartz. (Dudeck and Peacock, 1985; Peacock and Dudeck, 1985) and *Stenotaphrum secundatum* (Walt.) Kuntze. (Dudeck et al., 1993).

Halopyrum mucronatum is a potential seed crop and it also could be used as a coastal dune stabilizer. There is little information available on the salt tolerance of this species. This study was conducted to determine the effect of salinity on ion accumulation, growth, water relations, and osmoregulation in *H. mucronatum*.

MATERIALS AND METHODS

Seeds of *H. mucronatum* were collected during the winter of 1994 from sand dunes located on the Arabian Sea coast at Sands Pit, Karachi, Pakistan where it occurs as a dominant species. Seeds were separated from the inflorescence and stored at 4°C. These seeds were brought to Ohio University, Athens, OH, and growth studies were started in May 1995. Seeds were surface sterilized using the fungicide phygon prior to germination.

Plants were grown in a growth chamber at a thermoperiod of 25±1°C:35±1°C (night:day), and a 12-hr photoperiod (200 µmol photons $m^{-2} S^{-1}$, 400-700 nm). Five replicates of 15 plants were grown for 90 d at 0, 90, 180, and 360 mol m^{-3} NaCl in sand culture. A half-strength Hoagland and Arnon no. 2 nutrient solution was used to supply the macronutrients and micronutrients. 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 with 30 day-old seedlings, salinity concentrations were gradually increased by 90 mol m^{-3} at 2-d intervals to reach the maximum salinity levels of 360 mol m^{-3} NaCl after 8 days.

Fresh and dry weight of the shoots and roots of a subsample of 5 plants from each treatment were measured at 30-d intervals after the highest salt concentration was reached. Dry mass was determined after drying plant material 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 adding the salt treatments. Thereafter, successive harvests were taken on days 30, 60, and 90 with 5 plants harvested per treatment. Dry mass at each harvest was used to calculate rate of growth, using the formula $RGR = (\ln mass_2 \ \ln mass_1)/time$. Plant water status was determined by measuring shoot xylem pressure potentials with a pressure bomb on five shoots from each replicated treatment. Osmotic potential was calculated from pressure volume curves.

For glycinebetaine and ion determinations, 0.5 g of plant material was boiled in 10 mL of distilled water for two hours at 100°C using a dry heat bath. Samples were diluted with a 50 mmol L^{-1} potassium dihydrogen phosphate buffer adjusted to a pH of 4.6. This was the carrier buffer that was also used in the HPLC system. The sample was cooled, filtered using a 0.45 µm membrane filter (Gelman, Ann Arbor, MI), and then used directly to measure glycinebetaine, using a Hewlett Packard HPLC model HP 1050 modular 3D HPLC system with quaternary pump, on-line degasser, autosampler, and diode array detector with a stainless steel flow cell (6 mm path length, 8 µL volume). Separations were performed on a 250x4 mm I.D.

TABLE 1. Results of three-way ANOVA characteristics by harvest time (T), plant part (P), and salinity (S) treatments.

Independent variable	Time (T)	Plant part (P)	Salinity (S)	T x P	T x S	P x S	P x T x S
Fresh weight (g plant^{-1})	15.1***	10.4**	13.4***	4.1*	9.4***	2.2 NS	1.3 NS
Dry weight (g plant^{-1})	12.1***	22.0***	8.9***	7.9***	4.9**	4.3**	2.9*
Tissue water (g g^{-1} dry weight)	21.8***	187.8***	16.3***	10.9***	23.2***	5.9**	1.5 NS
Tissue water (mg plant^{-1})	15.3**	6.7*	14.3***	2.8 NS	10.4***	1.6 NS	0.8 NS

stainless steel column with 10 µm Nuleoside 100-10SA (Phenomenex, St. Torrance, CA). Flow rate was at 1.2 mL min^{-1}. Glycinebetaine and choline standards were run at 1, 10, and 100 mmol L^{-1}, while trigonelline standards were run at 0.1, 1, and 10 mmol L^{-1}. One mL of hot water extract was diluted with distilled water for ion analysis. Chloride content was measured with a Beckman specific ion electrode. Cation content of plant organs was analyzed using a Perkin Elmer model 360 atomic absorption spectrophotometer (Norwalk, CT). The Na and K content of plant tissue were assayed by flame emission and Ca and Mg content was determined by atomic absorption spectrophotometry.

