

CHAPTER 17

COMPARATIVE SALT TOLERANCE OF PERENNIAL GRASSES

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Abstract. Salt tolerance mechanisms of three perennial halophytic grasses (*Aeluropus lagopoides* (Linn.) Trin. ex Thw., *Sporobolus ioclados* (Trin.) C.E. Hubbard and *Urochondra setulosa* (Nees ex Trin.) Nees) were studied to determine if local species employ similar strategies to tolerate high salinity. We found different patterns of growth, water relations and ion uptake among the species tested. *Aeluropus lagopoides* and *U. setulosa* were grown in 0-1000 mM NaCl while *S. ioclados* in 0-500 mM NaCl under ambient conditions. Plants from non-saline controls had larger fresh and dry weights. Increasing concentrations of salinity from 600 – 1000 mM NaCl for *A. lagopoides* and *U. setulosa* and 500 mM NaCl for *S. ioclados* caused high salinity stress. Water and osmotic potential of the plants increased with increasing salinity and pressure potential decreased slightly in all species. Stomatal conductance in all grasses decreased substantially with the increase in salinity. Ash content remained low (~12%) in both shoot and root of all grasses and showed little change with the increase in salinity except for *S. ioclados*, where in root it increased up to 35%. Na⁺ and Cl⁻ concentrations showed a small increase while Ca²⁺, Mg²⁺ and K⁺ remained constant with increasing salinity. Various ion ratios for shoot and root also showed variation between the species tested.

1. INTRODUCTION

Soil salinity is a major constraint to food production because it limits crop yield and restricts use of previously uncultivated land (Yokoi et al., 2002). Coastal areas of Pakistan have limited supply of good quality water, however, the coast of Balochistan, despite few seasonal rivers, does not have enough fresh water. Most of the sub-surface water is brackish with various levels of salinity and not fit for the cultivation of conventional crops. Therefore, use of brackish water is the only affordable alternative left to improve the ecology of the deserted lands and to produce cash-crops for alleviating the economic hardship of local populations. The coastal area of Pakistan is reported to have about 100 halophytes and a significant number of them are grasses (Khan & Gul, 2001). Salt tolerant perennial grasses could be an alternate source of forage and fodder because they can be grown with

brackish water irrigation (Khan, 2002). We selected three of the most common grasses viz. *Aeluropus lagopoides* (Linn.) Trin. ex Thw., *Sporobolus ioclados* (Nees ex Trin.) Nees, and *Urochondra setulosa* (Trin.) C.E. Hubbard to determine their comparative salt tolerance and suitability as forage crop for the region.

Perennial grasses are reported to be highly salt tolerant (Russell, 1976; Shannon, 1978; Venables & Wilkins, 1978; Marcum & Murdoch, 1990; Lissner & Shierup, 1997; Bajji et al., 2002; Bell & O'Leary, 2003; Shen et al., 2003; Alshammary et al., 2004; Debez et al., 2004). Similar reports are also available on the salt tolerance of some of the local grasses (Ashraf et al., 1986; Shamsi & Ahmed, 1986; Kumar, 1990; Ashraf & Naqvi, 1991; Bodla et al., 1995; Mahmood et al., 1996; Khan et al., 1999, Gulzar et al., 2003ab; Gulzar et al., 2005). These reports indicate that the salt tolerance of grasses could vary from 300 mM NaCl to 800 mM NaCl (Gulzar et al., 2005). Grasses like *Aeluropus lagopoides* and *Urochondra setulosa* could survive in up to 1000 mM NaCl (Bodla et al., 1995; Gulzar et al., 2003ab) while a number of them survived salinity (550 to 600 mM NaCl) approaching seawater (Glenn, 1987; Hester et al., 1996, 2001). Some grasses grew in soil salinity ranges between 300 to 500 mM NaCl (Mahmood et al., 1996; Bell & O'Leary, 2003; Peng et al., 2004) while others could not survive in salt concentrations above 300 mM NaCl (Khan et al., 1999; La Peyre & Row, 2003).

Osmotic adjustment under increased salinity occurred concurrent with increased shoot sodium and chloride concentrations, decreased shoot potassium concentration, and decreased shoot succulence (Marcum & Murdoch, 1990; Gulzar et al., 2003ab, 2005). Water and osmotic potential in *Halopyrum mucronatum* increased with increase in salinity while turgor decreased (Khan et al., 1999). Osmotic adjustment and maintenance of positive turgor under salt stress also occurred in *Paspalum vaginatum* (Peacock & Dudeck, 1985) and *Stenotaphrum secundatum* (Dudeck et al., 1993).

