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Physiological responses to salt stress in young umbu plants☆

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Abstract

Soil salinity affects plant growth and development due to harmful ion effects and water stress caused by reduced osmotic potential in the soil solution. In order to evaluate the effects of salt stress in young umbu plants, research was performed in green house conditions at the Laboratory of Plant Physiology at Federal Rural University of Pernambuco, Brazil. Growth, stomatal behaviour, water relations, and both inorganic and organic solutes were studied aiming for a better understanding of the responses of umbu plants to increasing salinity. Plants were grown in washed sand with Hoagland and Arnon nutrient solution with 0, 25, 50, 75, and 100 mM NaCl. Growth, leaf water potential, transpiration, and diffusive resistance were evaluated. Na^+, K^+, Cl^-, soluble carbohydrates, and free amino acid contents were measured in several plant organs. Most variables were affected with salinity above 50 mM NaCl showing decreases in: number of leaves, plant height, stems diameter, and dry masses, and increases in root-to-shoot ratio. Reductions in ψ_{pd} were observed in plants grown under 75 and 100 mM NaCl. All salt levels above zero increased Na^+ and Cl^- contents in leaves. However, K^+ content was not affected. Na^+ and Cl^- in stems and roots reached saturation in treatments above 50 mM NaCl. Organic solute accumulation in response to salt stress was not observed in umbu plants. These results suggest that umbu plants tolerate salt levels up to 50 mM NaCl without showing significant physio-morphological alterations.
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Keywords: *Spondias tuberosa*; Water potential; Transpiration; Organic solutes; Sodium; Chloride

1. Introduction

Soil salinization is a serious problem in the entire world and it has grown substantially causing loss in crop productivity. It has been estimated that about 954 million hectares of land around the world are already salinized and 4.5% of these lands are located in Brazil (Dias et al., 2003). Although the information about the saline areas in Brazil is not well defined, it is estimated that 20–25% of the irrigated areas near rivers and intermittent streams face salinity and/or drainage problems. Irrigated perimeters in the Northeastern Brazil are approximately 23,000 ha and 25% are already salt affected (FAO, 2006).

Salinity reduces plant growth due to osmotic and ionic effects on soil solution (Marschner, 1990; Munns, 2002). Short-term effects include reduction on growth by salt due to osmotic effects, which reduces cell expansion. Long-term effects include excessive salt absorption, which causes plants to suffer ionic stress, leading to premature leaf aging following a reduction in the available photosynthetic area to maintain growth (Munns, 2002). In both long and short term, reductions on growth are generally attributed to low photosynthetic rates due both stomatal and non-stomatal limitations.

Stomatal closure is likely the first plant defence against desiccation and an important factor to control carbon fixation. Non-stomatal limitations on photosynthesis have been attributed to reductions in the carboxylation efficiency (Bethke and Drew, 1992; Robinson et al., 1997). Thus, independent of the limitation type, salinity affects growth and can alter leaf water potential, stomatal conductance, and transpiration (Sultana et al., 1999; Parida and Das, 2005).

Salt stress tolerance in plants is a complex phenomenon that may involve developmental changes as well as physiological and biochemical processes (Delauney and Verma, 1993; Hare and Cress, 1997). In halophytes, salt tolerance is a result of inorganic

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ion accumulation, mainly Na^+ and Cl^-, which are compartmentalized in the vacuole. While organic solutes accumulate in cytoplasm balancing water potential through several cellular compartments (Greenway and Munns, 1980; Marschner, 1990; Robinson et al., 1997; Serraj and Sinclair, 2002). In addition to their role in cell water relations, organic solutes accumulation may also contribute to the maintenance of ionic homeostasis and stabilization of some macromolecules and organelles such as proteins, protein complexes and membranes (Bohnert and Shen, 1999; Bray et al., 2000).

Umbu tree (*Spondias tuberosa* Arr. Cam.) is a xerophytic tree belonging to the Anacardiaceae which produces fruit edible to humans and animals. It is from the semi-arid region of the Brazilian Northeast. The tuberous roots (xylopodium) help to adapt it to the climate due to their ability to store water, mineral salts, and organic solutes essential to its survival during dry seasons (Epstein, 1998; Duarte et al., 2004).

The effects of salt stress on umbu tree physiology have been little studied. Neves et al. (2004) classified the umbu tree as moderately tolerant to salinity using the percentage reductions on dry mass as an evaluation standard. Considering the increase of salinization on arable lands and that the umbu tree is a native species in arid environments, this study was carried out to test the hypothesis that salinity induces changes in the ionic and osmotic relations in salt-stressed umbu plants, with consequences in the gas exchanges, growth, and solutes accumulation. Thus, this study may contribute for a better understanding of the responses of umbu plants to increasing salinity and improve knowledge of the physiology and ecology of this important species and perhaps other drought tolerant species.

2. Material and methods

2.1. Plant material, growth, and treatment conditions

Research was carried out in greenhouse conditions at the Laboratory of Plant Physiology of Federal Rural University of Pernambuco, Brazil, between July and September, 2004. Umbu seeds coming from Embrapa – CPATSA, Petrolina, Pernambuco state were sown in washed sand trays and watered daily. Thirty days after emergence, uniform, 1-month-old seedlings, of 13 cm height, four leaves, and 0.2 cm stem diameter, were transplanted to pots containing 8 kg of washed sand. Plants were irrigated daily with full strength Hoagland's nutrient solution (Hoagland and Arnon, 1950) for 30 days prior to starting salt treatments. After this period, a stress period was imposed in which plants of all treatments were irrigated daily until the free drainage with full strength Hoagland's nutrient solution with 0, 25, 50, 75 or 100 mM NaCl for 36 days.

2.2. Growth measurement

Each week, shoot length, the number of leaves, and stem diameter were measured. At the end of the experimental period, plants were carefully removed from the substrate, the roots were washed with distilled water, and plants were partitioned in different organs. Sigma Scan program SPSS Inc. was used to determine total leaf area (LA). After drying at 65 °C in an oven until constant dry weight, mass of leaves, stem, and root dry was determined. These data were used to calculate biomass allocation to leaves, stem, and roots as well as root-to-shoot ratio (R/Sh) as described by Benincasa (1988).

