

Full Length Research Paper

Effect of salinity on water relations of four turfgrasses

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Little information is available concerning turfgrass water relations characteristics in response to salinity. Two greenhouse studies were conducted at Colorado State University to determine if water relations characteristics were associated with salt tolerance of Kentucky bluegrass (KBG), tall fescue (TF), alkaligrass (AG), and saltgrass (SG). Grasses were grown in saline solution at 2.0, 4.7, 9.4, 14.1, 18.8, and 23.5 dS/m. Salinity reduced leaf water content (LWC) of all species. The pressure potential (Ψ_p) of KBG, TF, and AG decreased with increasing salinity, whereas SG Ψ_p did not change. Osmotic adjustment (OA) occurred in all grass species under salinity stress, however, in KBG and TF, the contribution of Na^+ and Cl^- to OA increased and these ions became the major contributors at high levels of salinity, whereas Na^+ and Cl^- contributions to OA in SG were maintained at stable levels. Saltgrass showed the highest proportion of K^+ at all levels of salinity than other grasses. As salinity increased, the contribution of unidentified osmolytes to OA increased in SG and decreased in KBG and TF. These interspecific differences in water relations may be, in part, attributed to the different salinity tolerance observed in these grasses.

Key words: Turfgrass, osmotic adjustment, Kentucky bluegrass, tall fescue, alkali grass, salt grass, leaf water potential, leaf osmotic potential, leaf pressure potential, salinity tolerance.

INTRODUCTION

The need for salt tolerant turfgrass has increased (Harivandi et al., 1992) because of salt accumulation in soils (Hoos, 1981), increased restrictions on the use of potable water for landscape irrigation (Devitt et al., 2004; Marcum, 2006; Lockett et al., 2008), and saltwater intrusion in the groundwater (McCarty and Dudeck, 1993; Murdoch, 1987). Turfgrass species and cultivars differ in their responses to salinity (Fu et al., 2005; Miyamoto and Chacon, 2006; Lockett et al., 2008; Shahba, 2010). In response to salinity, some plants can adjust osmotically to maintain growth and turgor. Osmotic adjustment under saline conditions can occur in plants by the uptake of inorganic ions from the medium, compartmentalizing ions in the cell vacuole, and balancing osmotic potential in vacuoles by the synthesis of compatible organic solutes in the cytoplasm (Ashraf and Harris, 2004; Qian and Fu, 2005; Abdel-Latef et al., 2009).

Proline in many halophytes, in particular grasses, has been suggested to be a compatible solute under saline conditions (Stewart and Lee, 1974; Abdel-Latef et al., 2009). Gorham et al. (1980) reported that the common

salt-marsh grass (*Puccinellia maritima* (Huds) Parl.) accumulated a high level of proline as a response to salt stress, and red fescue (*Festuca rubra* L.) and common salt-marsh grass accumulated sugars and proline under salt stress (Briens and Larher, 1982). Meanwhile, there is lack of information concerning the potential relationships between water relations and salinity tolerance of these selected grasses. Hence, the major objectives of this study were to: (1) examine water relations of KBG, TF, AG, and SG in response to salinity, and (2) determine if water relation characteristics were associated with salt tolerance for the selected grasses.

MATERIALS AND METHODS

Plant materials, growth conditions and salinity treatment

Two hydroponic experiments were carried out in a greenhouse at Colorado State University. 'Challenger' Kentucky bluegrass (*Poa pratensis* L.) (KBG), 'Arid' tall fescue (*Festuca arundinacea* Schreb) (TF), 'Fults' alkali grass (*Puccinellia distans* (L.) Parl.) (AG), and a

salt grass (*Distichlis spicata* (Torr.) Beetle) (SG) were planted into plastic cups (9 cm in diameter and 4 cm deep). The cups were filled with 1 cm layer of coarse, sterilized silica sand. The bottom of the cup was removed and covered with nylon screen to hold sand and allow roots to grow through. Twelve cups were placed into the holes of a plywood lid and suspended over a 50 liter tank, each tank containing 48 L of full strength Hoagland solution, which was replaced weekly. Air-stones connected to an electric pump provided aeration in each tank.