Halophytic grasses exclude salt effectively and use water loss to concentrate solutes for osmotic adjustment (Glenn, 1987; Munns, 2002; Parida & Das, 2005). Monocotyledonous halophytes generally have much lower water content, $\text{Na}^+ : \text{K}^+$ ratios and mineral content than dicotyledonous halophytes growing at the same location (Gorham et al., 1980; Glenn, 1987). Sodium exclusion method of salt tolerance appears less efficient than sodium accumulation particularly in the succulent xerophytes (Wang et al., 2004; Debez et al., 2004). At higher salinity, *Sporobolus arabicus* accumulated more Na^+ in comparison to other species studied (Mahmood et al., 1996). Khan et al. (1999) reported higher accumulation of Na^+ and Cl^- and corresponding decrease in K^+ , Ca^{2+} and Mg^{2+} with increasing salinity in *Halopyrum mucronatum*.

High intracellular concentrations of Na^+ and/or Cl^- may inhibit the activity of many enzymatic systems and some cellular processes, such as protein synthesis or mRNA processing (Serrano, 1996; Yeo, 1998; Zhu, 2001; Forment et al., 2002). Sodium interferes with the uptake of essential cations, especially K^+ and Ca^{2+} and promotes oxidative stress through generation of "reactive oxygen species" (ROS)

(Serrano & Gaxiola, 1994; Yeo, 1998; Zhu, 2001). Substantial differences in Na^+ and K^+ accumulation between salt-resistant species may be due to differences in the selective ion transport capacities at root level (Hester et al., 2001; Wang et al., 2002). Salt secreting species would be expected to have the weakest selective transport capacity for K^+ over Na^+ as most of the salt would have to be transported up to the stem and excluded from the leaf via salt glands. *Aeluropus lagopoides* did show high selectivity for K^+ by retaining greater amounts of Cl^- and Mg^{2+} in roots than in shoots (Gulzar et al., 2003a), while *U. setulosa* shoots did not show high K^+ selectivity (Gulzar et al., 2003b) although countless salt crystals accumulate on its leaf surface. Salinity induced inhibition of plant growth may occur due to the effects of high Na^+ , Cl^- or SO_4^{2-} by decreasing the uptake of essential elements such as P, K^+ , NO_3^- and Ca^{2+} , ion toxicity or osmotic stress (Zhu, 2001, 2002). *Sporobolus spicatus* was found to secrete 93% NaCl by weight of salts secreted by plants from 4 different sites while K^+ , Ca^{2+} , Mg^{2+} and SO_4^{2-} constituted only 5% of salts (Ramadan, 2001).

Ion ratios could be helpful in categorizing the physiological response of a plant (salt-excluding, salt-secreting or salt-diluting) in relation to ion selectivity under increasing substrate salt concentrations (Wang et al., 2002). However, the influence of various ion ratios on salt tolerance is quite complex and attempts to draw general conclusions have not been successful (Grieve et al., 2004). Sodium–potassium ion ratio is among the most important of these ion ratios and plants tend to maintain a low Na^+/K^+ ratio in the cytoplasm and low cytosolic Na^+ content below some crucial value (Greenway & Munns, 1980; Maathuis & Amtmann, 1999; Tyerman & Skerrett, 1999).

This research compares the effects of salinity on mechanisms of growth, water relations and ion uptake of three halophytic grasses (*Aeluropus lagopoides* (Linn.) Trin. ex Thw., *Sporobolus ioclados* (Nees ex Trin.) Nees, and *Urochondra setulosa* (Trin.) C.E. Hubbard from Pakistan.

2. MATERIALS AND METHODS

Propagules of *Aeluropus lagopoides* and *Sporobolus ioclados* were collected from University of Karachi campus and *Urochondra setulosa* from Hawkes Bay, at the Arabian Sea coast near Karachi. Seeds were separated from the hull and stored in a refrigerator at 4 °C. Growth experiments were carried out in the University of Karachi under ambient atmospheric conditions. Seeds were germinated in 10 cm x 8 cm plastic pots filled three fourths with sandy soil. Plants were raised on half strength Hoagland and Arnon solution No. 2 (Moore, 1960) for two weeks until they achieved a height of about 5 cm. Plants were thinned to five similar sized plants in each pot. Pots were sub-irrigated 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. Six salinity treatments with five replicates each were employed: 0, 200, 400, 600, 800 and 1000 mM NaCl for *A. lagopoides* and *U. setulosa* and 0, 100, 200, 300, 400 and 500 mM NaCl for *S. ioclados* after a

preliminary test for salinity tolerance. Salinity levels were raised gradually at daily intervals. At the end of the experiment, plants were harvested and fresh and dry weights of stem and root were measured. Plants were oven-dried at 80°C for 48h before dry weight was determined. Water potential was measured on punched disks from randomly chosen leaves in a C-52 chamber with the help of a HR-33 dew point micro-voltmeter (Wagtech). Similarly, press sap technique on Whatman No. 1 filter paper disks was used for measuring leaf osmotic potential. Leaf turgor pressure was estimated from the difference of leaf osmotic and water potentials. Leaf stomatal conductance was determined with an AP-4 Porometer (Delta-T Devices). Chloride ion was measured with a Beckman specific ion electrode. Cation content of plant root and shoot parts were analyzed using a Perkin Elmer model 360 atomic absorption spectrophotometer. The Na⁺ and K⁺ levels of the plant were examined by flame emission spectrometry. Statistical analyses were performed with the help of SPSS (SPSS, 2002).

