Effects of Salinity on Seashore Paspalum Cultivars at Different Mowing Heights

Mohamed A. Shahba,★ Saad F. Alshammary, and Mohamed S. Abbas

ABSTRACT

The objective of this research was to evaluate the effects of salinity on turf quality, clipping yield, root mass, canopy photosynthetic rate (Pn), total nonstructural carbohydrate content (TNC), shoot reducing sugar content (RSC), proline content, and K^+/Na^+ in shoots and roots of seashore paspalum (*Paspalum vaginatum* Swartz) cultivars (Salam, Excalibur, and Adalayd). These cultivars were evaluated at different mowing heights using a hydroponics system in the greenhouse. Salam achieved 11.9, 24.2, 36.5, and 55.7% more clipping yield than Adalayd at 0, 16, 32, and 44 dS m^{-1} salinity levels, respectively, under the highest mowing level. At the highest mowing height, the root mass of Salam, Excalibur, and Adalayd increased by 162.9, 170.0, and 204.0%, respectively, as salinity increased from 0 to 44 dS m^{-1}. The values of Pn in Salam were the highest (16.66, 19.89, and 25.85 µmol CO_2 M^{-2} S^{-1} at 25-, 35-, and 45-mm mowing heights, respectively) at 44 dS m^{-1}. The TNC decreased by 44.2, 29.2, and 25.5% in Salam while RSC increased by 49.3, 44.3, and 40.3% at 25-, 35-, and 45-mm mowing heights, respectively, as salinity increased from 0 to 44 dS m^{-1}. In Salam, as salinity levels increased from 0 to 44 dS m^{-1}, proline content increased by 417.7, 429.5, and 438.7% at 25-, 35-, and 45-mm mowing heights, respectively. Paspalum had its highest selectivity of K^+/Na^+ when maintained at 45-mm mowing height. Salinity tolerance of seashore paspalum cultivars can be enhanced by increasing mowing height.

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Abbreviations: EC, electrical conductivity; Pn, canopy photosynthetic rate; RSC, shoot reducing sugar content; TNC, total nonstructural carbohydrate content.

S ALINITY IS A MAJOR FACTOR affecting turfgrass sites in arid and semiarid regions where soil salinity is high and precipitation is limited. Worldwide, salt-affected soils impact nearly 10% of the land surface (Carrow and Duncan, 1998; Rengasmy and Olsson, 1991). The main effects of salinity on turfgrass growth include osmotic stress, ion toxicity, nutritional disturbances (Greenway and Munns, 1980; Lauchli, 1986; Cheeseman, 1988), damage to photosynthetic systems by excessive energy (Brugnoli and Bjorkman, 1992), and structural disorganization (Flowers et al., 1985).

In Egypt, salt-related problems have increased where turfgrass is managed, especially during the last 30 yr as new urban communities are established. Tourism development in Egypt's north coast, specifically between Alexandria and Al-Alamein, is also growing rapidly, and extensive use of turfgrass is occurring while at the same time potable water is limited. Accordingly, the need for salt-tolerant turfgrasses has increased.

Turfgrass species, and cultivars within a species, vary in their salinity tolerance. These variations probably result from genetic variations, especially in genes relating to salinity tolerance

mechanisms and their interaction with environments (Duncan and Carrow, 1999). Seashore paspalum (*Paspalum vaginatum* Swartz) has demonstrated superior salt tolerance compared to other turfgrasses (Peacock and Dudeck, 1985; Marcum and Murdoch, 1990; Shahba, 2010a). It has considerable interspecific diversity for various environmental stresses, including salinity, drought, wear, pests, and soil acidity (Duncan, 1999; Trenholm et al., 1999; Lee et al., 2004b).

The interaction of soil salinity and close mowing has been shown to cause a severe decline in turf quality (Suplick–Ploense et al., 2002; Fu et al., 2005; Shahba, 2010b). Close mowing has been shown to cause reductions in turf quality (Salaiz et al., 1995; Shahba, 2010b), root production (Krans and Beard, 1975; Salaiz et al., 1995; Shahba, 2010b), photosynthesis (Krans and Beard, 1975; Hull, 1987; Liu and Huang, 2003; Shahba, 2010b), and total nonstructural carbohydrate content (Huang and Fry, 1999; Shahba, 2010b). The balance between carbohydrate production and consumption will impact the ability of turfgrass species to cope with salinity stress (Huang and Fry, 1999; Lee et al., 2008a, 2008b), while the decline in salinity tolerance under close mowing can be associated with reduced carbohydrate availability and lessened effectiveness of Na^+ exclusion and K^+ active uptake and transport (Qian and Fu, 2005; Lee et al., 2007; Shahba, 2010b).

Proline accumulates in larger amounts than other amino acids in salt-stressed plants (Lee et al., 2008b). Proline accumulation is the first response of plants exposed to salt stress and water–deficit stress to reduce injury to cells (Ashraf and Foolad, 2007). Maggio et al. (2002) suggested that proline may act as a signaling/regulatory molecule, able to activate multiple responses that participate in the adaptation process to elevated salinity levels. Rapid accumulation of proline in tissues of many plant species in response to salt, drought, or temperature stress has been attributed to enzyme stabilization and/or osmoregulation (Flowers et al., 1977; Levitt, 1980). Ahmad et al. (1981) measured proline content fluctuations under high salinity levels in salt-tolerant and –sensitive ecotypes of creeping bentgrass (*Agrostis stolonifera* L.) and concluded that the salt-tolerant ecotype accumulated more proline in response to high salinity levels. Lee et al. (2008b) concluded that proline was the primary organic osmolyte for osmotic adjustment and proline accumulation was higher in salt-tolerant seashore paspalum genotypes. However, some other reports indicated no positive or even negative effect of proline on salinity tolerance. Marcum (2002) mentioned that proline accumulates in grasses under salinity stress with insufficient content to achieve osmotic adjustment. Torello and Rice (1986) concluded that proline accumulation has no significant osmoregulatory role in salt tolerance of five turfgrass species ('Fults' alkaligrass [*Puccinellia distans* (Jacq.) Parl.], 'Dawson' red fescue [*Festuca rubra* L. var. *trichophylla* Ducros ex Gaud.], 'Jamestown' red

fescue [*Festuca rubra* L. var. *commutata* Gaud.], 'Adelphi' and 'Ram I' Kentucky bluegrass [*Poa pratensis* L.]) following their exposure to 170 mM NaCl salinity stress. Because of these contrasting reports on the role of proline in salt tolerance, its use as selection criterion for salt tolerance has been questioned (Ashraf and Harris, 2004) and, as a result, proper testing is required before making any conclusion regarding proline role in salinity tolerance in any specific species.

Turfgrass managers suggested a mowing height range of 25 to 50 mm for seashore paspalum cultivars. However, mowing at 25 mm or less is a better option because the reduction in mowing height increases turf density and produces plants with shorter internodes. Mowing heights above 50 mm reduce turfgrass density and increase thatch (Lee et al., 2002, 2004c; Brosnan and Deputy, 2009). In a companion study, Shahba (2010a) noted that, mowing at 25.0-mm height, the cultivar Salam showed acceptable quality at the salinity level of 32.0 dS m^{-1}, the cultivar Excalibur showed acceptable quality at the salinity level of 16.0 dS m^{-1}, while Adalayd did not show acceptable quality at either of these tested salinities. No published information is available that addresses the influence of mowing height and frequency on seashore paspalum salinity tolerance. Most studies comparing salinity tolerance among different grass species have been conducted under a single mowing regime or under unmowed conditions (Youngner et al., 1967; Marcum, 2001; Qian et al., 2004; Shahba, 2010a). The interaction effects of salinity and mowing on seashore paspalum are not well understood. Knowledge of these effects would help to identify physiological factors involved in salinity and close mowing tolerance, leading to better management of seashore paspalum turf sites.