2.3. Transpiration, diffusive resistance, and water potential measurements

Transpiration (E) and diffusive resistance (r_s) were measured using a steady-state porometer, model LI-1600 (LI-COR, Inc. Lincoln, NE, USA), which set the null point near humidity in the greenhouse. As the porometer gave us the values of E in $\mu g\,cm^{-2}\,s^{-1}$, the values were converted to $mmol\,m^{-2}\,s^{-1}$. Two mature and fully expanded leaves located 5–7 leaves from the shoot tip on each plant were sampled. The measurements were carried out over one day (8–16 h at 2 h intervals) each week. Photosynthetic active radiation (PAR) varied from 14.8 to 776.9 $\mu mol\,m^{-2}\,s^{-1}$, air temperature (T_{air}) varied from 25.5 to 33.7 °C and vapour pressure deficit (VPD) from 1.42 to 2.96 kPa, respectively, exhibiting peaks at midday. At the end of the experimental period, the same leaves used for transpiration measurement were sampled to determine pre-dawn water potential using a model 3035 pressure chamber (Soil Moisture Equipment Corp, Santa Barbara, CA, USA).

2.4. Na^+, K^+, Cl^-, amino acid, and soluble carbohydrate contents

The extracts used for determination of sodium, potassium, chloride, amino acids, and soluble carbohydrate contents were prepared by grinding 0.5 mg of dry mass tissue with 10 mL of distilled water at 25 °C for 10 min. The homogenate was centrifuged at 3000 × g for 15 min, and the supernatant was filtered through qualitative filter paper. An aliquot of filtrate was used for Na^+ and K^+ determination by flame photometry (Sarruge and Haag, 1974) and Cl^- by precipitation titration with silver nitrate by Mohr's method (Azevedo Neto and Tabosa, 2001). Soluble carbohydrates were determined according to Dubois et al. (1956), using D(+)-glucose as standard. For free amino acid determination, 0.5 mL of 10% trichloroacetic acid was added to an aliquot of 0.5 mL of the water extract and the mixture was kept at 25 °C for an hour. This mixture was then centrifuged at 12,000 × g for 5 min, and the supernatant was used for amino acid determination (Yemm and Cocking, 1955), using L-leucine as standard.

2.5. Experimental design and statistical analysis

The experimental design was completely randomized with five salt levels and six replicates. Data were submitted to analysis of variance (ANOVA) and the means compared by Tukey's multiple range test ($P < 0.05$).

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3. Results

3.1. Growth

Salt stress induced significant differences on plant growth during the experimental period. After 15 stress days, decreases in plant height were observed in plants grown with 75 and 100 mM NaCl ($P < 0.01$) (Fig. 1A). At the end of the stress period (36 days), only plants submitted to 25 mM NaCl did not show significant differences compared to control plants. The means values of plant height were 58.4, 54.6, 52.4, 49.9 cm, and 48.4 cm for treatments of 0, 25, 50, 75, and 100 mM NaCl, respectively.

The number of leaves was more sensitive than plant height, showing a significant reduction ($P < 0.01$) 7 days after the beginning of the treatments (Fig. 1B). After 36 days, the mean values of number of leaves were, respectively, 9.7, 7.7, 8.4, 6.2, and 5.8 to 0, 25, 50, 75, and 100 mM NaCl. Thus, salinity reduced number of leaves at all NaCl levels. It was especially visible in plants submitted to 75 and 100 mM of NaCl (37 and 40%, respectively).

Stem diameter was less sensitive to NaCl levels than plant height and number of leaves. The means values of stem diameter at the end of the experimental period were 0.79 cm (control), 0.80 cm (25 mM), 0.75 cm (50 mM), 0.63 cm (75 mM), and 0.58 cm (100 mM) as shown in Fig. 1C. Significant reductions in stems diameter were verified only in plants submitted to 75 and 100 mM of NaCl (Fig. 3). This represents 20 and 26%, respectively, in comparison with control plants.

Salt stress resulted in considerable decreases in leaves, stem, and total dry masses verified in NaCl levels of 75 and 100 mM. These reductions were approximately 39 and 47%; 46 and 52%; 31 and 34%, respectively (Fig. 2A, B and D). Contrasting these results, root dry masses increased 45% in plants submitted to 25 mM NaCl, decreasing to the same control values in the other treatments (Fig. 2C). Root-to-shoot ratio (R/Sh) increased with salt stress, having been more visible in plants under 100 mM NaCl (93%) as shown in Fig. 2E.

Leaf area reduced as salt concentration increased (Fig. 2F). It occurred in plants submitted to severe levels of NaCl at 75 and 100 mM, these reductions being 46 and 55%, respectively, compared with control plants.

According to Table 1, specific leaf area (SLA) and leaf area ratio (LAR) were not affected by salinity irrespective of the considered treatment.

Biomass allocation varied with the NaCl levels applied and with the plant organs (Fig. 3). Thus, level of 100 mM NaCl increased biomass allocation to roots by 45% and decreased stems by 25% and leaves by 20% when compared with control plants.