The greenhouse mean temperatures were maintained between 25°C day and 18°C night. Grasses were transplanted and grown for 8 weeks in non-saline water in order to achieve full establishment. One day before starting salinity treatments, roots were clipped at the base of the cups, giving a common baseline for subsequent root measurements, and shoots were clipped to a 3-cm height. After grasses were well-established, saline water (a mixture of 1 NaCl: 1 CaCl₂) at 0.2 (control), 4.7, 9.4, 14.1, 18.8, and 23.5 dS/m were used and to avoid salinity shock; salinity levels were gradually increased by daily increments of ~2.35 dSm⁻¹. After the targeted salinity levels were achieved, salinity treatments were continued for a period of 8 weeks.

Data collection

Leaf water content

Leaf water content (LWC) was measured 7 weeks after salinity treatments were imposed. To determine LWC, leaves were cut from plants and quickly placed in a clean, dry glass vial and capped. After determining fresh weight (FW), leaves were dried in an oven at 70°C for 24 h to determine dry weight (DW). The leaf water content was calculated as:

$$\text{LWC (\%)} = [\text{FW} - \text{DW} / \text{FW}] \times 100$$

Leaf water, osmotic and pressure potentials

Leaf water potential (Ψ_w) and leaf osmotic potential (Ψ_o) were measured 7 weeks after salinity treatments were imposed. To determine Ψ_w , leaf pieces along the mid-section of the leaf blades were cut and placed directly into clean and dried psychrometer sample cups. The sample cups were immediately sealed with parafilm and brought to the laboratory in a cooler. In the laboratory, the sample cups were loaded into the psychrometer wells (model SC10 A, Decagon Devices Inc., Pullman, WA), and Ψ_w was measured after 2 h vaporpressure equilibration (Brown and Collins, 1980). To determine Ψ_o , the sample cups containing leaf samples were unloaded from psychrometer wells, sealed with a parafilm and frozen at -20°C for at least 24 h (Voltaire and Thomas, 1995). After removal from the freezer and thawed for 30 min, the sample cups were immediately loaded into the psychrometer wells, and Ψ_o was determined after 2 h of equilibration. The leaf pressure (turgor) potential (Ψ_p) was calculated as the difference between Ψ_w and Ψ_o .

Osmotic adjustment

Osmotic adjustment (OA) was calculated as the difference in leaf osmotic potential at full turgor (Ψ^{100}_o) between non-stressed (one day prior to salinity treatment) and stressed leaves (7 weeks of salinity treatment). To determine Ψ^{100}_o , leaves were brought to full hydration by submerging them in distilled water for 4 h (Babu et al., 1999). Samples were gently wiped to remove external moisture. Fully hydrated samples were placed in microcentrifuge tubes and frozen at -20°C for at least 24 h. Frozen samples were thawed and

crushed in a hydraulic press to release plant sap, and Ψ^{100}_o was measured by a vapor pressure osmometer (Wescor model 5520, Wescor, Inc., Logan, UT).

Proline determination

The shoot's proline content was determined 7 weeks after the initiation of salinity treatments. Based on the method described by Bates et al. (1973), about 0.5 g leaf tissue was homogenized in 10 ml of 3% aqueous sulfosalicylic acid. After filtration, 2 ml of extract was reacted with 2 ml glacial acetic acid and 2 ml acid-ninhydrin in a test tube for 1 h at 97°C. The reaction mixture was cooled in an ice bath, 4 ml toluene was added, and it was mixed vigorously. The separated top toluene layer was used for proline measurement with a spectrophotometer (Beckman DU-50, Beckman Instruments, Inc. Fullerton, CA); proline concentration was presented as $\mu\text{mole proline/g FW}$.

Osmotic adjustment contributions

The relative contributions of ions and proline to whole cell OA were estimated using data on leaf sap ion concentrations, proline content, and sap Ψ_o as described in the Van't Hoff equation (Salisbury and Ross, 1992), assuming an osmotic coefficient of 1 for proline and 0.9 for ions (Lang, 1967). Leaf sap ion concentrations were determined 7 days prior to experiment termination. Intact leaves were thoroughly rinsed with distilled water to remove all external salt. After air drying, leaf samples were clipped and frozen with dry ice. Leaf samples were later thawed, and the sap was obtained using a hydraulic press. The sap was analyzed for sodium (Na), calcium (Ca), magnesium (Mg), and potassium (K) by inductively coupled plasma atomic emission spectrometry (ICP-AES). Chloride was determined with a Cl-selective electrode (Orion Ionplus Chloride combination electrode). Concurrent with leaf sap ion concentration sampling, leaves were sampled to determine sap Ψ_o . To determine sap Ψ_o , leaf pieces along the mid-section of the leaf blades were cut and placed directly into microcentrifuge tubes and frozen at -20°C for at least 24 h. Frozen samples were thawed and crushed in a hydraulic press to release plant sap, and sap Ψ_o was measured with a vapor pressure osmometer (Wescor model 5520, Wescor, Inc., Logan, UT).