3. RESULTS

Best growth was recorded in the non-saline medium for all species (Figure 1). *Aeluropus lagopoides* had the highest fresh and dry weights for shoot and root as well as the highest number of tillers per plant. *Sporobolus ioclados* exhibited a progressive decrease in shoot fresh weight, root fresh weight, dry weight of shoot, dry weight of root, shoot length, root length, number of leaves and tillers with an increase in substrate salinity. However, *A. lagopoides* and *U. setulosa* showed little effect at 200 mM NaCl but a further increase in salinity level (200-1000 mM NaCl) substantially inhibited growth. *Urochondra setulosa* maintained greater root length at all salinities tested and shoot length at 400-1000 mM NaCl concentration as compared to *A. lagopoides* which had greater shoot length at 0 and 200 mM NaCl. In *A. lagopoides*, number of tillers per plant at 0 to 600 mM NaCl were twice those of *U. setulosa*, while the number of leaves was almost identical between these two species. Although *S. ioclados* had the highest shoot length of about 60 cm as compared to the other grasses in control, it had much lower root length at all salinity levels and both shoot and root length declined substantially with rising medium salinity (Figure 1). Shoot to root ratio on a dry weight basis increased with increase in salinity in *A. lagopoides* and *S. ioclados* in comparison to control while it decreased slightly in *U. setulosa* (Figure 2). Tissue water content on a dry weight basis declined at the higher NaCl concentrations in all the species but *A. lagopoides* and *S. ioclados* showed some increase at moderate salinities (Table 1).

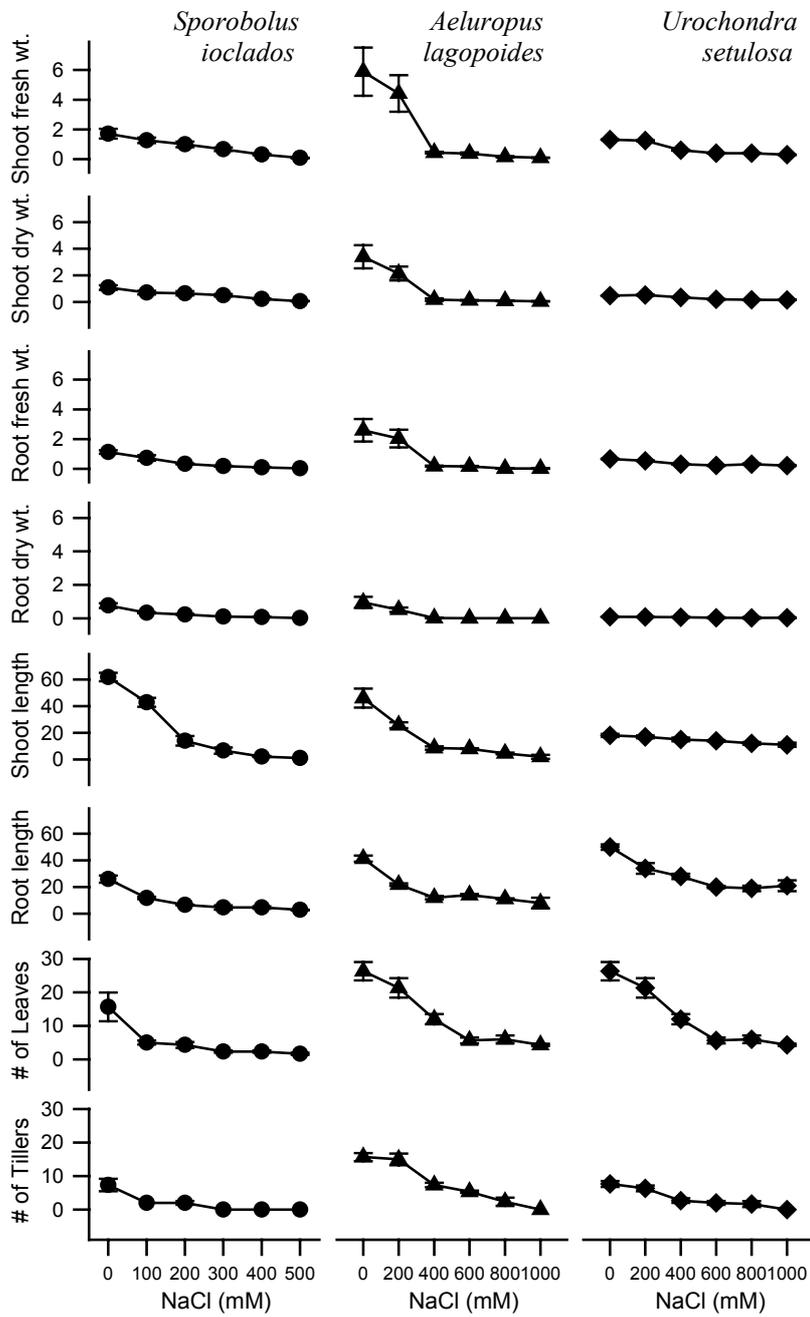


Figure 1. Effect of increasing salinity on the growth parameters of *S. ioclados*, *A. lagopoides* and *U. setulosa*. Values for shoot and root weight are in g and of length in cm.