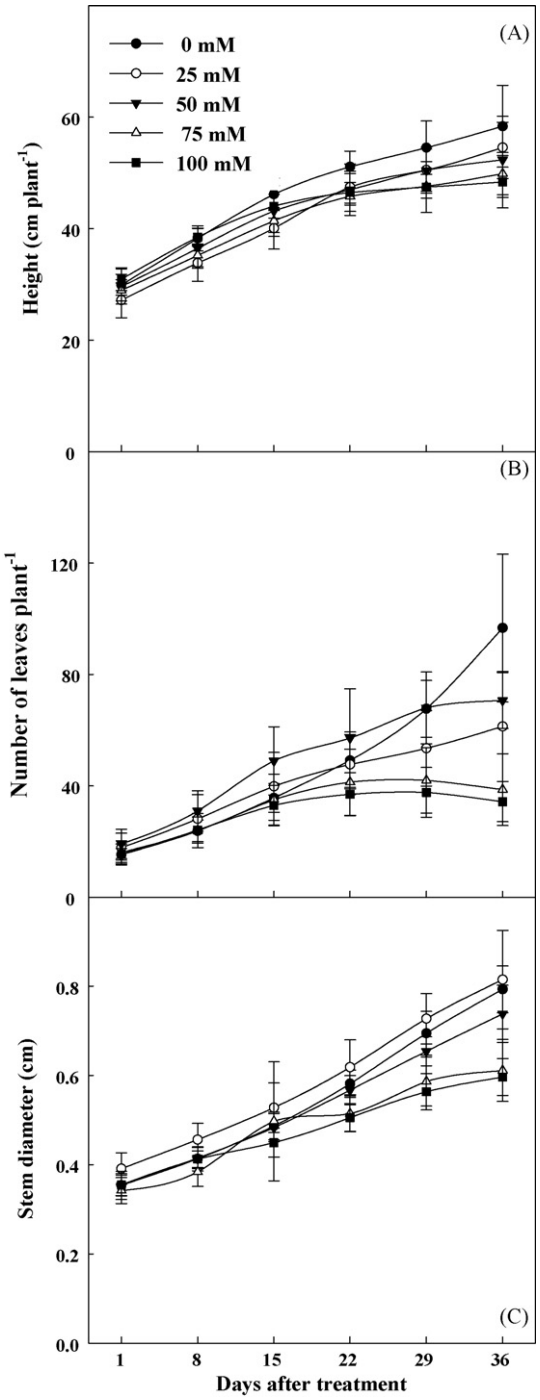

Fig. 1. Plant height, number of leaves, and stem diameter of young umbu plants cultivated at increasing NaCl levels. Means of six replicates ± S.D. are shown.

3.2. Transpiration, diffusive resistance, and water potential

Young umbu plants showed a peak of transpiration at 12 h (noon) in all assessments (Fig. 4A, C, E, and G). However,

Table 1
Specific leaf area (SLA) and leaf area ratio (LAR) of young umbu plants under increasing NaCl levels after 36 days of stress

NaCl levels (mM)	Specific leaf area (cm^2/g LDM)	eaf area ratio (cm^2/g TDM)
0	211.07 ± 21.94a	75.22 ± 13.92a
25	159.22 ± 66.34a	49.13 ± 20.68a
50	211.28 ± 47.91a	71.50 ± 15.89a
75	187.88 ± 43.60a	58.14 ± 16.29a
100	180.46 ± 26.79a	50.25 ± 7.55a

Means of six replicates ± S.D. are shown. Values followed by different letters differ significantly according to Tukey's multiple range tests at $P < 0.05$.

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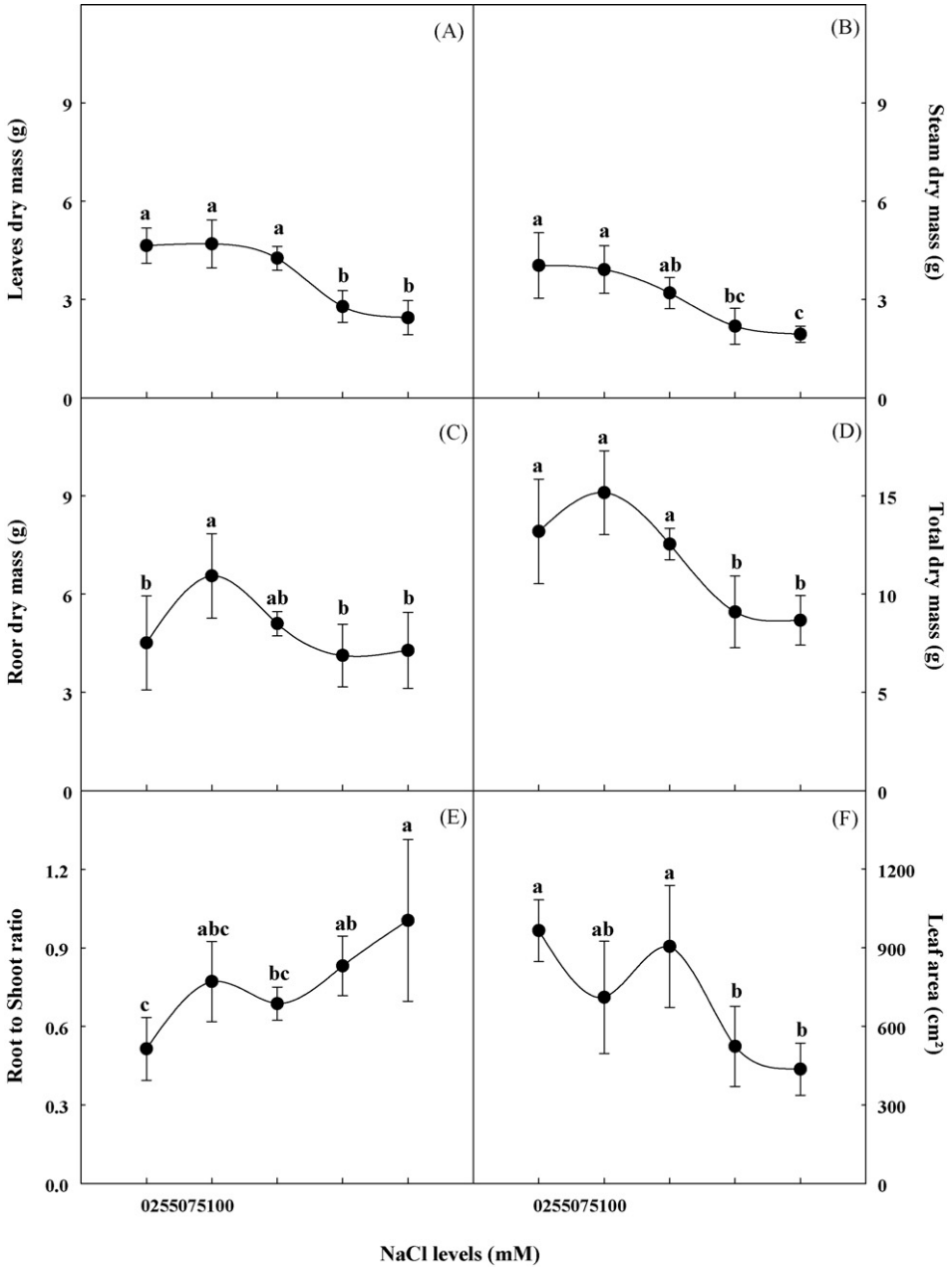

Fig. 2. Leaves (A), stem (B), root (C), and total dry masses (D), root-to-shoot ratio (E) and leaf area (F) of young umbu plants after 36 days at increasing salt levels. Means of six replicates ± S.D. are shown. Different letters denote statistical difference by Tukey's test ($P < 0.05$) among treatments.

transpiration rates (E) were lower at 21 and 28 days than observed in the beginning of the experimental period (Fig. 4E and G). Irrespective of the evaluation day, salinity reduced E in plants grown under 75 and 100 mM NaCl. In addition, the lowest values of E were observed at 16 h. Plants submitted to 100 mM NaCl in nutrient solution showed the smaller values of E at 28 treatment days when compared with the other treatments, independent of the time of assessment (Fig. 4G).