Data analyses

A split plot design was used with salt treatment (tank) being the main plot, and grass species within each tank being the subplot. Each treatment had 3 replications. Since experiment (time) \times treatment interactions were not significant, data from both experiments were combined; therefore the number of replications was doubled. Combined data were analyzed by analysis of variance (SAS Institute 1989). The treatment means were separated by Fisher's protected LSD. Regression analysis was used to determine the relationships between each variable and the salinity level.

RESULTS

Increasing salinity reduced LWC for all grasses (Figure 1). Alkali grass and SG maintained a stable LWC as salinity increased from control to 9.4 dS/m, whereas LWC of TF decreased at salinity ≥ 4.7 dS/m. The leaf water content of KBG dramatically decreased with increasing

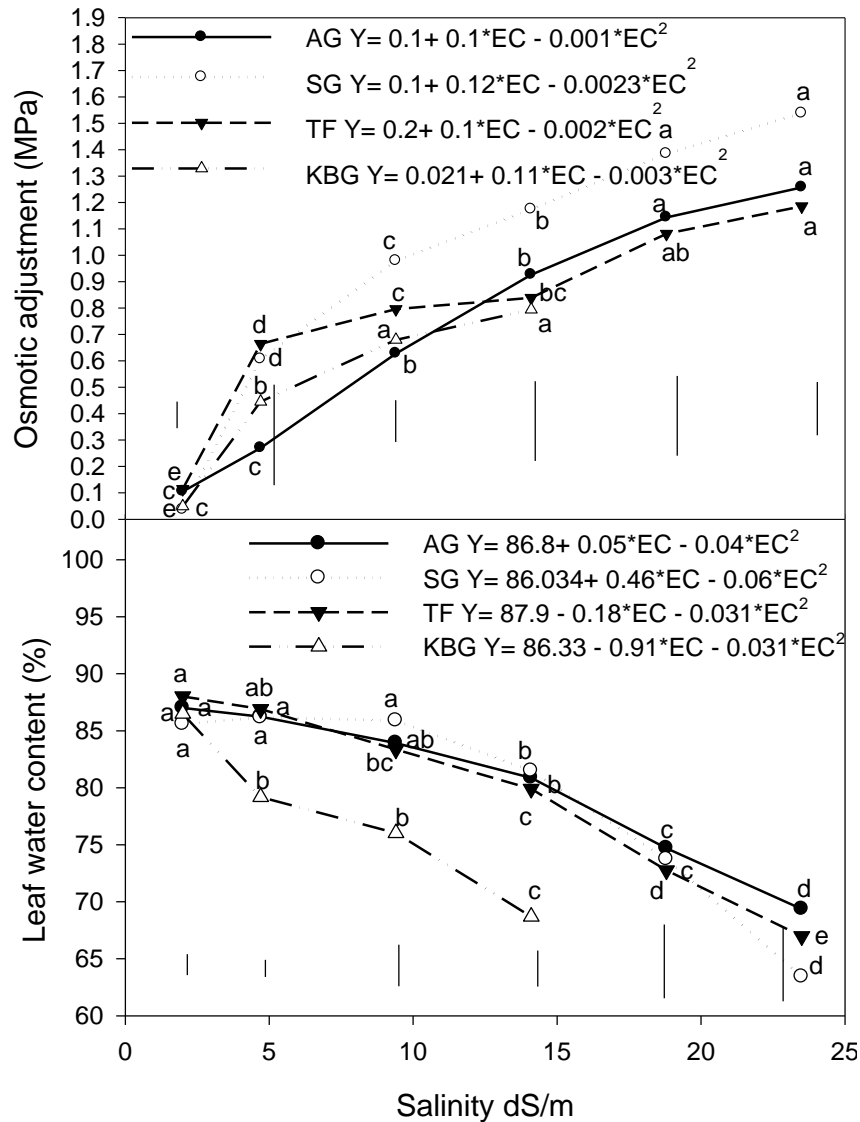


Figure 1. Leaf water contents of alkali grass (AG), salt grass (SG), tall fescue (TF), and Kentucky bluegrass (KBG) grown in saline solution at 2.0, 4.7, 9.4, 14.1, 18.8, and 23.5 dS/m. Vertical bars indicate least significant difference ($P=0.05$) among species within a given salinity level. Letters indicate significant difference ($P=0.05$) among salinity treatments for each species.