A progressive increase in water potential and osmotic potential was observed with the increase in salinity in all species while stomatal conductance showed a progressive decrease (Figure 3). *Aeluropus lagopoides* showed the ability to maintain water potential, osmotic potential and stomatal conductance at salinities between 200-600 mM NaCl but salinities of 800 mM NaCl and above had inhibitory effects. All species maintained a higher osmotic potential than the water potential at each salinity concentration. Pressure potential did not vary much with the increase in salinity (Figure 3).

Table 1. Effect of increasing salinity on the tissue water content of *Aeluropus lagopoides*, *Sporobolus ioclados* and *Urochondra setulosa*. Different letters in columns represent significant differences between mean tissue water content of each species.

NaCl (mM)	Tissue water ($g\ g^{-1}$ dry wt.)				
	Sporobolus ioclados	NaCl (mM)	Aeluropus lagopoides	NaCl (mM)	Urochondra setulosa
0	0.57 ^a ± 0.23	0	0.73 ^a ± 0.08	0	2.69 ^a ± 0.14
100	0.78 ^a ± 0.18	200	1.61 ^b ± 0.53	200	2.04 ^a ± 0.20
200	0.52 ^a ± 0.11	400	1.26 ^b ± 0.28	400	1.00 ^b ± 0.09
300	0.31 ^b ± 0.06	600	2.11 ^c ± 0.43	600	1.00 ^b ± 0.00
400	0.33 ^b ± 0.12	800	0.58 ^a ± 0.15	800	0.91 ^b ± 0.16
500	0.14 ^c ± 0.05	1000	0.40 ^a ± 0.20	1000	0.69 ^b ± 0.16

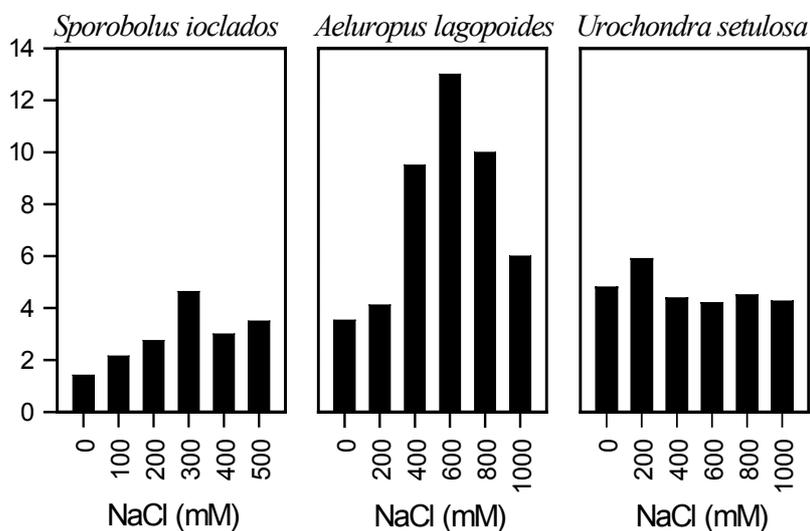


Figure 2. Effect of increasing salinity on the shoot to root dry weight ratio of *A. lagopoides*, *S. ioclados* and *U. setulosa*.

Ash content of shoots and roots of *A. lagopoides* and *U. setulosa* and shoots of *S. ioclados* was generally low (< 15% of dry weight) while *S. ioclados* roots had about 35% ash content (Figure 4). Ion content did not vary much in *A. lagopoides* and *U. setulosa* with an increase in salinity except for Cl^- which increased in roots of *A. lagopoides* with increase in salinity. Ion content was comparatively higher in