Salinity did not induce stomatal closure during the experimental period. However, increases in r_s became more conspicuous at 28 days of treatment and the highest value of r_s was observed at 4 p.m., particularly in plants under 75 and 100 mM NaCl (Fig. 4B, D, F and H).

Pre-dawn water potential in plants submitted to 25 and 50 mM NaCl remained unchanged, while plants grown under 75 and 100 mM NaCl treatments showed reduced ψ_{pd} (−0.96 and −0.89 MPa, respectively) in comparison to control plants.

3.3. Na^+, Cl^-, K^+, carbohydrates, and amino acids

Na^+ content in leaves increased linearly with increases in NaCl levels, reaching the highest value in plants submitted to 100 mM NaCl (Fig. 6). Na^+ content in the stem and roots increased in plants submitted to 25 mM NaCl, however remained relatively stable at the other salt levels. Comparing the different plant organs when plants were submitted to 100 mM NaCl, Na^+

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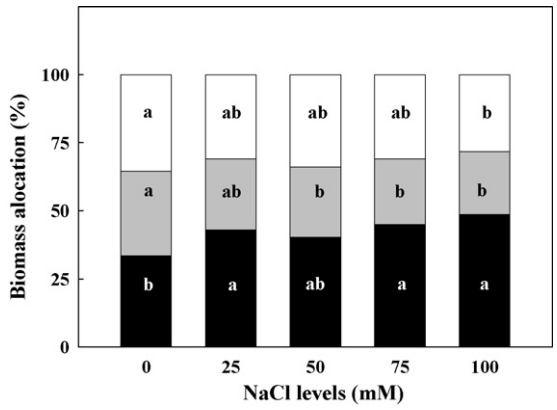

Fig. 3. Biomass allocation to roots (■), stem (▩) and leaves (□) in young umbu plants after 36 days at increasing salt levels. Different letters denote statistical difference by Tukey's test ($P < 0.05$) among treatments.

content in leaves was about 3- and 2-fold higher than in stem and roots, respectively.

Cl^- content in leaves increased linearly up to levels of 75 mM NaCl. In the stem and roots, Cl^- increased also up to 50 mM NaCl. However, differences among salt levels above 50 mM were not observed (Fig. 6). The chloride content in the leaves was about 2- and 1.5-fold higher than in stem and roots at the highest salt level. Chloride content was substantially higher than sodium in all organs.

Salinity did not significantly affect K^+ contents in the leaves, stems and roots ($P < 0.01$) (Fig. 7). Na^+/K^+ ratio increased linearly in leaves with increases in NaCl levels (Fig. 7). In stems and roots, the Na^+/K^+ ratio was significantly lower for the 0 NaCl treatment than all the higher treatments that did not differ.

The carbohydrate content in leaves showed a small but significant increase (18%) in plants grown above 50 mM NaCl