The objective of this study was to examine the effects of salinity on turf quality, growth response, canopy photosynthesis (Pn), proline content, total nonstructural carbohydrate content (TNC), shoot reducing sugar content (RSC), Na^+/K^+ ratio in shoots, and roots of three seashore paspalum cultivars commonly used in Egypt at three mowing heights.

MATERIALS AND METHODS
Plant Materials and Growth Conditions

Sod pieces (10 cm in diam.) of seashore paspalum cultivars Salam, Excalibur, and Adalayd were collected from different golf courses in Egypt. After removing soil by hand-washing, sod pieces were planted into 144 plastic cups (48 cups per cultivar). These cups (10 cm in diam. by 5 cm deep) were filled with coarse, acid-washed silica sand. The cup bottom was removed and covered with nylon screen to hold sand and allow roots to grow through. The cups were placed into holes of a 2.0-cm-thick plywood lid suspended over a tank containing 15.0 L of constantly aerated full-strength Hoagland solution. Full-strength Hoagland solution was used to produce maximum growth (Kang and van Iersel, 2004). The nylon screen bottom of each cup was submersed 3.0 cm into the solution. A total of

16 tanks were used, with each accommodating nine cups, representing each of the three mowing heights for each of the three cultivars. Plants were grown in the greenhouse with the daytime temperature ranging from 25.0 to 30.0°C, within optimal ranges for warm-season grasses (Beard, 1982), and nighttime temperature ranging from 20.0 to 25.0°C. Photosynthetically active radiation above the canopy at 1000 h was approximately 1000 μmol m^{-2} s^{-1}. Plants were grown for 2 mo, allowing root and canopy to establish before treatments were imposed. During this 2-mo period, turf in one-third of the cups was hand-clipped every 2 d at 50.0 mm. Turf in the remaining cups was clipped to the lower mowing height treatments, with clipping occurring gradually to avoid scalping. Before treatment initiation, roots were clipped off at the base of the cups.

Treatments

Salinity treatments were applied to each tank by adding equal weights of $CaCl_2$ and NaCl gradually during a 10-d period to obtain electrical conductivity (EC) values of 2.2 (control), 16.0, 32.0, and 44.0 dS m^{-1} measured at 25°C by an Orion EC meter (Model 160, Boston). The EC and pH values were checked every 2 d to assure stability and adjustment were made as needed. The pH of the nutrient solution ranged from 6.0 to 6.5. Nutrient solutions were changed weekly, preventing any change in treatment levels. Concurrent to the initiation of the salinity treatments, mowing treatments were started. Mowing treatments included hand-clipping one time weekly at 45.0 mm, two times weekly at 35.0 mm, and three times weekly at 25.0 mm. Treatments continued for 4 mo. The experiment was conducted once in August 2008 and repeated in August 2009.

Measurements

Collected data were turf quality, clipping yield, root dry weight, Pn, TNC, RSC, proline, and tissue Na$^+$ and K$^+$ content for each treatment.

Visual turf quality was rated biweekly based on color, density, and uniformity using a scale of 0 (brown, dead turf) to 9 (optimum color, density, and uniformity), with a rating of 6.0 or higher indicating acceptable quality. Clipping yield was determined every 2 wk by collecting clippings, determining oven-dried mass, and then calculating daily growth. At the end of the experiment, all roots were harvested at the base of each cup and root mass was determined.

Canopy net photosynthetic rate was measured biweekly between 1000 and 1500 h with a portable CO_2 gas analyzer system (Model CI-301, QC CID, Inc., Vancouver, WA). During each measurement, the whole turf canopy of individual cups was enclosed in a transparent Plexiglas chamber (7.6 cm in height and 10 cm in diam.) for 2 min. The canopy chamber was attached to the CO_2 gas analyzer system to determine CO_2 uptake. Canopy net photosynthetic rate was expressed as CO_2 uptake per unit canopy area.

The TNC content, RSC, tissue Na$^+$ and K$^+$, and proline contents were determined at the termination of the experiment. Aboveground tissues (shoots and stolons) were harvested and washed with cold distilled water to remove plant debris for carbohydrate analysis. Then, approximately 5 g of samples were freeze-dried (Genesis 25 LL Lyophilizer, Virtis, Gardiner, NY). After freeze-drying, samples were ground with a Wiley mill,

sieved through a screen with 425-μm openings, and kept in airtight vials at -20°C. The TNC content was measured using the method described by Chatterton et al. (1987). In brief, 25 mg of freeze-dried samples were transferred to 5 mL 0.1% (w/w) clarase solution and incubated at 38°C for 24 h. Then, 0.5 mL of hydrochloric acid (50% [v/v]) was added to the incubation solution. After the solution was incubated at room temperature for 18 h, the pH value of the solution was adjusted to between 5 and 7 with 10 and 1 M NaOH. This solution was used to determine TNC content using a spectrophotometer at 515-nm wavelength (Model DU640, Beckman).

To measure the free reducing sugar, 25 mg of the freeze-dried, ground, and sieved sample was extracted with 10 mL 0.1 M phosphate buffer (pH = 5.4) for 24 h at room temperature. An extracted aliquot (0.2 mL) was used to determine the reducing sugar content by using the same method as was used to measure TNC.

To measure ion content, about 5 g of shoots and roots were harvested, washed with deionized water, and dried at 70°C for 24 h. Dried shoots and roots were ground in a Wiley mill to pass through a screen with 425-μm openings. Approximately 1 g of screened and dried sample was weighed and ashed for 7 h at 500°C. Ash was dissolved in 10 mL of 1 M HCl and diluted with deionized water. Solution aliquots were analyzed for Na$^+$ and K$^+$ by inductively coupled plasma atomic emission spectrophotometry (Model 975 Plasma Atomcomp, Thermo Jarrell Ash Corp., Franklin, MA).

Actual proline tissue accumulation levels were determined according to the method of Bates et al. (1973) as modified by Torello and Rice (1986) with approximately 0.5 g fresh weight of tissue. Samples were ground with liquid nitrogen in a mortar. Each sample was homogenized in 10 mL of 3% (w/w) aqueous sulfosalicylic acid followed by agitation for 1 h before filtration through No. 2 Whatman filter paper. After filtration 2 mL of extract from each sample was reacted with 2 mL of ninhydrin reagent (1.25 mg ninhydrin in 30 mL of glacial acetic acid and 20 mL of 6 M H_3PO_4) and 2 mL of glacial acetic acid followed by 1 h of heating at 100°C in an enclosed water bath. Samples were then quickly cooled by immersion in an ice bath and total proline was determined spectrophotometrically at 520 nm. Actual proline tissue accumulation levels were determined by subtracting mean control data from salinity treatments data for all cultivars during the entire experimental period.