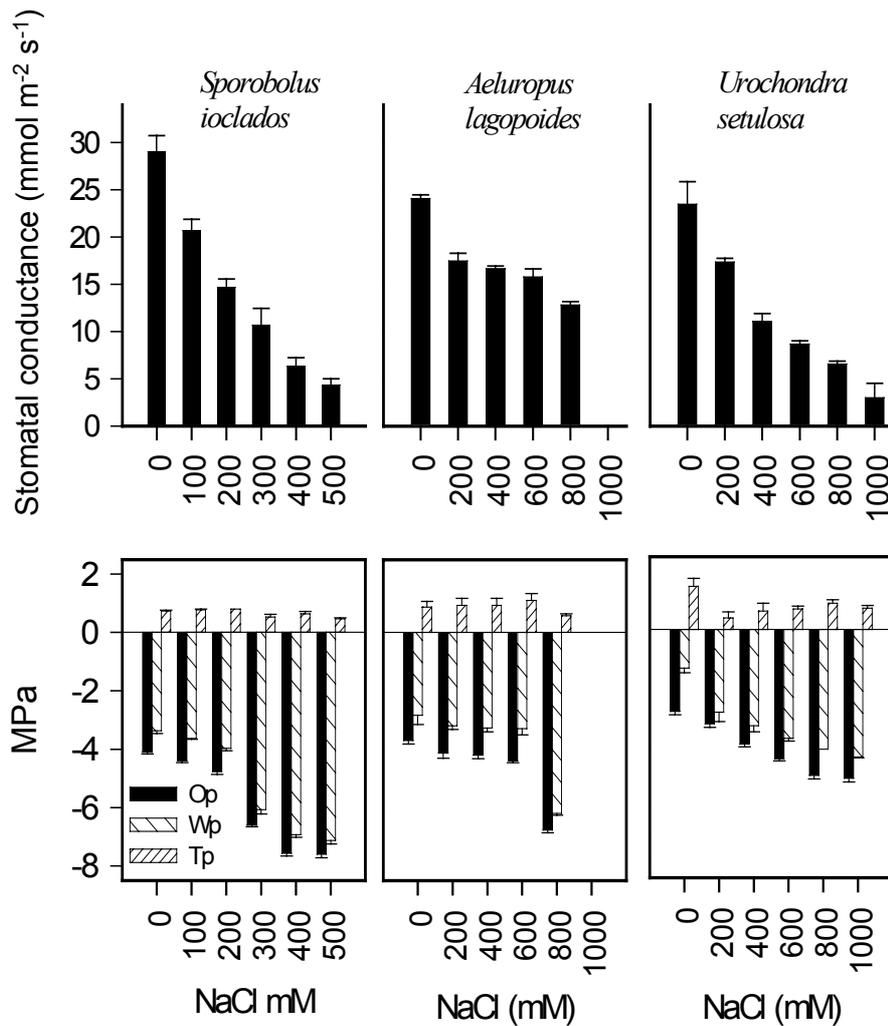


Figure 3. Effect of increasing salinity on the water relations of *A. lagopoides*, *S. ioclados* and *U. setulosa*.

roots of *A. lagopoides* but it was higher in shoot of *Urochondra setulosa*. In both the species mentioned Na^+ increased but K^+ , Ca^{2+} and Mg^{2+} levels remained relatively unchanged. *Sporobolus ioclados* showed a different pattern of ion accumulation with rise in salinity. Sodium increased considerably while K^+ , Ca^{2+}

and Mg^{2+} decreased concomitantly with increase in salinity concentrations (Figure 4).

These ratios were mostly higher in root than in shoot. At the highest salinities, *S. ioclados* roots had the highest Na^+/K^+ , Na^+/Mg^{2+} and K^+/Ca^{2+} ratios. *Aeluropus lagopoides* showed comparatively lower ion ratios among the three species selected with little variations between salinity treatments.