salinity. At ≥ 4.7 dS/m, SG, AG, and TF had significantly higher LWC than KBG. At 23.5 dS/m, AG had a higher LWC (69.4%) than SG (63.4%). Tall fescue maintained an intermediate LWC and was not statistically different from AG or SG at 23.5 dS/m. The leaf water potential and Ψ_o of all the species decreased as salinity level increased (Figure 2). However, the reduction rates were $AG < TF = SG < KBG$ for Ψ_w and $AG < TF < SG = KBG$ for Ψ_o .

However, salinity reduced Ψ_p of KBG, TF, and in AG relative to control, but Ψ_p of SG did not change as salinity level increased from control to 23.5 dS/m (Figure 2). At ≥ 14.1 dS/m, the Ψ_p of KBG was lower than those of TF,

SG, and AG; leaf pressure potential of TF and AG was lower than that of SG. The osmotic adjustment of all grasses increased significantly with increasing salinity (Figure 1). At 4.7 dS/m, TF exhibited greater OA than AG, and OA of SG and KBG was not different from that of either AG or TF. However, at ≥ 14.1 dS/m, OA in SG (1.17 MPa) was higher than in AG (0.93 MPa), TF (0.84 MPa), and KBG (0.79 MPa).

The shoot proline content of all grasses increased with increasing salinity (Table 1). When salinity was ≤ 9.4 dS/m, AG had 68 to 222% higher mean proline content than all other grasses. At 14.1 dS/m, AG had 262 and 23% higher proline than SG and TF, respectively, but did