The results of growth, ion content, glycinebetaine content, and plant water status were analyzed by 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 three-way ANOVA showed a significant individual effect of salinity, plant part, time of harvest, and their interactions in affecting fresh and dry weights of *H. mucronatum* plants (Table 1). Fresh weight of shoots was similar in the first two harvests, while a significant growth enhancement was observed in the third harvest (Figure 1). Fresh weight of shoots was highest at low salinity (90 mol m^{-3} NaCl) and decreased with any further increase in salinity. Plants died at 360 mol m^{-3} NaCl between the second and final harvest. Root fresh weight was highest at low salinity and decreased with increasing salinity, and was usually lower than that of shoot fresh weight (Figure 1). The most substantial increase in weight occurred between the second and third harvest (Figure 1). Both root and shoot growth was optimal at 90 mol m^{-3} NaCl and declined with any further increased salinity. Plants died between 60 and 90 days in the 360 mol m^{-3} NaCl treatment (Figure 1).

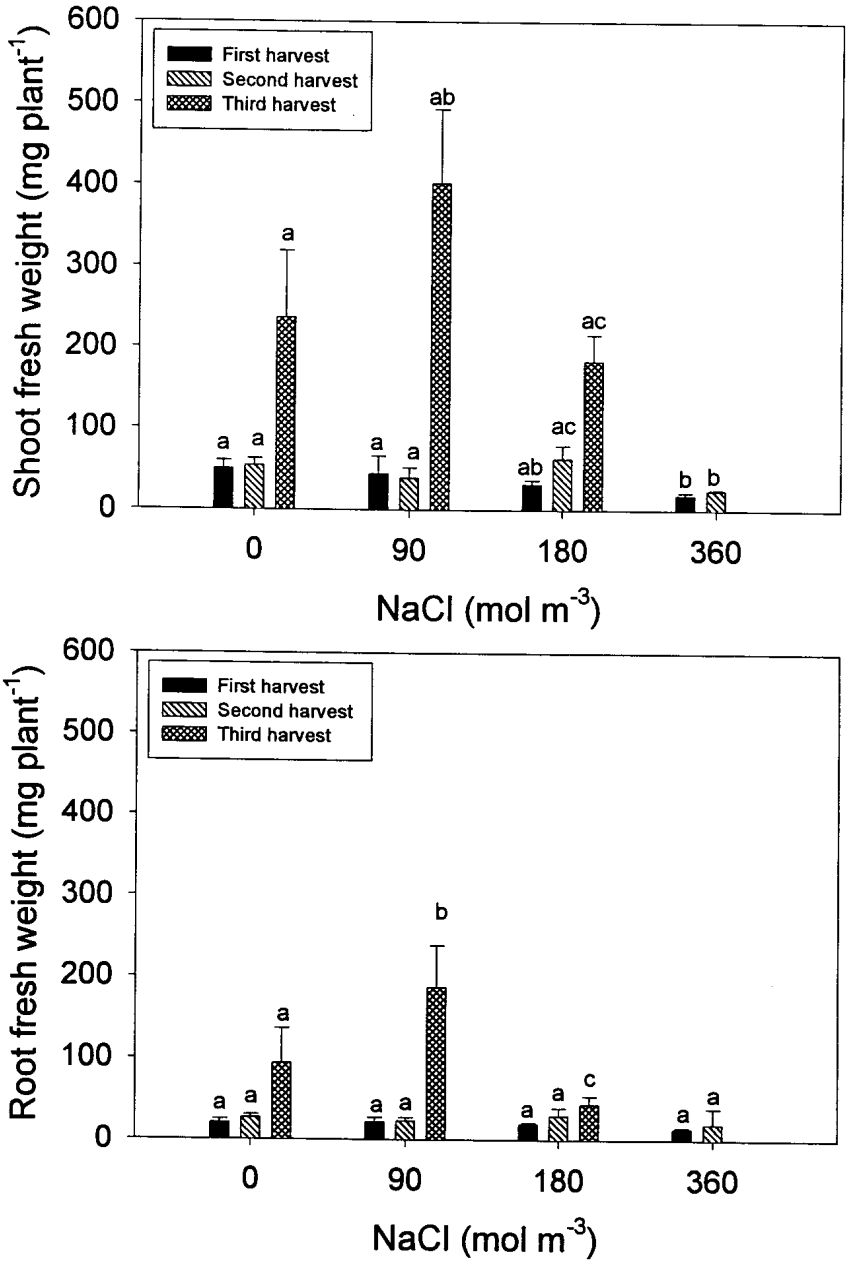

FIGURE 1. Effect of NaCl (0, 90, 180, and 360 mol m^{-3}) on the shoot and root fresh weight of *Halopyrum mucronatum* plants after 30, 60, and 90 days. Bar represents mean ± standard error. Bars for a harvest time at different salt treatment levels with different letters are significantly different ($P<0.05$).