Statistical Analysis

A split-split plot experimental design was used with salinity treatment being the main plot, mowing heights being the subplots, and cultivars being the sub-subplot factor. Each treatment had four replications. The data of the two experiments were subjected to ANOVA to test the experiment effect and the interaction between treatments and experiments. The experimental run was not significant. Therefore, data were pooled over experiments to test the effects of salinity, mowing, cultivar, and their interactions using ANOVA (SAS Institute, 2006). Turf quality and clipping yield were analyzed on individual measurement dates to examine salinity, mowing, and cultivar effects over time. Because significant interaction of mowing regime and salinity level was often observed, comparisons of salinity treatments within individual mowing heights are

presented and means were separated by least significant difference at the 0.05 level of probability. Regression analysis was performed to determine the relationship between the measured parameters at the end of the study (dependent variables) and the salinity levels (independent variable). Analysis of covariance was used to test the variations among Pn vs. salinity levels and both mowing heights and cultivars (SAS Institute, 2006).

RESULTS AND DISCUSSION
Turf Quality

Comparisons of turf quality among cultivars, different mowing heights, and salinity levels clearly showed significant differences (Table 1). All treatments exhibited desirable turf quality (ranged from 8 to 9 on a 0-to-9 scale, 9 = the best) at the beginning. With higher salinity, turf quality declined over time to unacceptable ratings (below 6). Turfgrass quality (at higher salinity) declined more rapidly and severely at lower mowing heights. In Salam, quality declined to the unacceptable rating of 4 and 5.2 when mowed to 25 and 35 mm, respectively, while quality was 6.0 at the mowing height of 45 mm under the salinity level of 44.0 dS m^{-1} (Fig. 1).

Turf quality decreased linearly with increasing salinity level under the three mowing heights. Regressions were strongly linear, with slope more negative at 25.0 mm than at either 35.0 or 45.0 mm (Table 2). Under all mowing heights, none of the cultivars showed an acceptable turf quality (rating of 6) at the highest salinity level of 44.0 dS m^{-1}, except for Salam, which showed acceptable quality when mowed at the highest height of 45 mm. At the salinity level of 32.0 dS m^{-1}, Salam showed acceptable quality at all mowing heights while Excalibur showed an acceptable quality (above 6) only at the higher mowing heights of 35.0 and 45.0 mm. Adalayd did not show acceptable quality at any mowing height at the salinity level of 32.0 dS m^{-1}. Adalayd showed acceptable quality at the salinity level of 16 dS m^{-1} only at the higher mowing heights of 35 and 45 mm (Fig. 1).
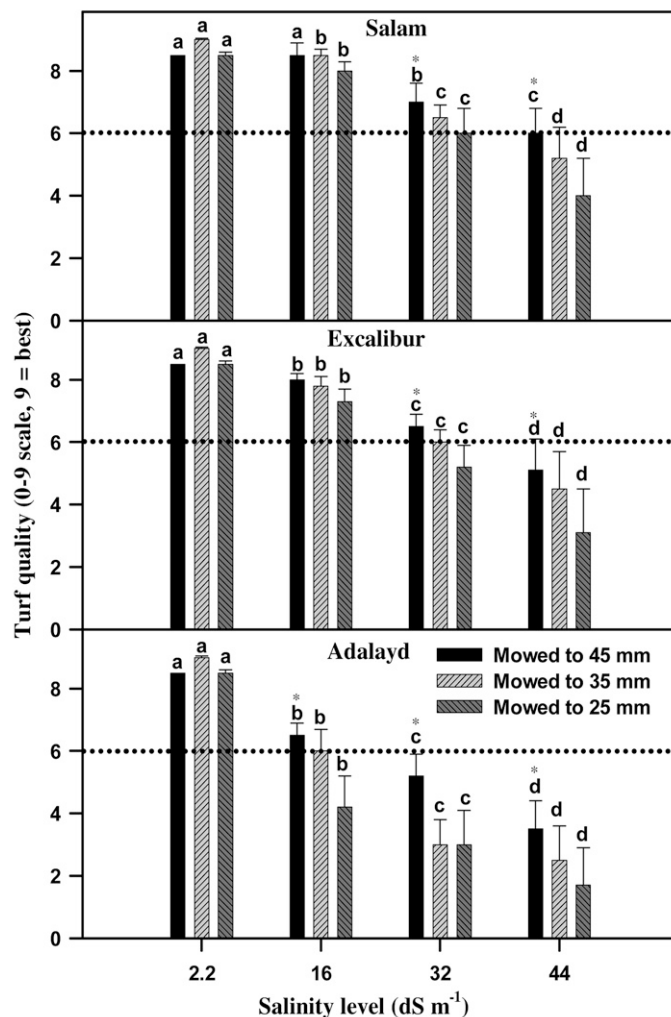

Figure 1. Effect of different salinity levels on turf quality of three seashore paspalum cultivars at 25-, 35-, and 45-mm mowing heights. Columns labeled with the same letters are not significantly different at $P = 0.05$ within the same mowing height. Columns labeled with an asterisk are significantly higher ($P = 0.05$) for mowing heights comparison within each salinity level. Vertical bars at the top of the columns represent standard error of the means. Dotted lines indicate the acceptable quality rating.

Table 1. Analysis of variances with mean square and treatment significance of turf quality (TQ), clipping yield (CY), root mass (RM), total nonstructural carbohydrate content (TNC), shoot reducing sugar content (RSC), proline content, root and shoot K$^+$ and Na$^+$ contents, and canopy photosynthetic rate (Pn) in seashore paspalum cultivars.

Source	TQ	CY	RM	Pn	TNC	RSC	Proline content	K$^+$		Na$^+$	
								Root	Shoot	Root	Shoot
	0–9 scale	mg cup^{-1} d^{-1}	mg cup^{-1}	μmol CO$_2$ m^{-2} s^{-1}	— mg g^{-1} dry wt. —		μg g^{-1} fresh wt.	————— mg g^{-1} dry wt. —————			
Cultivars (C)	8.1**	1.28**	3.68**	37.9**	7722**	33,111**	31,256**	145.0**	18,500**	45.0**	87,650**
Mowing height (H)	7.8*	1.17**	2.66**	57.6**	5421**	3,355**	2,113**	101.0**	33,200**	89.0**	67,685**
Salinity (EC)	66.5**	4.22**	4.22**	90.0**	988**	897**	1,056**	664.0**	188,000**	982.0**	33,557**
C × H	6.4*	0.16*	0.12*	42.8*	2355*	1,012*	1,200*	72.0*	9,980*	49.0*	6,521*
EC × H	5.4*	2.8*	2.22*	38.9*	626*	366*	355*	265.0*	8,650*	254.0*	9,754*
EC × C	76.5*	1.2*	2.45*	35.4*	562*	36.7*	56.9*	334.0*	8,745*	454.0*	10,897*
C × EC × H	0.06 NS†	0.07 NS	0.15 NS	9.7 NS	43.0 NS	25.6 NS	32.2 NS	28.0 NS	2,344 NS	54.0 NS	4,689 NS

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

† NS, not significant.

Table 2. Linear regression of different parameters of seashore paspalum cultivars measured at the end of the experiment vs. salinity.