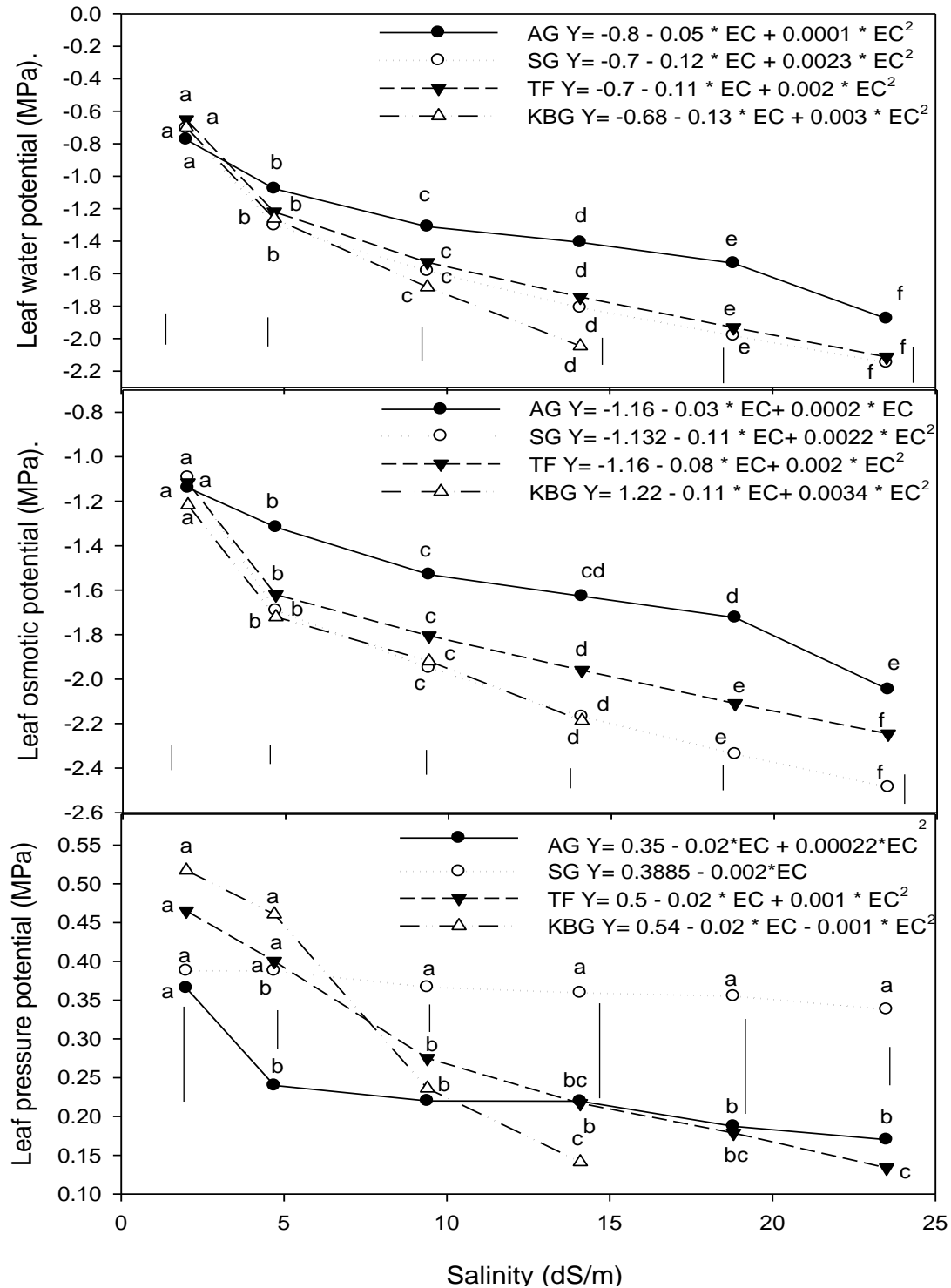


Figure 2. Leaf pressure potential, osmotic potential, and water potential of alkali grass (AG), salt grass (SG), tall fescue (TF), and Kentucky bluegrass (KBG) grown in saline solution at 2.0, 4.7, 9.4, 14.1, 18.8, and 23.5 dS/m. Vertical bars indicate least significant difference (P=0.05) among species within a given salinity level. Letters indicate significant difference (P=0.05) among salinity treatments for each species.

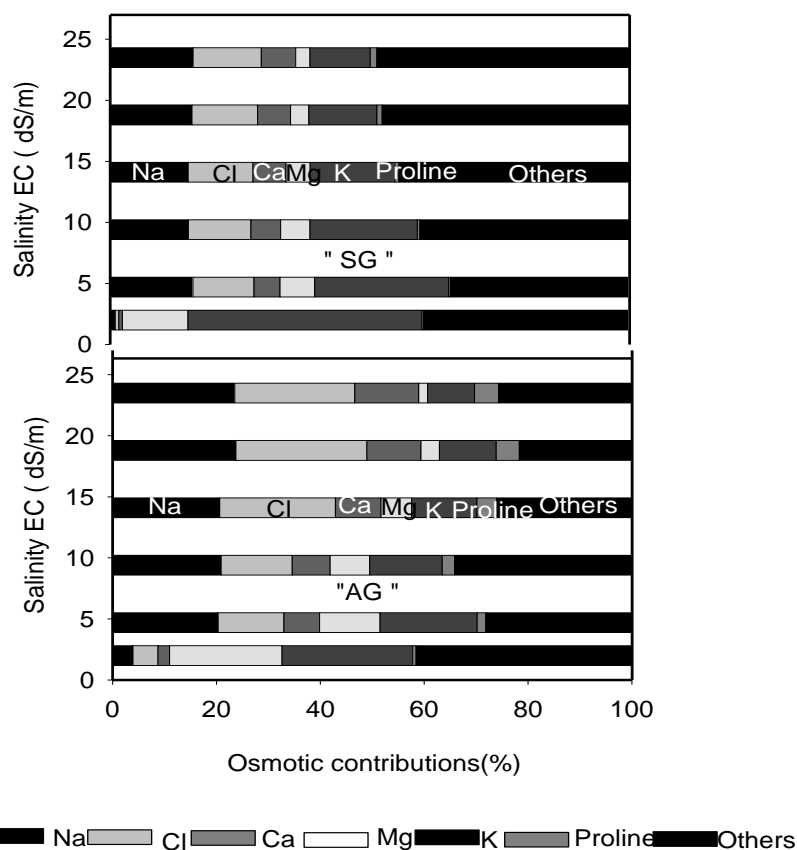
not differ from KBG for proline content. Salt grass produced the lowest proline content under salinity treatments. On the other hand, Kentucky bluegrass exhibited

lower proline content than other grasses under control conditions, but it increased almost 50-fold as salinity level increased from control to 14.1 dS/m, the relative

Table 1. Shoot proline contents ($\mu\text{mole/g FW}$) for alkaligrass, saltgrass, tall fescue, and Kentucky bluegrass exposed to different salinity levels.