TABLE 2. Effect of NaCl on relative growth rates (RGR) (mean ± standard error) of *Halopyrum mucronaum* shoots at three time intervals during the growth season: between 0 and 30 d, between 30 and 60 d, and between 60 and 90 d after the highest salinity was reached.

NaCl (mM)	RGR ($g\ g^{-1}\ d^{-1}$) for 3 time periods		
	0-30 d	30-60 d	60-90 d
0	0.031^a	0.021^b	0.038^b
90	0.020^b	0.026^a	0.077^a
180	0.021^b	0.017^b	0.038^b
360	0.003^c	0.015^c	0.0^c

Relative growth rate (RGR) of shoots was calculated at various time intervals during the growth period. Plants growing in 90 mol m^{-3} NaCl had the greatest growth at all of the time intervals (Table 2). Relative growth rate decreased with a further increase in salinity at all intervals. The period between the second and third harvest in each salt treatment showed the highest growth rate in all cases, except for highest salinity treatment where no plants survived.

A three-way ANOVA showed significant individual effects of harvest time, plant tissue, salinity, and their interactions in affecting water content of tissue (Table 1). The interaction between plant tissues and salinity was not significant (Table 1). Tissue water content (mg $plant^{-1}$) was greatest at 90 mol m^{-3} NaCl in the final harvest (Figure 2). There were no significant differences between first and second harvest, while in the third harvest the tissue water content was substantially higher than that in the first two harvests (Figure 2).

A two-way ANOVA showed significant individual effects of salinity, and the interaction between time of harvest and salinity in affecting the water potential of *H. mucronatum* (Table 3). Water potential and osmotic potential decreased with an increase in salinity, but harvest time did not affect these values (Figure 3). Pressure potential generally decreased with an increase in salinity.

A two-way ANOVA showed significant ($P<0.05$) individual effects of plant tissue and salinity on ion content (Table 4), but their interaction was only significant for Na ($P<0.01$). Element levels in the shoots were comparatively higher than those in roots (Table 5). Sodium and Cl content of shoots increased with an increase in salinity to 180 mol m^{-3} NaCl. Concentrations of K, Mg, and Ca decreased with an increase in salinity (Table 5).

A two-way ANOVA showed a significant ($P<0.05$) individual effect of harvest time, salinity, and their interaction on glycinebetaine content when expressed both on a dry weight as well as on a concentration basis (Table 3). Glycinebetaine expressed both as a total amount as well as a concentration showed little increase