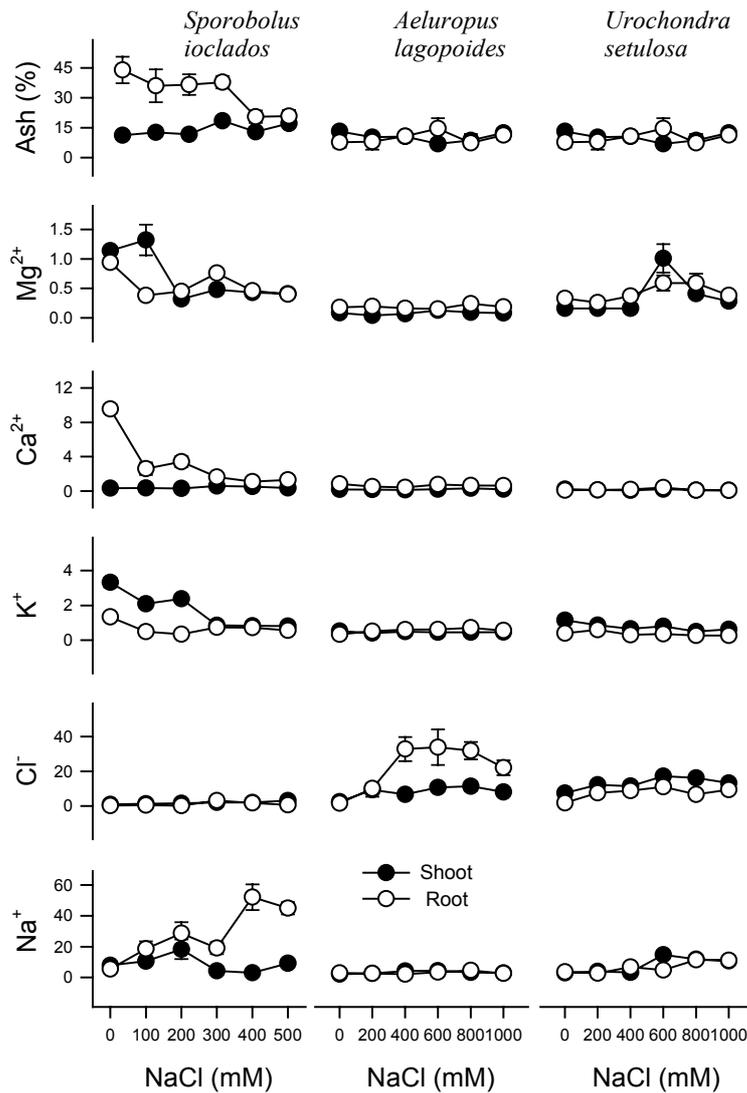


Figure 4. Effect of increasing salinity on the shoot and root concentrations of Na^+ , Cl^- , K^+ , Ca^{2+} , Mg^{2+} and ash in *A. lagopoides*, *S. ioclados* and *U. setulosa*. Tissue ion concentrations are expressed in $mmol\ g^{-1}$ dry weight.

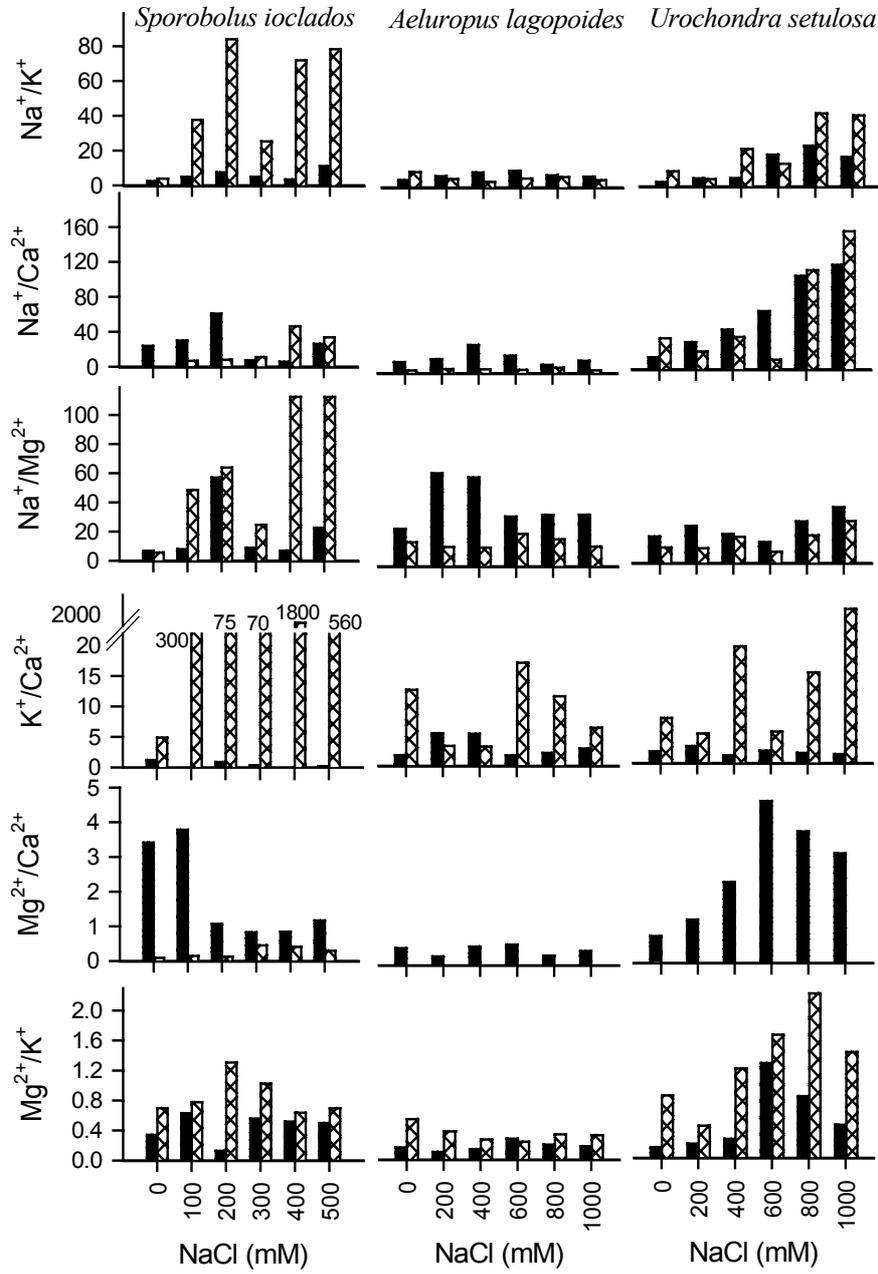


Figure 5. Effect of increasing salinity on the Na/K, Na/Ca, Na/Mg, K/Ca, Mg/Ca and Mg/K ion ratios in shoot and root of *S. ioclados*, *A. lagopoides* and *U. setulosa*.