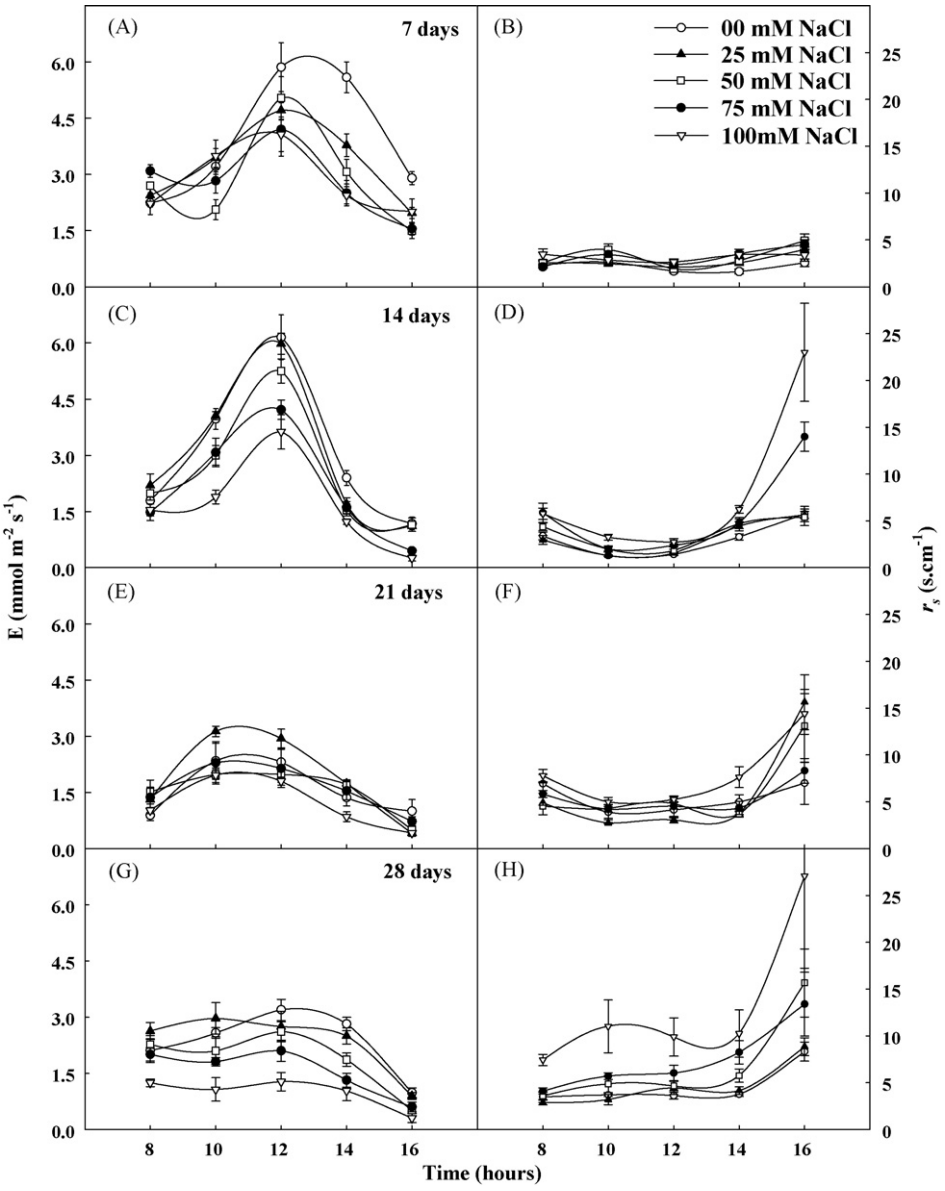

Fig. 4. Daily course of transpiration (E) and diffusive resistance (r_s) in young umbu plants cultivated at increasing NaCl levels. Measurements were accomplished after 7 (A and B), 15 (C and D), 21 (E and F), and 28 (G and H) days of salt stress. Means of six replicates ± S.D. are shown.

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($P < 0.01$) (Fig. 8). In stems, carbohydrate contents increased 40% in plants submitted to 25 mM NaCl. However, it returned to the same as the control level in the other treatments. In roots, a reduction of 32% in the soluble carbohydrate content was observed at salt levels of 50, 75, and 100 mM NaCl.

In relation to the amino acid content of leaves, there was a decrease of 53% in the highest NaCl level when compared with control plants (Fig. 8). In contrast, amino acid content increased nearly 110% in stems of plants grown under higher salt levels (75 and 100 mM NaCl). In the roots, significant differences in free amino acid content were not observed as a result of NaCl levels applied.

Under salt stress, carbohydrate content in leaves and roots was, respectively, 3- and 87-fold higher than amino acid content.

4. Discussion

Salinity inhibits plant growth for two reasons: first, water-deficit and second due to salt-specific or ion-excess effects (Munns et al., 2006). Different plant species have developed different mechanisms to cope with these effects (Munns, 2002). In this work, reductions in plant height, number of leaves, and stem diameter in stressed plants were observed (Fig. 1A–C). However, growth inhibition was not verified during the experimental period. Stem diameter was less affected by salt stress than plant height and number of leaves, corroborating the results obtained by Neves et al. (2004) in umbu plants. Reductions in stem diameter were also observed in avocado (Bernstain et al., 2001). Seedlings of *Leucaena leucocephala* showed reduced shoot growth by 60% when submitted to 100 mM NaCl, while seedlings of *Prosopis juliflora* were reduced just 15% under the same salt conditions (Viégas et al., 2003).

Salt tolerance has usually been assessed as the percentage biomass production in saline versus control conditions over a prolonged period of time (Munns, 2002). Plants submitted to high salinity (75 and 100 mM NaCl) decreased both leaf and stem dry masses (Fig. 2A and B). Contrasting with these results, root dry mass increased in plants grown in the lowest NaCl level (25 mM) while plants submitted to 50, 75, and 100 mM NaCl did not differ from control plants (Fig. 2C). Several researchers have shown that shoot growth is more sensitive to salinity than root growth (Shalhevet et al., 1995; Azevedo Neto and Tabosa, 2000; Bernstain et al., 2001). Our results also demonstrate that the shoot of young umbu plants is more sensitive to salinity than the root system (Fig. 2E). According to Munns (1993), this sensitivity could be explained due to an imbalance among cations as a result of the complex interaction in the xylem transport system. Alternatively, when compared with shoots, this phenomenon could be associated to both a faster osmotic adjustment and a slower turgor loss in the roots (Shalhevet et al., 1995).

Leaf area was the most sensitive growth parameter in response to high salt levels in the nutrient solution (75 and 100 mM NaCl) (Fig. 2F). For example, in young guava plants leaf area was reduced by 92% compared to control when plants were submitted to 150 mM NaCl (Távora et al., 2001). The same was observed for mangabeira plants (*Hancornia speciosa* Gomes) which showed a 47% reduction in leaf area when cultivated in sand with 125 mM NaCl (Albuquerque, 2004). Leaf area is a function of leaf size. Considering that leaf area was more affected than number of leaves, our results suggest that salinity also affected cell elongation ratio, therefore decreasing leaf size.

The increases in salinity did not significantly affect SLA and LAR (Table 1) suggesting that the effect of salt stress on leaf area was as intense as the effect on dry mass yield. Similar results were found in maize by Azevedo Neto and Tabosa (2000). The contrary was found in mangabeira plants where LAR increased 41% when NaCl levels increased (Albuquerque, 2004).

The increasing of biomass allocation to roots to the detriment of the shoot induced a raise in R/Sh ratio (Figs. 2E and 3). These results differ from those found by Neves et al. (2004) in young umbu plants in which the authors verified reductions in R/Sh with the increases in NaCl levels in the medium. In contrast, other authors found similar results with other crops as to those obtained in this work (Azevedo Neto and Tabosa, 2000; Bernstain et al., 2001; Chartzoulakis et al., 2002), while in other research, R/Sh remained unchanged (Albuquerque, 2004).

Stomatal closure was not observed with the increase of NaCl in nutrient solution. In stressed plants, however, significant reductions in transpiration rate were verified, primarily in high evaporative demand hours (Fig. 4A, C, E and G). Decline in transpiration rates usually occurs in both halophytes and glycophytes when salinity of the root zone increases. Short-term results indicate that the reduction in E occurs due to decrease in water potential in roots. Long-term results indicate that high salt concentrations are associated with the inhibition of photosynthesis caused by the accumulation of salts in the mesophyll and increases in intercellular CO_2 concentration which reduces stomatal apertures (Robinson et al., 1997).