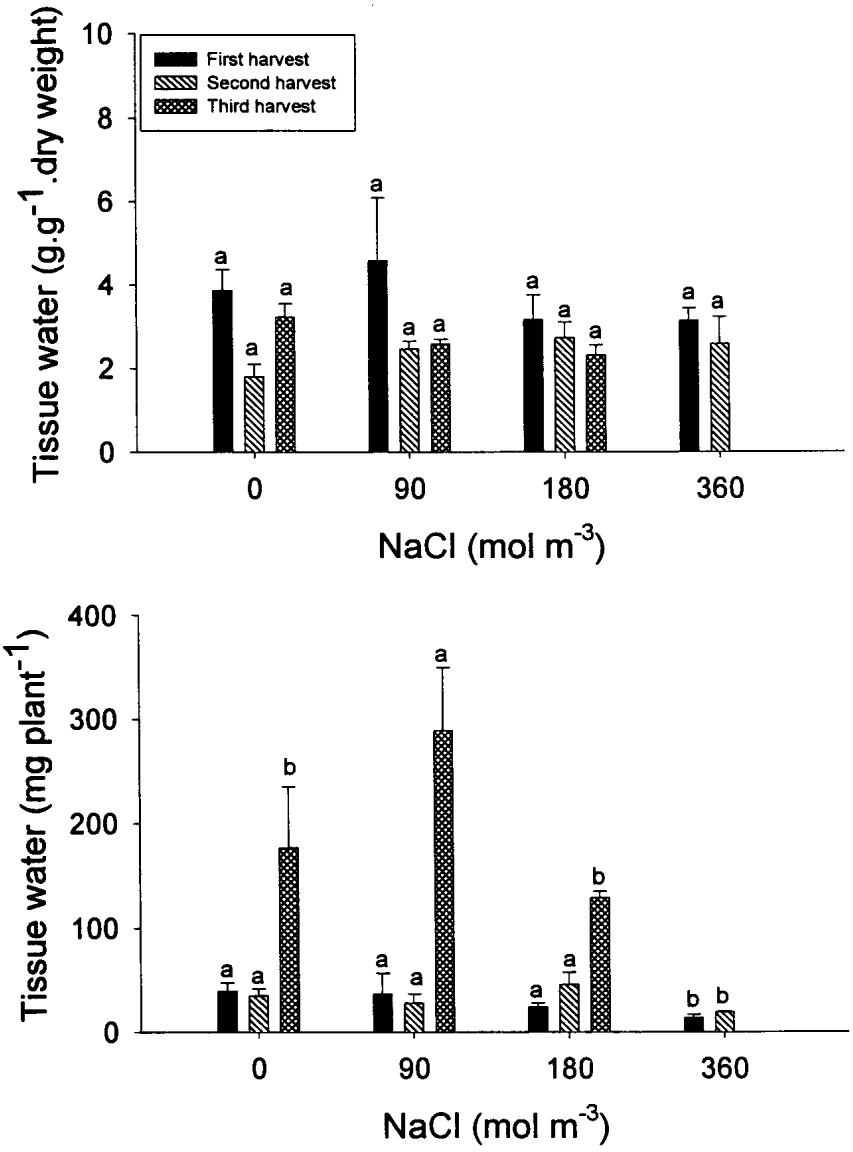

FIGURE 2. Effect of NaCl (0, 90, 180, and 360 mol m^{-3}) on tissue water content (mg $plant^{-1}$) of *Halopyrum mucronatum* after 30, 60, and 90 days. Bars represent mean ± standard error. Bars for a harvest time at different salt treatment levels with different letters are significantly different ($P<0.05$).

TABLE 3. Results of two-way analysis of variance of characteristics by salinity (S) and time of harvest (T).

Dependent variable	Salinity (S)	Time of harvest (T)	S x T
Betaine (mmol kg^{-1} dry weight)	3.4*	5.1**	2.8*
Betaine (mmol L^{-1} tissue water)	4.1*	4.6*	3.2*
Water potential (-MPa)	11.6***	1.6^{NS}	26.3***

Note: Numbers represent F values—*P<0.01, **P<0.00, ***P<0.0001, ^{NS}=non-significant.

at low salinity over the harvest period (Figure 4). However, plants grown at the highest salinity had a substantial increase in glycinebetaine over the harvest period.

DISCUSSION

Growth of *H. mucronatum* was substantially promoted at low salinity (90 mol m^{-3}), but decreased with a further increase in salinity. At later stages of growth, plants grown under 360 mol m^{-3} NaCl did not survive. A true halophyte can be defined as one which could complete its life cycle in saline conditions, with growth promoted at moderate salinity and survival in up to 340 mol m^{-3} NaCl (Flowers et al., 1977; Flowers and Yeo, 1986; Ungar, 1991). Consequently, *Halopyrum mucronatum* would be classified as a facultative halophyte. Grasses are known to vary in their salt tolerance (Mahmood et al., 1996; Pearen et al., 1997). A few species showed growth promotion at 450 mol m^{-3}, while others did not survive in more that 300 mol m^{-3} NaCl. Bodla et al. (1995) showed that *Aeluropus lagopoides* could grow in up to 110 dS m^{-1} NaCl (1,500 mol m^{-3}). Other graminoid species like *Paspalum distichum* L. (Bodla et al., 1995), *Cyperus rotundus* L. (Shamsi and Ahmed, 1986), *Leptochloa fusca* (L.) Kunth. (Ahmed, 1987), and *Cynodon dactylon* (Kumar, 1990) have also been shown to survive in high medium salinity (40 dS m^{-1} NaCl or 500 mol m^{-3}).