Cultivar	Mowing height	Quality Regression	R^2	Clipping yield Regression	R^2	Root mass Regression	R^2
	mm	——— 0–9 scale ———		——— mg cup^{-1} d^{-1} ———		——— mg cup^{-1} ———	
Salam	25	$Y = 8.99 - 0.06X$	0.90**	$Y = 148.0 - 0.99X$	0.87**	$Y = 467.4 + 13.7X$	0.62*
	35	$Y = 9.56 - 0.09X$	0.96**	$Y = 138.1 - 1.19X$	0.86**	$Y = 418.5 + 12.9X$	0.95**
	45	$Y = 9.20 - 0.11X$	0.94**	$Y = 132.95 - 1.52X$	0.98**	$Y = 360.5 + 13.1X$	0.97**
Excalibur	25	$Y = 8.98 - 0.08X$	0.96**	$Y = 142.4 - 1.2X$	0.94**	$Y = 431.9 + 11.9X$	0.59*
	35	$Y = 9.37 - 0.11X$	0.99**	$Y = 125.3 - 1.3X$	0.98**	$Y = 382.1 + 11.5X$	0.66**
	45	$Y = 9.06 - 0.13X$	0.98**	$Y = 111.8 - 1.36X$	0.99**	$Y = 323.3 + 11.8X$	0.94**
Adalayd	25	$Y = 8.63 - 0.12X$	0.99**	$Y = 131.7 - 1.88X$	0.92**	$Y = 390.2 + 11.4X$	0.55*
	35	$Y = 8.92 - 0.16X$	0.95**	$Y = 111.8 - 1.83X$	0.95**	$Y = 302.1 + 11.8X$	0.87**
	45	$Y = 7.95 - 0.15X$	0.90**	$Y = 93.4 - 2.13X$	0.90**	$Y = 235.9 + 11.9X$	0.90**

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

Several previous studies indicated similar results to our findings. Qian et al. (2001) and Fu et al. (2005) indicated a decline in the turf quality of 'Brilliant' Kentucky bluegrass and 'L-93' creeping bentgrass irrigated with high–salinity water compared to those irrigated with fresh water. The decline was more severe and more rapid when L-93 creeping bentgrass was mowed at 6.4 mm than at 12.7 or 25.4 mm (Fu et al., 2005). These data suggested that salinity damage becomes much more severe under shorter mowing heights. Hybrid bermudagrass [*Cynodon dactylon* (L.) Pers. var. *dactylon*] has been reported to tolerate relatively high salinity levels (Francois, 1988), with variation in salinity tolerance between intraspecific and interspecific cultivars (Dudeck et al., 1983; Francois, 1988; Marcum and Murdoch, 1990; Shahba, 2010a, 2010b). In a previous study (Shahba, 2010a), 'Tifgreen' and 'Tifdwarf' showed acceptable turf quality at the salinity level of 16.0 dS m^{-1} while 'Tifway' did not when both mowed to 25.0 mm. Shahba (2010b) indicated that neither Tifgreen nor Tifdwarf showed an acceptable quality at the same salinity level when mowed to 15 mm. Marcum (2001) reported variations among Kentucky bluegrass cultivars and variations among different mowing heights within the same cultivar in salinity tolerance.

Clipping Yield

Clipping yield is another indicator of turf vigor. Clipping yield varied significantly ($P < 0.05$) among cultivars under different salinity levels, among mowing heights within cultivars, and among salinity levels within cultivars and within mowing heights (Table 1). Clipping yield declined with higher salinity. The decline in clipping yield under higher salinity was more severe and more rapid at lower mowing heights for all cultivars (Fig. 2). Clipping yield decreased linearly with increasing salinity level under the three mowing heights. Regressions were strongly linear,
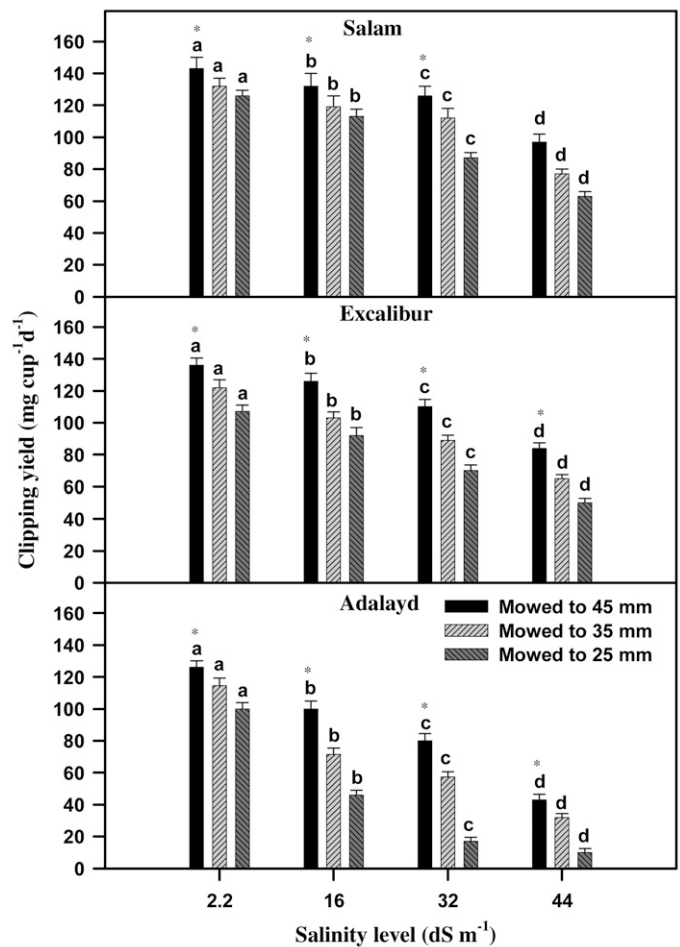

Figure 2. Effect of different salinity levels on clipping yield of three seashore paspalum cultivars at 25-, 35-, and 45-mm mowing heights. Columns labeled with the same letters are not significantly different at $P = 0.05$ within the same mowing height. Columns labeled with an asterisk are significantly higher ($P = 0.05$) for mowing heights comparison within each salinity level. Vertical bars at the top of the columns represent standard error of the means.

with slope more negative at 25.0 mm than at either 35.0 or 45.0 mm (Table 2). Salam showed higher clipping yield under all mowing heights and salinity levels compared to Excalibur and Adalayd (Fig. 2). Adalayd had the lowest clipping yield at all salinity levels. At the highest mowing height, Salam had 4.9, 4.5, 16.7, and 13.4% more clipping yield than that of Excalibur and 11.9, 24.2, 36.5, and 55.7% more than that of Adalayd at 2.2 (control), 16, 32, and 44 dS m^{-1} salinity levels, respectively (Fig. 2).

Previously, salinity levels that resulted in 25% clipping yield reduction have been used as indicator of salinity tolerance (Qian et al., 2001, 2004, 2007; Suplick-Ploense et al., 2002; Lee et al., 2004a, 2004c; Fu et al., 2005; Shahba, 2010a, 2010b). Using regression equations and the clipping yield of the control treatment at each mowing height, the salinity levels at which a 25% clipping yield reduction would occur were calculated for each tested cultivar. For Salam, salinity levels that resulted in 25% clipping yield reduction were 25.3 dS m^{-1} at 25-mm mowing height, 32.9 dS m^{-1} at 35-mm mowing height, and 41.4 dS m^{-1} at 45-mm mowing height. The salinity levels that resulted in 25% clipping yield reduction in Excalibur were 23.2 dS m^{-1} at 25-mm mowing height, 26.0 dS m^{-1} at 35-mm mowing height, and 33.7 dS m^{-1} at 45-mm mowing height. Adalayd showed the lowest salinity tolerance, and salinity levels that resulted in 25% reduction in its clipping yield were 8.6 dS m^{-1} at 25-mm mowing height, 14.2 dS m^{-1} at 35-mm mowing height, and 19.8 dS m^{-1} at 45-mm mowing height. Clipping yield data also suggested that salinity had fewer adverse effects on paspalum at higher mowing heights.