Salinity (dS/m)	Alkaligrass	Saltgrass	Tall Fescue	Kentucky bluegrass
2.0	2.98 ^{fAZ}	1.41 ^{fB}	2.14 ^{eB}	0.48 ^{dC}
4.7	8.76 ^{eA}	2.54 ^{eC}	4.27 ^{eB}	4.40 ^{cB}
9.4	14.66 ^{dA}	3.76 ^{dC}	9.23 ^{dB}	10.18 ^{bB}
14.1	24.89 ^{cA}	6.88 ^{cC}	20.32 ^{cB}	23.37 ^{aA}
18.8	31.17 ^{bA}	9.45 ^{bC}	24.09 ^{bB}	-
23.5	38.42 ^{aA}	12.79 ^{aC}	26.68 ^{aB}	-
Significance	L ^{***}	L ^{***}	L ^{***}	L ^{**}

Lowercase letters indicate significant differences ($P=0.05$) among salinity treatments for each species. Uppercase letters indicate significant differences ($P=0.05$) among species within a given salinity level. *, **, and *** indicate significance of linear (L) or quadratic(Q) relationship at $P=0.05$, 0.01 , and 0.001 level, respectively.

**Figure 3.** Contributions of ions, proline and other solutes to the osmotic adjustment of alkali grass (AG), salt grass (SG) shoots at 2.0, 4.7, 9.4, 14.1, 18.8 and 23.5 dS/m.

contributions of proline to whole cell OA were estimated to be 3.8, 2.7, 2.5 and 0.8% in AG, KBG, TF, and SG, respectively, at 14.1 dS/m, and 4.7, 2.8, and 1.3% in AG, TF, and SG, respectively, at 23.5 dS/m (Figures 3 and 4).

In this experiment, we also determined leaf sap ion content (data not presented). The concentration of Na^+ and Cl^- in the shoot sap increased rapidly as salinity

increased. In KBG and TF, the contribution of Na^+ and Cl^- to osmotic adjustment increased as the level of salinity increased, and became the major contributors at high levels of salinity. The contribution of Na^+ and Cl^- in KBG was 58% at 14.1 dS/m and 46% in TF at 23.5 dS/m. In SG, however, Na^+ and Cl^- contribution to OA were stable (15% by Na and 13% by Cl) as salinity increased from