Salinity tolerance is better expressed as a reduction in the relative growth rate with increased salinity in comparison to absolute growth (Maas and Hoffman, 1977; Marcum and Murdoch, 1994). The relative growth rate of *H. mucronatum* showed a substantial salinity effect 90 days after the final salinity concentrations were reached. Growth was highest in the 60-90 day growth period and a substantial increase in growth was recorded in the low salinity treatment compared to both higher and lower salinities. A similar stimulation in growth at low salinity was also reported for *Stenotaphrum secundatum* (Marcum and Murdoch, 1994). The relative growth rate of *H. mucronatum* decreased at the highest salinity. This is similar to

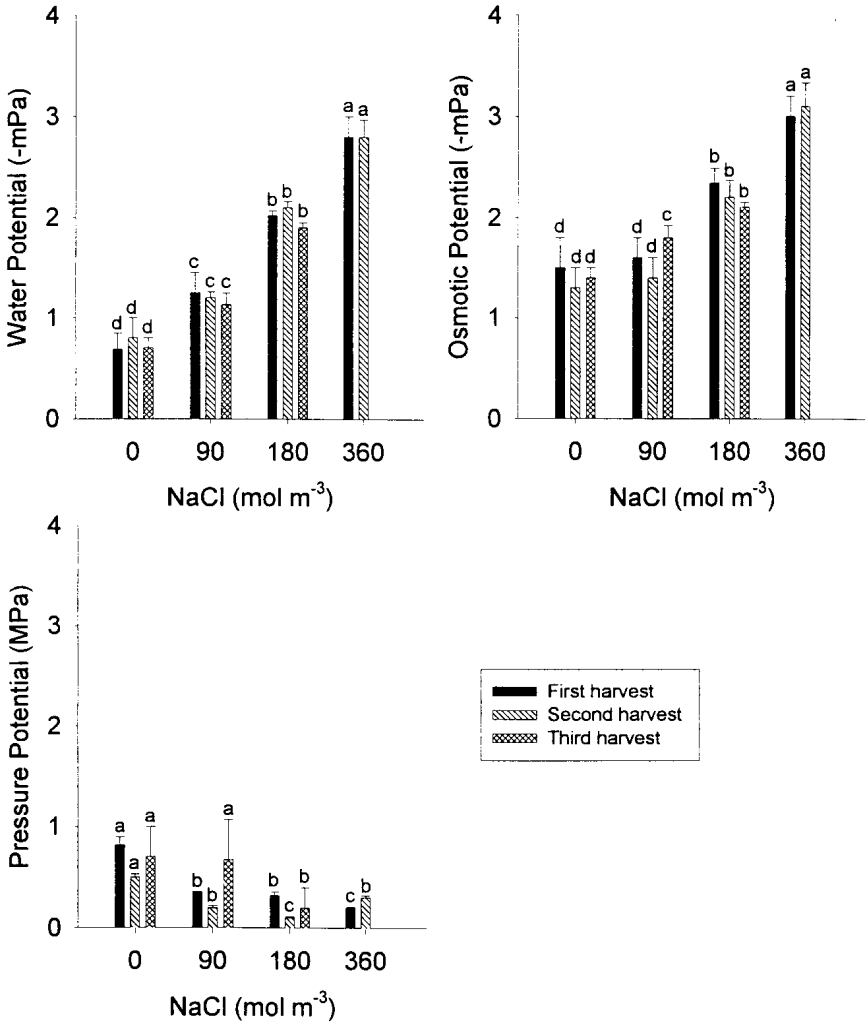

FIGURE 3. Effect of NaCl (0, 90, 180, and 360 mol m^{-3}) on the water potential, osmotic potential, and pressure potential of *Halopyrum mucronatum* shoots at different times during the growing season. Bar represents mean ± standard error. Bars for a harvest time at different salt treatment levels with different letters are significantly different ($P<0.05$).

TABLE 4. 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
Calcium	8.4***	4.1*	0.1^{NS}
Chloride	8.8***	59.1***	0.1^{NS}
Potassium	0.2^{NS}	21.0***	0.1^{NS}
Magnesium	5.8**	7.1**	0.3^{NS}
Sodium	9.8***	82.4***	5.2**

Note: Numbers represent F values—*P<0.01, **P<0.00, ***P<0.0001, ^{NS}=non-significant.

the reduction in relative growth rate of *Distichlis spicata* (L.) Greene at high salinity (500 mol m^{-3} NaCl) from 0.057 to 0.019 g g^{-1} d^{-1} (Kemp and Cunningham, 1981).