Pessarakli and Touchane (2006) found that the reduction in biomass production due to salinity stress is more obvious than the reduction in shoot lengths in bermudagrass. The decrease in plant biomass production due to salinity may be attributed to low or medium water potential, specific ion toxicity, or ion imbalance (Greenway and Munns, 1980). In addition, elevated salinity may adversely affect photosynthesis and, as a result, adversely affect plant biomass production through less accumulation of carbon products (Munns and Termatt, 1986).

Root Mass

Generally, there was a significant increase in root mass as salinity increased. There was no significant difference ($P < 0.05$) in root mass among cultivars within the same mowing height in the control treatment. However, as salinity increased there were significant differences in root mass among cultivars within the same mowing heights (Table 1). Salam had higher root mass at all salinity levels, except for the control treatment followed by Excalibur and Adalayd. By comparing the increase in root mass under the salinity level of 44.0 dS m^{-1} to the corresponding control treatment (across mowing heights), we found the increase

in root mass in Salam was 133.0, 142.5, and 162.9% and was 129.3, 137.8, and 170.0% in Excalibur, and was 131.6, 161.3, and 204.0% in Adalayd at 25-, 35-, and 45-mm mowing heights, respectively (Fig. 3).

In agreement with previous studies (Krans and Beard, 1975; Salaiz et al., 1995; Fu et al., 2005; Shahba, 2010b), mowing height significantly affected the total root mass of paspalum cultivars (Fig. 3). Regression analysis indicated a significant positive association between root mass and salinity levels at all mowing heights (Table 2). The ranking of mowing heights for total root mass in all cultivars was 45 > 35 > 25 mm (Fig. 3). Salinity stress generally increased root growth. Marcum (1999) reported root mass increased under saline conditions of several grasses at mowing heights ranging from 35 to 75 mm. Also, root growth stimulation under saline conditions has been reported in salt-tolerant grasses, as well (Dudeck et al., 1983; Peacock and Dudeck, 1985). Fu et al. (2005) found an increase in
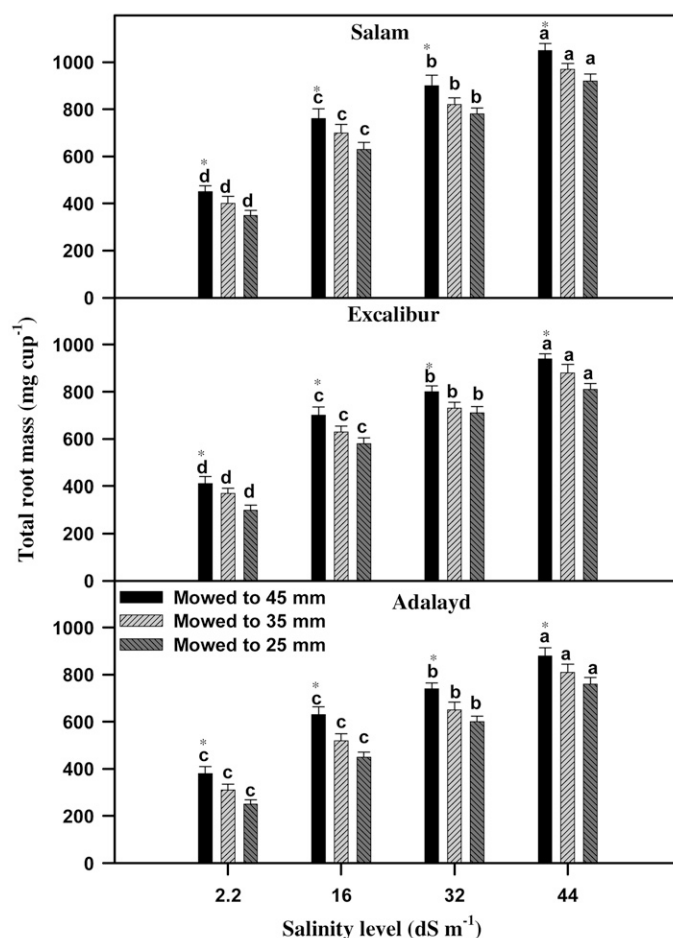

Figure 3. Effect of different salinity levels on total root mass of seashore paspalum cultivars at 25-, 35-, and 45-mm mowing heights. Columns labeled with the same letters are not significantly different at $P = 0.05$ within the same mowing height. Columns labeled with an asterisk are significantly higher ($P = 0.05$) for mowing heights comparison within each salinity level. Vertical bars at the top of the columns represent standard error of the means.

total root mass ranging from 30 to 66% and 39 to 89% at the 25.4-mm mowing height than at 12.7- and 6.4-mm mowing heights, respectively, when salinity was between the control level and 10 dS m^{-1}. Qian et al. (2000, 2007) also found a similar increase in root mass with increases in the salinity of growth solutions for zoysiagrass (*Zoysia* spp.) and saltgrass [*Distichlis spicata* var. *stricta* (Greene)]. Shahba (2010b) reported 33.0, 40.0, and 31.0% increases in root mass of Tifgreen, Tifdwarf, and Tifway, respectively, when salinity level increased from 0 to 20.0 dS m^{-1}. It was suggested that these grasses may require sodium or chloride for growth (Munns and Termatt, 1986). Rozema and Visser (1981) indicated that increased rooting and the associated increase in root absorbing area is an adaptive mechanism to the osmotic and nutrient deficiency stresses occurring under saline conditions. Higher root mass production in Salam may explain its higher salinity tolerance compared to Excalibur and Adalayd. Although our study and the study of Rozema and Visser (1981) were performed in hydroponics, while Fu et al. (2005) used polyvinyl chloride tubes filled with a clay loam soil, they also found a significant relationship between increasing total root mass and increasing salinity. This supports the argument that the response of the roots of grasses under salinity stress in a hydroponics system might be similar to those observed in the field.

Canopy Photosynthetic Rate

Photosynthetic rate varied significantly among cultivars, mowing heights, and salinity levels. The interaction among cultivars, salinity levels, and mowing heights was not significant, while the interaction of salinity and mowing treatments was significant (Table 1). Reduced mowing heights along with increasing salinity resulted in more decreased canopy photosynthesis in paspalum (Table 3). The decrease in Pn was higher at lower mowing heights than at the higher mowing heights of all cultivars when subjected to the same salinity levels. In Salam, as salinity levels increased from control to 44.0 dS m^{-1}, average canopy photosynthetic rate decreased by 33.3, 31.2, and 25.5% at 25-, 35-, and 45-mm mowing heights, respectively. The decrease was intermediate in Excalibur where the average canopy photosynthetic rate decreased by 42.1, 41.9, and 29.1% at 25-, 33-, and 45-mm mowing heights, respectively, where it was the highest in Adalayd where it decreased by 74.6, 76.0, and 46.7% at 25-, 35-, and 45-mm mowing heights, respectively. Although Pn is less sensitive to salinity compared to other growth parameters (Fu et al., 2005), it does add additional proof to the superior salinity tolerance of Salam as compared to Excalibur and Adalayd. Previous studies documented the adverse effects of salinity on Pn in other species (Chartzoulaki et al., 2002; Liu and Cooper, 2002; Qian and Fu, 2005; Shahba, 2010b). In creeping bentgrass, Liu and Cooper (2002) reported a 20% decrease in Pn when salinity increased from 0.0 to 16 dS m^{-1}, while Qian and Fu (2005) reported a 40% decrease for the same species when salinity increased from control (0.2 dS m^{-1}) to 15 dS m^{-1}. Shahba (2010b) indicated that increasing salinity and reducing mowing heights of bermudagrass cultivars additively decreased canopy photosynthesis. A significant difference ($P < 0.05$) in slope among mowing heights within the same cultivar and among cultivars was found, which suggested that mowing height has a significant impact on the change in Pn. Growth responses are in agreement with the physiological parameters. The combination of salinity and close mowing caused greater reduction in Pn and carbohydrate availability. Photosynthetic capacity can be reduced in the presence of high salinity due to stomata closure, damage to photosynthetic systems by excessive energy, structural disorganization, or reduction in photochemical quenching (Flowers et al., 1985; Lee et al., 2004b).