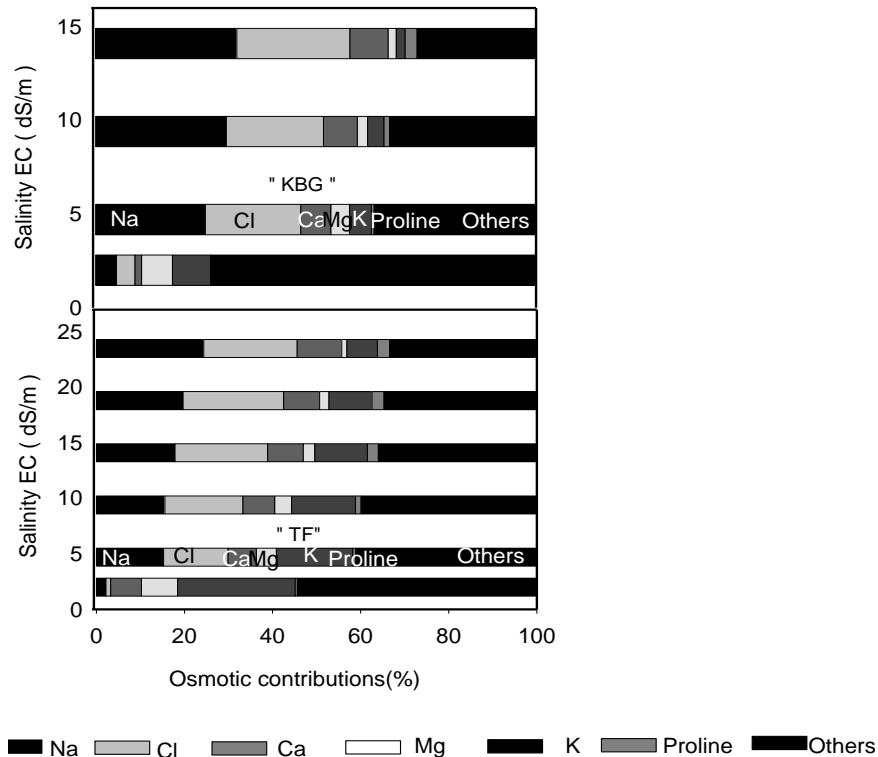


Figure 4. Contributions of ions, proline and other solutes to the osmotic adjustment of tall fescue (TF), and Kentucky bluegrass (KBG) shoots at 2.0, 4.7, 9.4, 14.1, 18.8, and 23.5 dS/m.

4.7 to 23.5 dS/m. Under non-saline condition, potassium was the major contributor compared with other ions in all grasses, but its contribution declined as salinity increased. Salt grass had the highest proportion of K^+ at all levels of salinity than did other grasses. The proportion of K^+ to OA in AG and TF was lower than in SG but higher than KBG. As salinity increased, the contribution of unidentified osmolytes to OA increased in SG and decreased in KBG and TF. The trend of the change in OA contribution by the unidentified osmolytes in AG was not clear.

DISCUSSION

Shoot dehydration and loss of turgor are common responses of plants to salinity (Neumann et al., 1988; Wyn Jones, 1981; Marcum and Murdoch, 1994). In this study we found that, the slope of LWC decrease was greatest for $KBG > TF = AG > SG$ as salinity increased from 2.0 to 23.5 dS/m. The relative slope of LWC reduction was associated with the relative effect on shoot growth reduction ($r = 0.65$), indicating that salinity tolerance may, in part, be attributed to the ability of plants to maintain a desired tissue hydration level. Leaf water content was also negatively correlated with leaf firing ($r = -0.76$) and positively correlated with turf quality ($r = 0.84$).

Reductions of Ψ_W and Ψ_O in our study were in agreement with results of Ackerson and Youngner (1975) with Bermuda grass (*Cynodon dactylon* L.); Peacock and Dudeck (1985) with Seashore pappasium (*Pappasium vaginatum* Swartz); Dudeck et al. (1993) with St. Augustine grass (*Stenotaphrum secundatum* Walt.) cultivars; and Qian et al. (2001) with two Kentucky bluegrass cultivars. The Ψ_W of KBG decreased more than Ψ_O , resulting in a loss of Ψ_P ; at 14.1 and 23.5 dS/m, SG maintained the highest; AG and TF the intermediate, and KBG had the lowest Ψ_P . The greater ability to maintain LWC and Ψ_P in SG, AG, and TF than in KBG could result from root growth stimulation of SG and AG and the extensive root system of TF under saline conditions, which likely contributed to more efficient water and nutrient uptakes. The severe shoot growth reduction of KBG under high salinity may be associated with the greater degree of tissue dehydration and the loss of turgor. Leaf turgor or cell volume maintenance has been suggested to be essential for sustained growth and development (Greenway and Munns, 1980; Munns and Termaat, 1986). Rajasekaran et al. (2000) stated that there is a significant correlation between Ψ_P and salt tolerance index in *Lycopersicon* spp. exposed to saline conditions.

As a response to salinity, plants in saline environments must adjust osmotically (Yeo, 1983). Osmotic adjustment is defined as the net accumulation of solutes in a cell in

Table 2. Pearson correlation coefficients for leaf proline (PR), relative shoot dry weight (SH), relative root dry weight (RO), relative root length (RL), root to shoot ratio (R/S), leaf firing (LF), turf quality (TQ), leaf water content (WC), leaf water potential (WP), leaf osmotic potential (OP), leaf pressure potential (PP), and osmotic adjustment (OA).