The regulation in the transpiration rate has an important role in controlling ion accumulation in the shoot because salt transport occurs via transpiration flow (Robinson et al., 1997). Lima Filho (2004) observed that umbu trees exhibit two peaks of transpiration during the daytime, at 10 and 16 h under field conditions. This shows that even in good soil with appropriate humidity conditions, umbu trees exert strict control over the

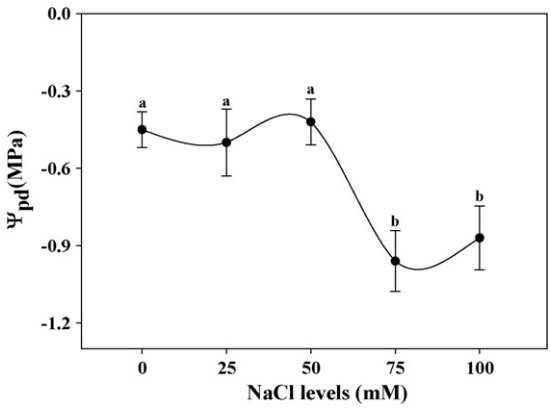

Fig. 5. Pre-dawn leaf water potential (ψ_{pd}) of young umbu plants cultivated under increasing NaCl levels. Means of six replicates ± S.D. are shown. Different letters denote statistical difference by Tukey's test ($P < 0.05$) among treatments.

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water loss through stomata by restricting transpiration at high evaporative demand hours, assuring a significant water economy (Lima Filho and Silva, 1998). We found no information about gas exchange in umbu tree within a saline environment in the literature. Hence, our results are the first report on this topic.

Salinity reduces water potential in guava (Távora et al., 2001), avocado (Chartzoulakis et al., 2002), Barbados cherry (Nogueira et al., 1998; Gurgel et al., 2003), mangabeira tree (Albuquerque, 2004), maize (Azevedo Neto et al., 2004), and sugar apple (Nogueira et al., 2004). However, information about the effects of salt stress on ψ_{pd} in umbu tree was not found in the literature. Plants cultivated under low and moderate salinity (25 and 50 mM NaCl) maintained high values of ψ_{pd}, while plants under high NaCl levels (75 and 100 mM) exhibit low values of ψ_{pd} (Fig. 5). These results suggest that salt-induced water stress led to non-recovering of water potential in the more stressed plants. It is well known that salt stress reduces hydraulic conductivity in roots, resulting in decreases of water flow from root to shoot. Thus, there is an alteration in water relations even in osmotically adjusted plants (O'Leary, 1994; Prisco, 1980).

The association between osmotic and ionic effects (ionic toxicity, nutritional deficiency and/or imbalance) has been reported as being the main reason of the growth reduction under salt stress (Yahya, 1998; Neves et al., 2004). Our results showed an increase in tissue Na^+ and Cl^- when salinity increased. However, this increase was more conspicuous in leaves than in roots (Fig. 6A, B, E, and F). The stabilization in Na^+ and Cl^- contents verified in moderate and high salinity in the roots suggests saturation in the sodium and chloride retention mechanism in this organ (Fig. 6E and F). Greater Na^+ and Cl^- accumulation in roots

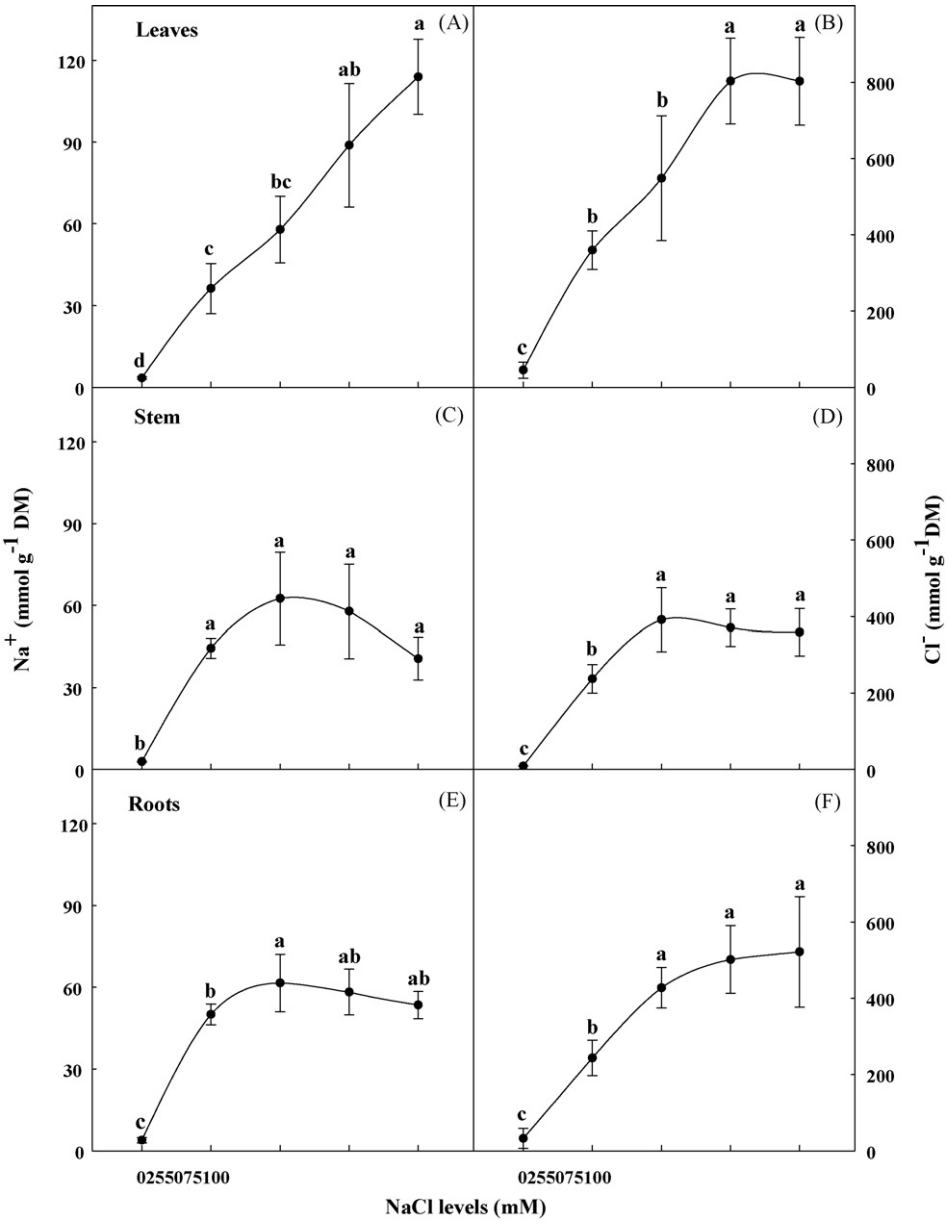

Fig. 6. Sodium (Na^+) and chloride (Cl^-) contents in leaves (A and B), stem (C and D), and roots (E and F) in young umbu plants cultivated under increasing NaCl levels. DM: dry mass. Means of six replicates ± S.D. are shown. Different letters denote statistical difference by Tukey's test ($P < 0.05$) among treatments.