Table 3. Average canopy net photosynthesis (Pn) response of seashore paspalum cultivars to three mowing heights and four salinity levels.

Cultivar	Mowing height	Pn				Regression	R^2
		Salinity level (dS m^{-1})					
		2.2	16	32	44		
	mm	μmol CO$_2$ m^{-2} s^{-1}					
Salam	25	24.9 c[†]	21.2 c	18.2 c	16.7 b	$Y = 24.9 - 0.20X$	0.82*
	35	28.9 b	26.3 b	20.8 b	19.9a	$Y = 29.9 - 0.23X$	0.96**
	45	34.7 a	30.3 a	27.8 a	25.9 a	$Y = 34.5 - 0.21X$	0.87*
Excalibur	25	23.2 c	16.4 c	14.3 c	13.4 b	$Y = 22.12 - 0.22X$	0.85*
	35	27.1 b	19.6 b	16.6 b	15.8 a	$Y = 25.97 - 0.26X$	0.94**
	45	33.2 a	26.7 a	24.5 a	23.6 a	$Y = 32.27 - 0.22X$	0.72*
Adalayd	25	12.2 c	6.9 c	4.9 c	3.1 b	$Y = 11.67 - 0.21X$	0.78*
	35	16.4 b	9.9 b	7.7 b	3.9 a	$Y = 16.15 - 0.28X$	0.95**
	45	22.1 a	17.6 a	14.6 a	11.8 a	$Y = 22.12 - 0.24X$	0.89**

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

[†] Values followed by the same letters within a column are not significantly different within each cultivar ($P = 0.05$) based on a Fisher's LSD test.

Shoot Total Nonstructural Carbohydrates and Total Reducing Sugar Content

Shoot TNC varied significantly among cultivars, mowing heights, and salinity levels. The interaction among cultivars, salinity levels, and mowing heights was not significant, while the interaction of salinity and mowing treatments was significant (Table 1). Increasing salinity and reducing mowing height additively decreased shoot TNC of seashore paspalum (Table 4). In Salam, as salinity levels increased from control to 44 dS m^{-1}, average TNC decreased by 44.2, 29.2, and 25.5% and the average TNC decrease in Excalibur shoots was 51.9, 43.3, and 38.4%, while the decrease in Adalayd was 54.8, 47.3, and 41.1% at 25-, 35-, and 45-mm mowing heights, respectively. A decline in TNC with mowing height reduction was recorded, most likely due to continued defoliation that removed photosynthetic tissues. High salinity escalated the reduction in TNC that resulted from close mowing. In the control treatment, mowing Salam at 25 mm reduced TNC by 6.7 and 14.8% in comparison with that mowed at 35 and 45 mm, respectively. As salinity increased to 44 dS m^{-1}, the mowing height effect on TNC intensified where TNC was reduced by 26.4 and 36.2% at 25-mm mowing height in comparison to those mowed at 35 and 45 mm. Regression analysis indicated a significant negative association between salinity and TNC content in all cultivars at all mowing heights (Table 4).

Shoot RSC varied significantly among cultivars, mowing heights, and salinity levels. The interaction among cultivars, salinity levels, and mowing heights was not significant, while the interaction of salinity and mowing treatments was significant (Table 1). The RSC response to different mowing heights under different salinity treatments followed a different trend than TNC (Table 5).

Table 4. Total nonstructural carbohydrates (TNC) in shoots of seashore paspalum cultivars subjected to three mowing heights and four salinity levels.

Cultivar	Mowing height	TNC				Regression	R^2
		Salinity level (dS m^{-1})					
		2.2	16	32	44		
	mm	——————— mg g^{-1} dry wt. ———————					
Salam	25	144.6 c[†]	109.8 b	89.2 b	80.7 b	$Y = 141.7 - 1.5X$	0.94**
	35	154.9 b	135.8 a	129.5 a	109.7 a	$Y = 155.8 - 1.0X$	0.69*
	45	169.8 a	141.5 a	135.1 a	126.5 a	$Y = 165.9 - 1.0X$	0.72*
Excalibur	25	143.8 c	99.7 b	83.8 b	69.2 b	$Y = 139.1 - 1.7X$	0.92**
	35	152.8 b	113.5 a	104.4 a	86.7 a	$Y = 148.7 - 1.5X$	0.74*
	45	165.8 a	118.5 a	107.6 a	102.2 a	$Y = 157.2 - 1.4X$	0.82**
Adalayd	25	141.8 c	95.2 b	75.2 b	64.1 b	$Y = 136.4 - 1.8X$	0.92**
	35	150.7 b	99.7 a	92.3 a	79.5 a	$Y = 142.3 - 1.6X$	0.84**
	45	163.9 a	114.2 a	104.5 a	96.5 a	$Y = 155.1 - 1.5X$	0.82**

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

[†] Values followed by the same letters within a column for each cultivar are not significantly different ($P = 0.05$) based on a Fisher's LSD test.

Table 5. Total reducing sugar content (RSC) in shoots of seashore paspalum cultivars subjected to three mowing heights and four salinity levels.

Cultivar	Mowing height	RSC				Regression	R^2
		Salinity level (dS m^{-1})					
		2.2	16	32	44		
	mm	——————— mg g^{-1} dry wt. ———————					
Salam	25	29.2 b[†]	32.5 b	37.6 b	43.6 c	$Y = 29.7 + 0.32X$	0.82*
	35	32.5 a	35.6 a	40.2 a	46.9 b	$Y = 30.9 + 0.34X$	0.97**
	45	36.2 a	39.7 a	44.4 a	50.8 a	$Y = 34.8 + 0.34X$	0.77*
Excalibur	25	27.9 b	30.6 b	35.6 b	41.6 c	$Y = 26.3 + 0.32X$	0.79*
	35	29.2 a	32.6 a	38.7 a	43.6 b	$Y = 27.9 + 0.35X$	0.96**
	45	32.5 a	35.8 a	40.6 a	46.7 a	$Y = 31.1 + 0.33X$	0.72*
Adalayd	25	22.9 b	25.9 b	30.8 b	36.8 c	$Y = 21.5 + 0.33X$	0.72*
	35	25.9 a	28.9 a	33.8 a	39.8 b	$Y = 24.4 + 0.32X$	0.95**
	45	27.8 a	30.9 a	35.7 a	41.9 a	$Y = 26.3 + 0.33X$	0.81*

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

[†] Values followed by the same letters within a column for each cultivar are not significantly different ($P = 0.05$) based on a Fisher's LSD test.