To avoid the toxic effects of salt, halophytes have developed a number of mechanisms, including succulence, exclusion, and secretion (Ungar, 1991). *Halopyrum mucronatum* substantially increased succulence at low salinity, but increases in salinity caused a substantial reduction in tissue water content. The growth of plants was apparently correlated with their level of succulence. When succulence was high, plants achieved more positive turgor and had a substantial promotion of growth. With a further increase in salinity, the water content of plants decreased and they lost turgor, which resulted in an inhibition of growth. *Halopyrum mucronatum* adjusted osmotically, maintaining a more negative osmotic

TABLE 5. Ion concentration in shoots and roots of *Halopyrum mucronatum* plants grown for 90 d after highest salinity was reached.

Plant part	NaCl (mM)	Na	K	Cl	Mg	Ca
		(μmol g^{-1} dry weight)				
Shoot	0	772^{b}	860^{a}	544^{b}	114^{a}	48^{a}
	90	856^{b}	730^{a}	590^{b}	56^{b}	20^{b}
	180	1685^{a}	340^{b}	1865^{a}	46^{b}	12^{c}
	360	-	-	-	-	-
Root	0	587^{a}	400^{a}	506^{a}	50^{a}	20^{a}
	90	464^{a}	280^{b}	618^{ab}	61^{b}	15^{a}
	180	786^{b}	240^{b}	711^{b}	30^{c}	11^{b}
	360	-	-	-	-	-

Values in each column having the same letter are not significantly different at P=<0.05, Bonferroni test.

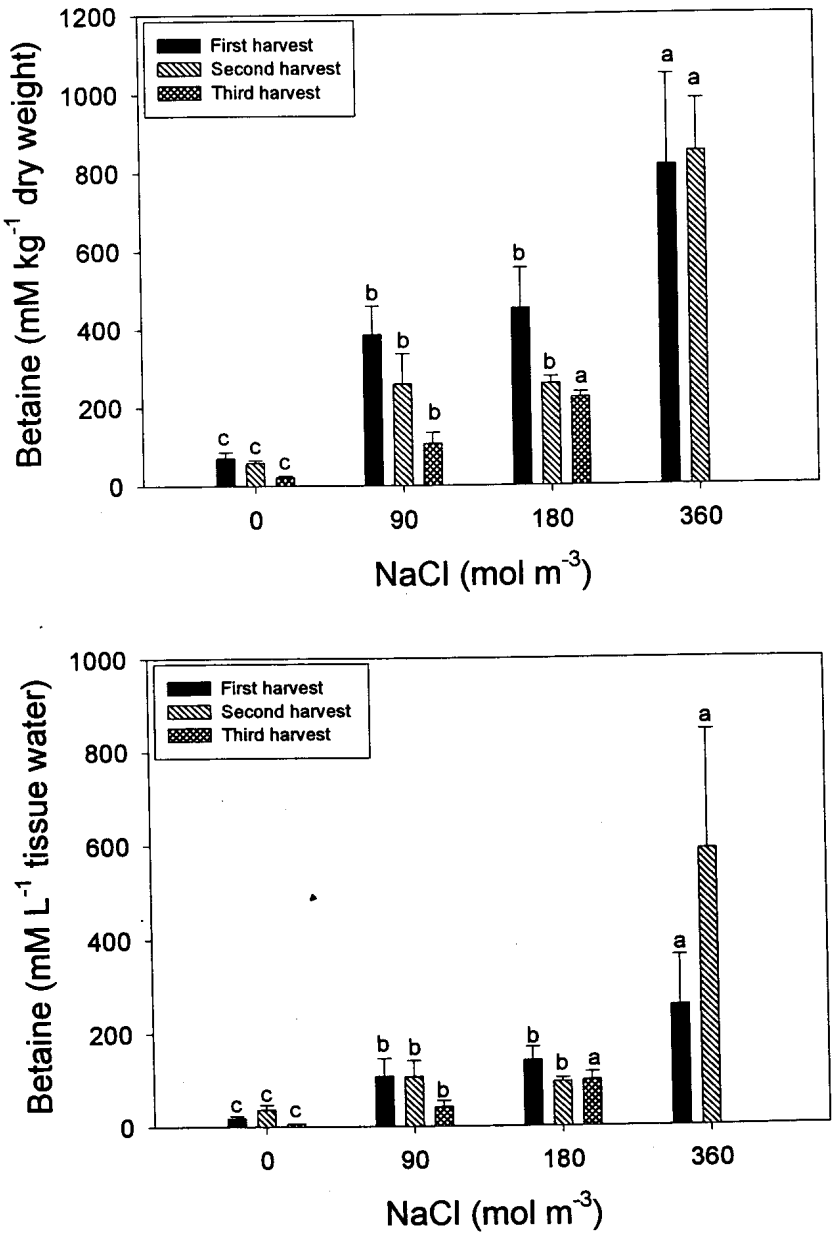

FIGURE 4. Effect of NaCl (0, 90, 180, and 360 mol m^{-3}) on glycinebetaine content in leaves of *Halopyrum mucronatum* after 30, 60, and 90 days. Bar represents mean ± standard error. Bars for a harvest time at different salt treatment levels with different letters are significantly different ($P<0.05$).