4. DISCUSSION

Grasses are quite variable in their tolerance to salinity at growth (Khan et al., 1999; Hester et al., 2001; Muscolo et al., 2003; Joshi et al., 2004). Muscolo et al. (2003) reported that *Panicum clandestinum* could tolerate 200 mM NaCl while growth was little affected by 100 mM NaCl. Leaf and root growth, leaf number, root and leaf length also decreased with increase in salinity. Increasing salinity to 200 mM NaCl had no effect on growth parameters of *A. lagopoides* compared to control. Salt tolerance increased with the age of plants and after 30 days seedlings showed maximum growth inhibition in comparison to 90 days old plants (Debez et al., 2004). Lesser shoot length and fresh weight, but greater root length and dry weight were observed in 70 d plants of *A. lagopoides* and *Panicum hemitomon* grown in 16-48 dS m⁻¹ seawater concentrations (Hester et al., 2001; Joshi et al., 2004). Khan et al. (1999) showed that growth of *Halopyrum mucronatum* was promoted at low salinity (90 mM NaCl) but decreased with increase in salinity. Bodla et al. (1995) showed that *A. lagopoides* could grow in up to 110 dS m⁻¹ NaCl (1,500 mM NaCl). Mauchamp and Mésleard (2001) reported that growth of plants decreased by 50% in comparison to control at 0.75% (150 mM NaCl) NaCl and plants died at 2% (342 mM NaCl) NaCl. Other graminoid species like *Paspalum distichum* L. (Bodla et al., 1995), *Cyperus rotundus* L. (Shamsi & Ahmed, 1986), *Cynodon dactylon* (Kumar, 1990), *Cenchrus pennisetiformis* Hochst. and Steud; *Panicum turgidum* Forssk. (Ashraf & Naqvi, 1991) reported to survive at moderate salinities. Slower growth is a general adaptive feature for plant survival under stress, allowing to re-direct cell resources (e.g., energy and metabolic precursors) towards the defense reactions against stress (Zhu, 2001). Among the three species, we found that *U. setulosa* had the slowest growth, while *S. ioclados* showed robust growth in a short time and maximum growth was achieved in only 20 days (Gulzar et al., 2005) after salinity treatments in comparison to 45 and 60 days for *A. lagopoides* and *U. setulosa*, respectively (Gulzar et al., 2003ab).

Succulence is one of the mechanisms that halophytes utilize to deal with the high internal ion concentrations (Debez et al., 2004). In *Suaeda fruticosa* (L.) Forssk., shoot tissue water content at 200 mM external NaCl was higher than in non-treated controls, but it decreased at higher salt concentrations (Khan et al., 2000). Succulence expressed on a dry weight basis increased at 200 mM NaCl and then declined at the higher NaCl concentrations in *A. lagopoides* and *S. ioclados* but increased about two-folds in *U. setulosa*. Succulence plays a key role in the survival and maintenance of halophytes under saline conditions by maintaining positive turgor (Khan et al., 1999). These plants also maintained a high water and osmotic potential with progressively lower stomatal conductance with the increase in salinity. However, *A. lagopoides* maintained higher turgor, stomatal conductance and water and osmotic potential up to 600 mM NaCl as compared to the other two grasses. Salt inhibits growth due to stomatal closure subsequently reducing CO₂ uptake and limiting photosynthesis (Zhu, 2001). At high salinity

water content of plants decreases and plants lose turgor causing growth inhibition and increase in mortality. Khan et al. (1999) reported that *H. mucronatum* adjusted osmotically, maintaining a more negative osmotic potential than that of the medium though the differences became less with increasing salinity. Antlfinger & Dunn (1983) found that species growing in higher soil salinities had more xylem pressure potential than plants growing in less saline areas. Xylem pressure potential for graminoids ranged from -2.2 to -2.9 MPa. Our data showed much higher ranges of water potential while growing under high salinity.

Salinity inhibits and delays growth due to primary (ion imbalance and hyper osmotic effects) as well as secondary (decrease in water uptake followed by an increase in ion uptake) stresses (Zhu, 2001). Delayed reserve mobilization from cotyledons (Gomes Filho et al., 1983; Prisco, 1987) and membrane stability due to increased leakage of materials from the embryo axis (Prisco, 1987). At the highest concentrations tested i.e., 200 mM NaCl, growth of *Cakile maritima* was inhibited but some plants appeared to maintain tissue hydration by Na^+ compartmentalization (Debez et al., 2004) for maintaining the osmotic potential (Blumwald et al., 2000). Evidently, this was not sufficient to overcome the Na^+ toxicity, particularly to the meristematic tissue involved in new leaf production (Debez et al., 2004). *Aeluropus lagopoides* and *U. setulosa* increased succulence for maintaining turgor by absorbing large quantities of Na^+ . *Sporobolus ioclados*, however, lost tissue water with the increase in salinity and maintained higher K^+ , Ca^{2+} and Mg^{2+} and lower chloride uptake in shoot in comparison to other two species, however, it was not successful in overcoming the Na^+ toxicity probably due to poor rate of secretion through leaf glands.