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than shoot has been considered a physiological trait indicator of salt tolerance in plants (Viégas et al., 2003). Studying four forest species, these authors verified that salt sensitivity was correlated with a lower Na^+ and Cl^- retention in roots. Additional support of this hypothesis is provided by some olive genotypes, moderately salt tolerant species, for which Na^+ and Cl^- accumulation in roots was greater than in leaves (Chartzoulakis et al., 2002).

The maintenance of K^+ content in both leaves and roots of stressed umbu plants (Fig. 7A and E) was reported for other forest species also (Viégas et al., 2003), suggesting that the absorption and transport processes were not affected by competition between this ion and Na^+ as shown by Azevedo Neto and Tabosa (2000) and Azevedo Neto et al. (2004).

Although salinity did not affect K^+ content, increases of Na^+ content in leaves and roots substantially raised Na^+/K^+ ratio in these organs (Fig. 7A, B, E, and F). Na^+/K^+ ratios equal to or smaller than 0.6 are necessary for an optimal metabolic efficiency in non-halophyte plants (Greenway and Munns, 1980). High Na^+ concentration can induce K^+ deficiency inhibiting the activity of enzymes that require K^+. Thus, the interaction between relative K^+ and Na^+ concentration has been considered a key factor in determining salt tolerance in plants (Willadino and Câmara, 2005). In this work, Na^+/K^+ ratios above 1.0 were found in the leaves (Fig. 7A), with values of 1.4 and 1.5 in plants submitted to 75 and 100 mM NaCl, respectively. These results suggest that the reduction in growth can

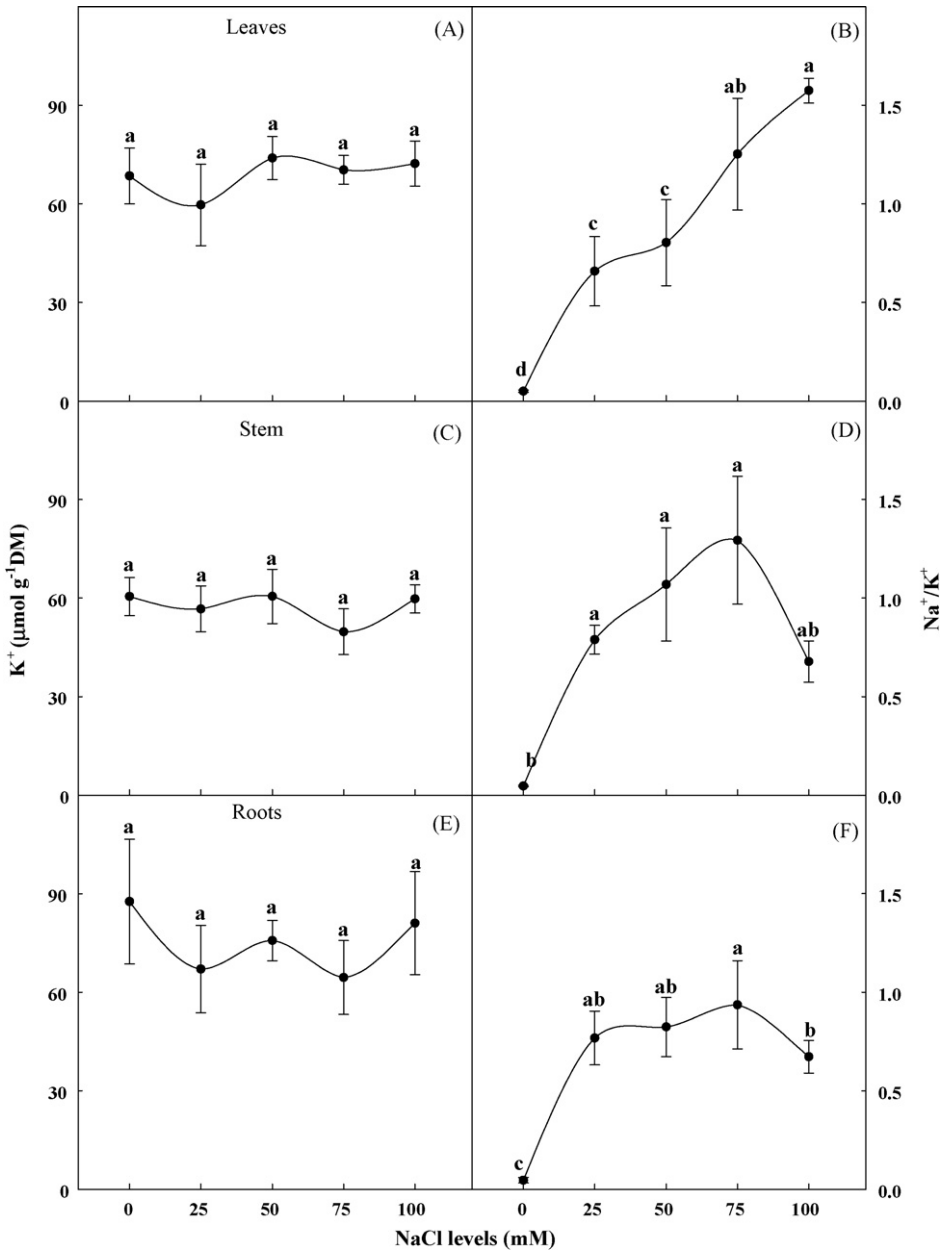

Fig. 7. Potassium content (K^+) and sodium/potassium ratio (Na^+/K^+) in leaves (A and B), stem (C and D), and roots (E and F) in young umbu plants cultivated under increasing NaCl levels. DM: dry mass. Means of six replicates ± S.D. are shown. Different letters denote statistical difference by Tukey's test ($P < 0.05$) among treatments.

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be, at least in part, related to metabolic disorders induced by salt.