potential than that of the medium though the differences became less with increasing salinity. Antlfinger and Dunn (1983) found that species growing in higher soil salinities had a greater xylem pressure potential than that of plants growing in less saline areas. Xylem pressure potential for graminoids ranged from 2.2 to 2.9 MPa. Our data showed a similar range of water potential for *H. mucronatum* plants growing in high salinity.

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). However, the supply of ions to the shoot of *H. mucronatum* was adequate for osmotic adjustment, since large quantities of Na and Cl were transported to the shoots. The cause of growth reduction in salt stressed monocots is poorly understood (Munns et al., 1983; Yeo, 1983), but may be the result of a specific ion toxicity.

Organic solutes, which cause a minimum amount of perturbation to macromolecular stability and cytoplasmic enzyme function, accumulate in eukaryotic plant cells as they adjust to low osmotic potentials (Storey et al., 1977). This adaptation may occur at concentrations above 350-400 mol m^{-3} (-1.4 to -1.6 MPa) (Wyn Jones et al., 1977). Glycinebetaine is reported to occur extensively in the Poaceae (Storey et al., 1977), but does not accumulate in all grass species. Albert (1975) described the physiotype of the salt resistant *Puccinellia maritima*, which did not accumulate glycinebetaine, and its tissues were high in K and relatively low in Na. *Spartina townsendii* belongs to second physiotype that accumulates both Na and glycinebetaine. *Chloris gayana* Kunth., *Ammophila arenaria* (L.) Link., and *Zea mays* L. are similar to this second type. *Halopyrum mucronatum* belongs to the Na accumulating physiotype and it also accumulates 400-600 mol m^{-3} glycinebetaine in high salinity treatments, which is sufficient to serve as an osmoticum.

CONCLUSIONS

In conclusion, *H. mucronatum* is a facultative halophyte, which is less salt-resistant than other coastal salt marsh species such as *Arthrocnemum indicum*, *Atriplex griffithii*, *Cressa cretica*, *Suaeda fruticosa*, and *Haloxylon recurvum*. Growth enhancement at lower salinities appears to be related to increased succulence. Sodium and Cl accumulate in organs rather than being excluded from tissues, and cellular NaCl tolerance is presumably related to the capacity of *H. mucronatum* to accumulate glycinebetaine as a compatible solute.

ACKNOWLEDGMENTS

We would like to thank the CIES for providing a Fulbright Scholar Research Grant and Ohio University for a Postdoctoral Fellowship to M. Ajmal Khan. This research was supported in part by National Science Foundation Research Grant INT-9730882.

REFERENCES

Ahmed, R. 1987. Saline agriculture at coastal sandy belt. Final Report (1981-86). Department of Botany, University of Karachi, Karachi, Pakistan.

Albert, R. 1975. Salt regulation in halophytes. Oecologia 21:57-71.

Antlfinger, A. and E.L. Dunn. 1983. Water use and salt balance in three salt marsh succulents. Am. J. Bot. 70:561-570.

Bodla, M.A., M.R. Chaudhry, S.R.A. Shamsi, and M.S. Baig. 1995. Salt tolerance in some dominant grasses of Punjab. pp. 190-198. In: M.A. Khan and I.A. Ungar (eds.), Biology of Salt Tolerant Plants. Department of Botany, University of Karachi, Karachi, Pakistan.

Dudeck, A.E. and C.H. Peacock. 1985. Effects of salinity on seashore *Paspalum* turfgrasses. Agron. J. 77:47-50.

Dudeck, A.E., C.H. Peacock, and J.C. Wildmon. 1993. Physiological and growth responses of St. Augustine grass cultivars to salinity. Hort. Sci. 28:46-48.

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., P.F. Troke, and A.R. Yeo. 1977. The mechanism of salt tolerance in halophytes. Annu. Rev. Plant Physiol. 28:89-121.