Chrysothamnus nauseosus appears to tolerate Na^+ toxicity equally well as compared to *Sarcobatus vermiculatus* but only in periodically wet times (Dodd & Donovan, 1999). However, decreasing soil moisture even under low saline conditions is inhibitory to seedling growth but not for *Sarcobatus vermiculatus* which takes up Na^+ to continue its growth (Dodd & Donovan, 1999). Sodium uptake by high salt tolerant plants promotes the water potential gradient between seedling and substrate and thus enhances the seedling ability to maintain turgor for growth. In other words under natural conditions osmotic and ionic effects act individually as well as interact with soil moisture content in affecting plant establishment in saline desert soils. Additionally, the proportion of various ions in the soil has been known to increase the chances of success for seedling establishment and hence the species distribution. The presence of Ca^{2+} for instance is known to improve the Na^+ and Mg^{2+} tolerance in saline soils to varying degrees in different halophytic species (Tobe et al., 2002).

A high cytosolic K^+/Na^+ ratio is important for maintaining cellular metabolism. Under salt stress, Na^+ competes with K^+ for uptake into roots (Zhu, 2003). The K^+/Na^+ ratios were considered to be an effective index for salt tolerance in wheat (Poustini & Siosemardeh, 2004). Potassium-sodium ratio in roots of *Puccinellia tenuiflora* (alkali grass) decreased from 1.64 at 3 mmol/L to about 0.6 at 100 mmol/L NaCl and remained at this level up to 300 mmol/L NaCl salinity in the

culture solution and was higher than K^+ uptake of wheat at 0.37 (Peng et al., 2004). This higher uptake was found to be due to higher K^+/Na^+ selectivity of plasma membrane. A higher K^+ uptake under non-saline and saline conditions was observed in alkali grass, which indicated that a high K^+/Na^+ selectivity of potassium transport systems might be critical in plants salt tolerance. However, molecular evidence involving complex mechanisms at the cellular level would be required. Preference for K^+ over Na^+ did not appear to be a good predictor of plant salt tolerance in 10 forages tested in greenhouse cultures and each species had unique shoot ion concentrations (Grieve et al., 2004). The K^+/Na^+ ratio of the more salt tolerant grasses was lower than the less tolerant ones. In the present study, at all salinity levels, shoot and root of all the three grass species had high Na^+/K^+ that is K^+/Na^+ ratios of less than ~ 0.5 .

Grieve et al. (2004) found that K^+/Mg^{2+} relations of grasses differed from legumes and did not change with the increase in either the external salinity from 15-25 dS m^{-1} or with an increase in Mg^{2+} from 14-28 mM. Similarly, a 50% decrease in Ca^{2+}/Mg^{2+} ratio in substrate from 0.8 to 0.4 did not affect grass species in contrast to alfalfa plants which showed subsequent decrease in Ca^{2+}/Mg^{2+} . The adequate range of Mg^{2+} between species varied mainly due to its competition with K^+ uptake. Magnesium is also strongly competitive with Ca^{2+} and may displace Ca^{2+} from extracellular binding sites within plant organs to further disrupt metabolic availability of Ca^{2+} . Plant growth may be reduced, when the external Mg^{2+}/Ca^{2+} increases above 1 (Carter et al., 1979). Complex ion ratios and balances in the saline irrigation waters did not adversely affect plant nutrient status and, with the exception of broadleaf trefoil (*Lotus ulginosus*), none of the forages showed symptoms of ion toxicities or deficiencies. Many researchers have suggested that the K^+/Na^+ ratio in tissues of glycophytes should be >1 to supply the K^+ necessary for the normal functioning of metabolic processes (Ashraf, 1994; Maathuis & Amtmann, 1999). The K^+/Na^+ and K^+/Na^+ selectivity ratios did not appear to be good indicators of plant salt tolerance (Grieve et al., 2004).

Aeluropus lagopoides, *S. ioclados* and *U. setulosa* varied in their growth, water relations and ion uptake responses with increasing salinity. Grass species studied showed various combinations of strategies for combating high salinity probably linked to their native soil and moisture conditions, the inherent salt and drought tolerating mechanisms as well the ability for intra- and inter-specific competition, unique for each species. Grasses like *A. lagopoides* and *U. setulosa* are highly salt tolerant and could be cultivated using seawater irrigation. *Sporobolus ioclados* is relatively less salt tolerant and suited for areas where brackish water is available. *Aeluropus lagopoides* and *U. setulosa* are good candidates for landscape development in highly saline areas. *Sporobolus ioclados* would be ideal for dune stabilization with good seepage where less saline water is available. These grasses could also be used for forage and fodder.

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