Soluble carbohydrates and free amino acids have been mentioned as important compounds in osmoregulation in plants under water and salt stresses (Hare et al., 1998). Accumulation of these compatible solutes reduces osmotic potential in the cytoplasm and contributes to maintaining water homeostasis among several cellular compartments (Sairan and Tyagi, 2004). Among all organic compounds, soluble carbohydrates represent about 50% of the total osmotically active organic solutes (Ashraf and Harris, 2004). However, salinity may increase carbohydrates in some plant species (Lacerda et al., 2003; Silva et al., 2003) or decrease in others (Agastian et al., 2000). In this work, carbohydrate content increased 18% in leaves (Fig. 8A) and decreased 32% in roots (Fig. 8E) when plants were grown at 50 mM NaCl and higher. In stems, substantial differences in soluble carbohydrates were not verified (Fig. 8C). The greater carbohydrate accumulation in leaves and the reduction in roots under stressed conditions may be associated with decreases in this compound exported from leaves to roots. It is interesting to observe that even in stressed conditions, soluble carbohydrate content was 3-fold higher in leaves, contributing therefore to water status maintenance in roots.

Free amino acid accumulation in plants under salt stress has often been attributed to alterations in biosynthesis and degradation processes of amino acids and proteins (Dhindsa and Cleland, 1975; Ranieri et al., 1989; Roy-Macauley et al., 1992). Considering that salinity significantly decreased the free amino acid content in leaves (Fig. 8B), but did not alter content in roots (Fig. 8F), our results could be related to an increase in amino acid

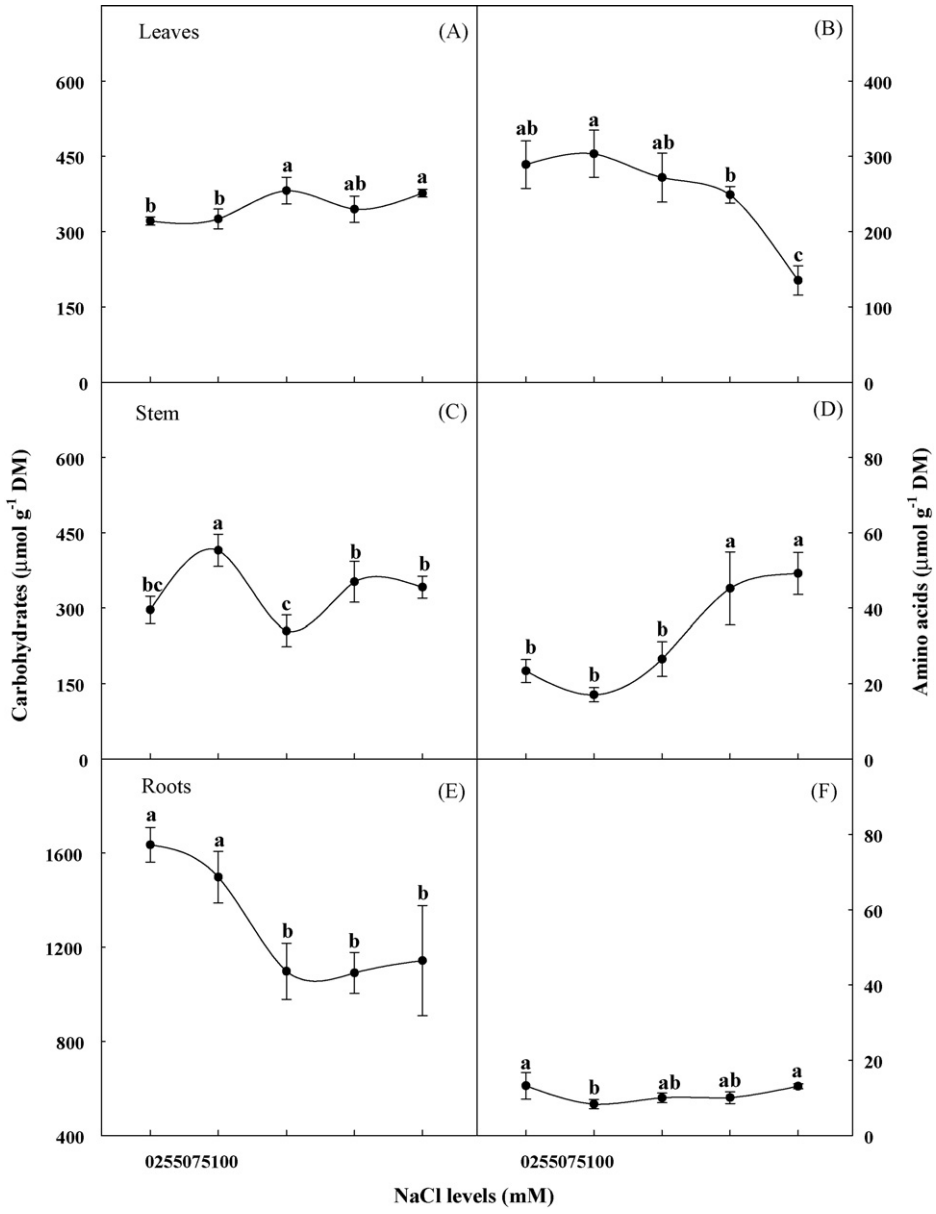

Fig. 8. Soluble carbohydrates and free amino acids content in leaves (A and B), stem (C and D), and roots (E and F) in young umbu plants cultivated under increasing NaCl levels. DM: dry mass. Means of six replicates ± S.D. are shown. Different letters denote statistical difference by Tukey's test ($P < 0.05$) among treatments.

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degradation or inhibition in synthesis jointly with reductions in degradation or increases in protein synthesis. Considering that soluble carbohydrate contents in leaves and roots were much higher than free amino acids, our results suggest a greater participation of carbohydrates than amino acids in maintaining water relations in both leaves and roots of umbu plants.

Summarizing, salt stress did not significantly affect the initial growth, transpiration, diffusive resistance, or leaf water potential of umbu plants grown in salt levels up to 50 mM NaCl. The low Na^+ and Cl^- retention capacity in stem and roots may be responsible for the high ion levels observed in the leaves. The organic solute accumulation at the salt levels studied was not shown to be a physiological trait in response to salt stress in umbu plants. These results suggest that young umbu plants tolerate salinity levels until 50 mM NaCl without showing significant physiomorphologic alterations in the initial developmental phase.

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