Reducing sugars in grass species mainly consists of glucose and fructose (Ball et al., 2002; Shahba et al., 2003). While nonstructural carbohydrates are energy reserves in grasses, soluble reducing sugars are thought to play an important role in salinity, drought and freezing tolerance as osmoregulators, and as protectants as they prevent cell desiccation (Popp and Smirnoff, 1995). Regression analysis indicated a significant positive association between salinity and RSC content in all cultivars at all mowing heights (Table 5). As salinity levels increased from control to 44 dS m^{-1}, average RSC increased by 49.3, 44.3, and 40.3% in Salam and by 49.1, 49.3, and 43.7% in Excalibur, and by 60.7, 53.7, and 50.7% in Adalayd at 25-, 35-, and 45-mm mowing heights, respectively. Comparing RSC among mowing heights within each salinity treatment indicated a decline in RSC with mowing height reduction. In agreement with our results, Qian and Fu (2005) found a decrease in TNC and an increase in RSC with increasing salinity level in shoots of L-93 creeping bentgrass. Also, Shahba (2010b) found an increase in RSC and a decrease in TNC with salinity increase and salinity effect was maximized at lower mowing heights in bermudagrass cultivars (Tifgreen, Tifdwarf, and Tifway). Carbon reduction could be related to the salt resistance mechanisms that are energy dependent. The results suggested that carbohydrate availability was a limiting factor for shoot growth under high salinity stress and close mowing height.

Soluble carbohydrates may interact with membrane phospholipids and proteins to stabilize their structures and prevent desiccation under salinity stress (Popp and Smirnoff, 1995). In agreement with our findings, Lee et al. (2008a, 2008b) reported a positive association between salinity tolerance and reducing sugars accumulation in seashore paspalums. Also, Qian and Fu (2005) indicated that salinity increased glucose and fructose content in bentgrass. Total nonstructural carbohydrate serves as the resource for the increased RSC under salinity conditions.

Shoot Proline Content

Shoot proline content varied significantly among cultivars, mowing heights (except at the control treatment), and salinity levels. The interaction among cultivars, salinity levels, and mowing heights was not significant, while the interaction of salinity and mowing treatments was significant (Table 1). Increasing salinity increased shoot proline content of paspalum. The increase in proline content was more obvious with increasing mowing heights (Table 6). As salinity levels increased from control to 44 dS m^{-1}, average proline content in shoots increased by 417.7, 429.5, and 438.7% in Salam, 387.6, 397.9, and 405.7% in Excalibur, and 250.8, 278.0, and 297.8% in Adalayd, at 25-, 35-, and 45-mm mowing heights, respectively. Comparing proline content among mowing heights within each salinity treatment indicated an increase in proline content as mowing height increased. At the control treatment, there was no significant difference among mowing heights in proline content. As salinity increased to 44 dS m^{-1}, the mowing height effect on proline content intensified where proline content was increased by 7.6, 7.0, and 17.6% at 25-mm mowing height in comparison with those mowed at 45 mm in Salam, Excalibur, and Adalayd, respectively. Regression analysis indicated a significant positive association between salinity and proline content in all cultivars at all mowing heights (Table 6). The role of proline in salt tolerance and its use as a selector for salt tolerance has been questioned (Ashraf and Harris, 2004). Our results suggested a positive role for proline in salinity tolerance of seashore paspalum cultivars. Accumulation of proline in plant tissues in response to salinity stress has been attributed to enzyme stabilization and/or osmoregulation (Flowers et al., 1977; Levitt, 1980). It could enhance membrane stability and mitigates the effect of NaCl on cell membrane disruption and protein structure, act as a sink for carbon and nitrogen for stress recovery, and can buffer cellular redox potential under salinity stress (Ashraf and Foolad, 2007). Maggio et al. (2002) suggested that proline

Table 6. Proline content in shoots of seashore paspalum cultivars subjected to three mowing heights and four salinity levels.

Cultivar	Mowing height	Proline content				Regression	R^2
		Salinity level (dS m^{-1})					
		2.2	16	32	44		
	mm	— µg g^{-1} fresh wt. —					
Salam	25	350.0	955.0 b[†]	1355.0 b	1812.0 c	$Y = 318.3 + 32.9X$	0.97*
	35	357.3	1120.0 a	1460.0 a	1892.0 b	$Y = 386.2 + 34.9X$	0.96*
	45	362.0	1280.0 a	1590.0 a	1950.0 a	$Y = 451.6 + 35.8X$	0.92*
Exacalibur	25	333.7	746.0 b	1090.0b	1627.0 c	$Y = 250.7 + 29.7X$	0.97*
	35	339.0	820.0 a	1180.0 a	1688.0 b	$Y = 277.2 + 30.9X$	0.98*
	45	344.1	890.0 a	1260.0 a	1740.0 a	$Y = 302.7 + 32.1X$	0.98*
Adalayd	25	318.7	518.0 b	770.0 b	1118.0 c	$Y = 242.4 + 18.6X$	0.97*
	35	325.4	622.0 a	840.0a	1230.0 b	$Y = 269.9 + 20.6X$	0.97*
	45	330.6	690.0 a	960.0 a	1315.0 a	$Y = 289 + 22.7X$	0.99*

* Significant at $P \leq 0.01$.

[†] Values followed by the same letters within a column for each cultivar are not significantly different ($P = 0.05$) based on a Fisher's LSD test.

may act as a signaling/regulatory molecule able to activate multiple responses that participate in the adaptation process to elevated salinity levels.