Gorham J. 1995. Mechanism of salt tolerance of halophytes. pp. 31-53. In: R. Choukr-Allah, C.V. Malcolm, and A. Hamdy (eds.), Halophytes and Biosaline Agriculture. Marcel Dekker, Inc., New York, NY.

Hellebust, J.A. 1976. Osmoregulation. Annu. Rev. Plant Physiol. 27:485-505.

Jafri, S.M.H. 1966. Flora of Karachi. University of Karachi, Karachi, Pakistan.

Kemp, P.R. and G.L. Cunningham. 1981. Light, temperature and salinity effects on growth, leaf anatomy and photosynthesis of *Distichlis spicata* (L.) Green. Am. J. Bot. 68:507-516.

Kumar, A. 1990. Forage yield of grasses as affected by the degree of soil sodicity and soil amelioration caused by their growth. pp. 435-444. In: Proceedings of Indo-Pak Workshop on Soil Salinity and Water Management. PARC, Islamabad, Pakistan.

Maas, E.V. and G.J. Hoffman. 1977. Crop salt tolerance-current assessment. Am. Soc. Civil Eng. J. Irrig. Drainage Div. 103:115-134.

Mahmood, K., K.A. Malik, M.A.K. Lodhi, and K.H. Sheikh. 1996. Seed germination and salinity tolerance in plant species growing on saline wastelands. Biol. Plant. 38:309-315.

Marcum, K.B. 1995. Salt tolerance in the grass (Poaceae) subfamily Chloridoideae. pp. 231-237. In: M.A. Khan and I.A. Ungar (eds.), Biology of Salt Tolerant Plants. Department of Botany, University of Karachi, Karachi, Pakistan.

Marcum, K.B. and C.L. Murdoch. 1990. Growth responses, ion relations, and osmotic adaptations of eleven C_4 turfgrasses to salinity. Agron. J. 82:892-896.

Marcum, K.B. and C.L. Murdoch. 1994. Salinity tolerance mechanisms of six C_4 turfgrasses. J. Am. Soc. Hort. Sci. 119:779-784.

Munns, R., H. Greenway, and G.O. Kirst. 1983. Halotolerant eukaryotes. pp. 59-83. In: O.L. Lang, P.S. Nobel, C.B. Osmond, and H. Ziegler (eds.), Encyclopedia of Plant Physiology. Springer-Verlag, Berlin, Germany.

Noor, M. and M.A. Khan. 1995. Factors affecting the germination of summer and winter seeds of *Halopyrum mucronatum* under salt stress. pp. 51-58. In: M.A. Khan and I.A. Ungar (eds.), Biology of Salt Tolerant Plants. Department of Botany, University of Karachi, Karachi, Pakistan.

Peacock, C.H. and A.E. Dudeck. 1985. Physiological and growth response of sea shore paspalum to salinity. Hort. Sci. 20:111-112.

Pearen, J.R., M.D. Pahl, M.S. Wolynetz, and R. Hermesh. 1997. Association of salt tolerance at seedling emergence with adult plant performance in slender wheatgrass. Can. J. Plant Sci. 77:81-89.

Ramakrishnan, P.S. and R. Nagpal. 1973. Adaptation to excess salts in an alkaline soil population of *Cynodon dactylon* (L.) Pers. J. Ecol. 61:369-381.

Shamsi, S.R.A. and B. Ahmad. 1986. Studies on salt tolerance of purple nutsedge (*Cyperus rotundus*). Ind. J. Exp. Biol. 24:499-504.

SPSS. 1996. SPSS 7.0 for Windows 95. SPSS, Inc., Chicago, IL.

Storey, R., N. Ahmed, and R.G. Wyn Jones. 1977. Taxonomic and ecological aspects of the distribution of glycinebetaine and related compounds in plants. Oecologia 27:319-332.

Ungar, I.A. 1991. Ecophysiology of Vascular Halophytes. CRC Press, Boca Raton, FL.

Wyn Jones, R.G., R. Storey, R.A. Leigh, N. Ahmed, and A. Pollard. 1977. A hypothesis on cytoplasmic osmoregulation. pp. 121-136. In: E. Marre and O. Ciferri (eds.), Regulation of Cell Membrane Activities in Plants. North Holland, Amsterdam, The Netherlands.

Yeo, A.R. 1983. Salinity resistance: Physiologies and prices. Physiol. Plant. 58:214-222.

Younger, V.B. and O.R. Lunt. 1967. Salinity effects on roots and tops of bermuda grass. J. Brit. Grassl. Soc. 22:257-259.