Parameter	WC	WP	OP	PP	OA	LF	TQ	SH	RO	RL	R/S
PR	-0.75***	-0.68***	-0.54***	-0.87***	0.58***	0.88***	-0.75***	-0.78***	-0.51***	-0.36*	0.68***
WC		0.88***	0.81***	0.65***	-0.78***	-0.76***	0.84***	0.65***	0.46***	0.54***	-0.29*
WP			0.98***	0.66***	-0.96***	-0.65***	-0.85***	0.58***	0.25 ^{ns}	0.21 ^{ns}	-0.37*
OP				0.48***	-0.95***	-0.59***	0.79***	0.52***	0.12 ^{ns}	0.14 ^{ns}	-0.15 ^{ns}
PP					-0.56***	-0.87***	0.74***	0.74***	0.47***	0.39**	-0.64***
OA						0.57***	-0.74***	-0.43**	-0.02 ^{ns}	-0.05 ^{ns}	0.28*
LF							-0.95***	-0.96***	-0.88***	-0.79***	0.39**
TQ								0.92***	0.67***	0.76***	-0.14 ^{ns}
SH									0.92***	0.85***	-0.44**
RO										0.89***	-0.11 ^{ns}
RL											0.08 ^{ns}

ns, *, **, and *** indicate non-significant or significant of correlations at $P = 0.05$, 0.01 , and 0.001 level, respectively ($n = 132$).

response to a fall in Ψ_w , independent of the effect of solute concentration due to tissue water loss (Turner and Jones, 1980). Osmotic adjustment under saline conditions can occur in plants due to the uptake of inorganic ions and compartmentalization of them in the cell vacuole (this is important to avoid enzyme deactivation), or by internal synthesis of organic solutes (compatible solutes) in the cytoplasm, or more generally by a combination of both. Osmotic adjustment solves several problems in cells (Morgan, 1984) as it helps to maintain turgor and cell volume, and maintains enzyme function due to the accumulation of compatible solutes in the cytoplasm. Our results, however, indicated that OA occurred in all grass species under salinity stress, even in salt sensitive KBG and the relative OA was negatively associated with salinity tolerance based on relative growth reduction and turf quality rating (Table 2).

Estimation of various components of whole cell OA indicated that in the most salt tolerant grass in our study, the OA contributed by Na^+ and Cl^- was stable as salinity increased from 4.7 to 23.5 dS/m. However, the proportion contributed by unidentified osmolytes increased with increasing salinity in SG. This result indicated that the ion homeostasis was maintained for up to 23.5 dS/m in SG. It seems that one of the major advantage of the more salt tolerant SG and AG over salt sensitive KBG in this study were not because of the degree of OA per se, but because of the more responsive control of Na^+ and Cl^- uptake and/or partition, and the more effective capacity to coordinate the increasing Na^+ and Cl^- with the synthesis of compatible solutes, which do not inhibit normal metabolic reaction. The accumulation of non-toxic ions (K^+) and organic solutes (not identified in our study) in the cytoplasm can balance cytoplasmic Ψ_o with that of the vacuole, and protect cytoplasmic enzymes against inactivation by inorganic ions (Pollard and Wyn Jones, 1979; Wyn Jones, 1984; Ball et al., 2002; Qian and Fu,

2005).

Proline is the most frequently reported solute accumulated in salt stressed plants (Wyn Jones, 1984;). The physiological significance of proline accumulation is controversial; some reported that it represents a form of injury, while others suggested that proline acts as a compatible solute. Although shoot proline content of KBG, TF, SG, and AG significantly increased with increasing salinity (Table 1), results of OA measurement indicated that proline made insubstantial cytoplasmic osmotic contributions in all grass species. Furthermore, proline was positively correlated with leaf firing ($r = 0.88$) and negatively correlated with turf quality ($r = -0.75$) (Table 2), and the most salt tolerant SG exhibited the lowest proline content in comparison with other grasses. Similar findings were reported by Huang and Redman (1995) who stated that proline appeared to be insufficient to influence leaf osmolality of barley cultivars since it accounted for less than 1% of the total osmotica. These results suggest that proline accumulation may be as a result of salt injury. However, alkali grass is an apparent exception in that salt injury was minimal under conditions leading to high proline content. Torello and Rice (1986) have reported that among cool season turfgrass species, AG had the highest proline content compared to red fescue and KBG. Therefore, proline accumulation is likely stress consequences in KBG, TF and SG, but may play a role as a compatible solute in AG. The results obtained also showed that salt grass seems to have higher ability for water uptake under physiological drought conditions by decreasing water potential along with decreased leaf osmotic potentials besides other factors that might have helped to maintain this osmotic balance.

In conclusion, this study demonstrated the different effects on water relations among the four turf grass species used here. The differences in salt tolerance among these species may be attributed to maintenance

of high LWC, Ψ_P , and accumulation of compatible solute. These water relation characteristics may play significant role in plants in coping with high salt concentration.

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