Shoot and Root K⁺/Na⁺ Ratio

Shoot and root K^+ and Na^+ varied significantly among cultivars, mowing heights, and salinity levels. The interaction among cultivars, salinity levels, and mowing heights was not significant, while that of salinity and mowing treatments was significant (Table 1). Increasing salinity and reducing mowing height additively decreased shoot and root K^+/Na^+ ratio (Fig. 4). As salinity increased, Na^+ content increased and K^+ content decreased for the three mowing heights in the three cultivars in both shoots and roots. Wyn Jones et al. (1979) suggested a threshold K^+/Na^+ ratio of 1 for normal growth of plants subjected to salinity. Our K^+/Na^+ ratio was ≥1 at higher salinity levels in Salam, as compared to Excalibur and Adalayd (Fig. 4). All cultivars had a K^+/Na^+ ratio <1 under all mowing heights at the salinity level of 44 dS m⁻¹. In agreement with Qian and Fu (2005) who studied the response of creeping bentgrass and Shahba (2010b) who studied the response of bermudagrass cultivars to salinity and mowing heights, our results showed increased Na^+ and decreased K^+ concentration in shoots and roots with the increase of salinity level and that was more obvious at lower mowing height. Storey and
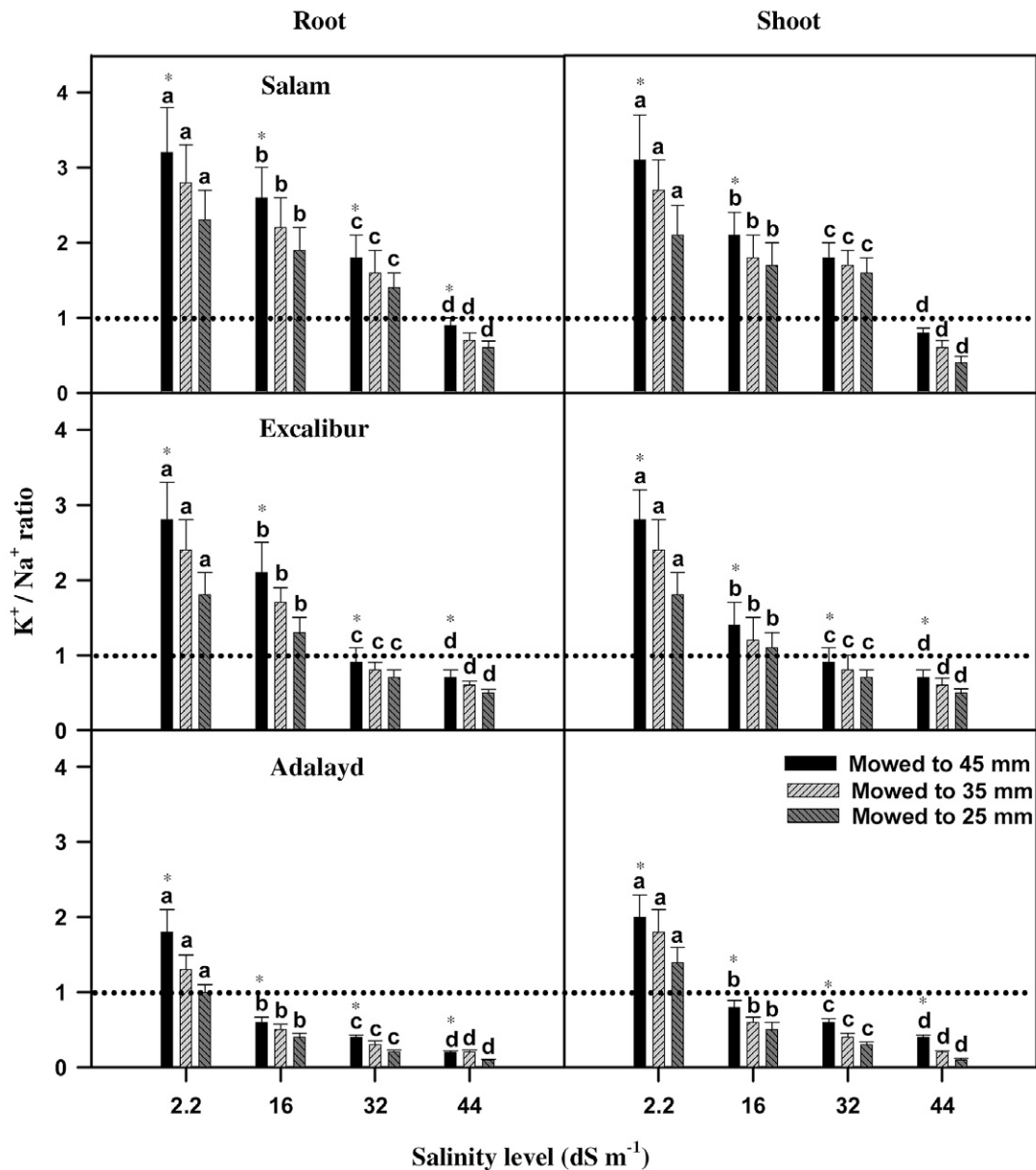
Figure 4. Effect of different salinity levels on root (left panel) and shoot (right panel) K⁺/Na⁺ ratio of seashore paspalum cultivars at 25-, 35-, and 45-mm mowing heights. Columns labeled with the same letters are not significantly different at P = 0.05 within the same mowing height. Columns labeled with an asterisk are significantly higher (P = 0.05) for mowing heights comparison within each salinity level. Vertical bars at the top of columns represent standard error of the means. Dotted lines indicate the suggested threshold K⁺/Na⁺ ratio for normal growth.

Wyn Jones (1979) suggested that the capacity to maintain high shoot K^+/Na^+ ratio is an important element of salt tolerance, especially in species that lack foliar salt-excretion mechanisms. Shannon (1978) studied salt tolerance of 32 lines of tall wheatgrass [*Agropyron elongatum* (Host) Beauv.] and found association between salinity tolerance and the maintenance of K^+/Na^+ ratio ≥ 1. This suggested that the increase in mowing height may help limit shoot Na^+ and improve K^+ concentrations in the shoot. Also, it has been demonstrated that salinity tolerance in several grass species (Gramineae) is associated with exclusion of Na^+ from shoot and the capacity to maintain high shoot K^+/Na^+ ratio (Torello and Rice, 1986; Qian et al., 2000, 2001; Qian and Fu, 2005; Shahba, 2010b). Grieve et al. (2004) found an increase in Na^+ concentration and a decrease in K^+ ion concentration when salinity increased from 15 to 25 dS m^{-1}, and concluded that neither K^+/Na^+ ratios nor $K^+{:}Na^+$ selectivity coefficients appear to be satisfactory indicators of relative salt tolerance of the forages examined in their study, in agreement with Lee et al. (2007) who concluded that K^+/Na^+ ratio did not appear to be related to seashore paspalum ecotypes' salinity tolerance.

Data on K and Na contents indicated that maintaining seashore paspalum at 45-mm mowing height increased the uptake of K^+ over Na^+, while close mowing reduced the uptake of K^+ under high salinity conditions and increased the uptake and transport of Na^+ to shoots. The proteins of the cell membrane play a significant role in the selective distribution of ions within the plant cells. These proteins include (i) primary H^+−ATPases that generate the H^+ electrochemical gradient. This gradient controls ion transport through the plasma membrane with high selectivity for K over Na; (ii) Na/H antiports in the plasma membrane for pumping excess Na out of the cell; and (iii) Na/H antiports in the tonoplast for extruding Na into the vacuole (Ashraf and Harris, 2004; Tester and Davenport, 2003). The selectivity of K over Na in the root uptake is an energy-dependent process and more likely regulated to a substantial degree by H^+ gradients across the plasma membrane which are maintained by H^+−ATPase activity. Low mowing height depletes TNC reserves that induce ATP deficit, resulting in the lack of energy to control active ion selectivity in uptake and transport (Qian and Fu, 2005; Shahba, 2010b).

Salt stress responses are tissue- and salinity-specific. For long-term performance and persistence in field situations under salt stress, it is essential that grasses exhibit both root and shoot tissue salinity tolerance (Carrow and Duncan, 1998). On the basis of the number of times in the best statistical category for turf quality, clipping yield, root growth, Pn, TNC, RSC, proline content, and K^+/Na^+ ratio, the cultivar Salam was found to have higher salt tolerance compared to Excalibur and Adalayd. Also, increasing salinity had fewer adverse effects on overall responses of all cultivars at higher mowing heights.

CONCLUSIONS

In summary, as salinity increased, seashore paspalum cultivars exhibited reduced turf quality, clipping yield, canopy photosynthesis, shoot TNC, and K^+/Na^+ ratio, and increased shoot total reducing sugars and proline contents. Salam showed higher salinity tolerance compared to other cultivars tested, and turf mowed at lower mowing heights was more sensitive to salinity stress. The tolerance of paspalum cultivars to moderate to high salinity stress can be enhanced by increasing the mowing height, related to increased carbon fixation as indicated in this study. Also, proline accumulation could add to the salinity tolerance through osmoregulation or by acting as carbon and nitrogen sink for stress recovery.

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