Available online at www.sciencedirect.com
ScienceDirect
Flora 203 (2008) 437–447
FLORA
www.elsevier.de/flora

Morphological and physiological responses of the halophyte, *Odyssea paucinervis* (Staph) (Poaceae), to salinity

Gonasageran Naidoo*, Rita Somaru, Premila Achar

School of Biological and Conservation Sciences, University of KwaZulu – Natal, P/B X54001, Durban 4000, South Africa

Received 28 March 2007; accepted 23 August 2007

Abstract

In this study, salt tolerance was investigated in *Odyssea paucinervis* Staph, an ecologically important C_4 grass that is widely distributed in saline and arid areas of southern Africa. Plants were subjected to 0.2%, 10%, 20%, 40%, 60% and 80% sea water dilutions (or 0.076, 3.8, 7.6, 15.2, 22.8, and 30.4 parts per thousand) for 11 weeks. Increase in salinity from 0.2% to 20% sea water had no effect on total dry biomass accumulation, while further increase in salinity to 80% sea water significantly decreased biomass by over 50%. Morphological changes induced by salinity included reductions in the number of culms, leaves and internodes as well as decreases in internode length and leaf length:leaf width ratios. Carbon dioxide exchange, leaf conductance and transpiration decreased at salinities of 40% and higher, while quantum yield of photosystem II (PSII), electron transport rate (ETR) through PSII and intrinsic photosynthetic efficiency generally decreased at salinities of 60% and higher compared to 0.2% sea water. Concentrations of Na^+ and Cl^- increased significantly with salinity increase in both roots and shoots. Na^+/K^+ ratios in the roots and shoots ranged from 0.66 to 3.28 and increased with increase in substrate salinity. The maximal rate of secretion at 80% sea water was 415 nmol cm^{-2} d^{-1} for Na^+ and 763 nmol m^{-2} d^{-1} for Cl^- with high selectivity for these two ions. Predawn and midday ψ decreased with increase in salinity and were more negative than those of the treatment solutions. The concentration of proline increased with increase in salinity in both roots and shoots. The data clearly indicated that *O. paucinervis* is a highly salt-tolerant species that is morphologically and physiologically adapted to a saline environment.

Keywords: Gas exchange; Ion relations; Salt secretion; Salt tolerance; Southern Africa; Water relations

Introduction

Odyssea paucinervis Staph, a perennial C_4 grass of the subfamily Chloridoideae (Clayton and Renvoize, 1986), is widely distributed in Namibia, Botswana and South Africa. The species commonly occurs in saline or alkaline desert soils adjacent to salt pans and flats and appears to be drought and salt tolerant. Ecologically, the species is often the major primary producer in saline areas and is an important component in food chains in these arid environments. It is of considerable forage value as it is grazed by many herbivores, especially on the margins of inland saline pans and flats. Its distribution suggests that the species may have potential for hay and pasture and as a low maintenance ground cover in saline areas.

Salt tolerance in halophytes, which has been reviewed extensively (Flowers et al., 1986; Munns et al., 1983; Yeo, 1998; Zhu, 2001), involves a range of adaptations

*Corresponding author. Tel.: +27 31 2607367; fax: +27 31 2607364.
E-mail address: naidoogn@ukzn.ac.za (G. Naidoo).

0367-2530/$ - see front matter © 2008 Elsevier GmbH. All rights reserved.
doi:10.1016/j.flora.2007.08.003

that includes germination responses (Ungar, 1982), selective uptake and transport of ions (Serrano et al., 1999), ion compartmentation (Epimashko et al., 2004; Leigh, 1997), production of compatible osmolytes (Huang et al., 2000; Rhodes and Hanson, 1993), succulence and salt secretion (Naidoo and Naidoo, 1998; Ramadan, 2000). These adaptations have been suggested to be under genetic control (Apse and Blumwald, 2002; Borsani et al., 2003).

Previous work established that *O. paucinervis* possesses bicellular salt glands on the abaxial leaf surface (Somaru et al., 2002) like other members of the Poaceae (Liphschitz and Waisel, 1982) and that the secreted material is predominantly Na^+ and Cl^-. No information, however, is available on growth, productivity and salt tolerance of this species. Determination of species-specific salt tolerance mechanisms contributes to a better understanding of species composition and zonation and their dynamics, as well as their competitive interactions with other species (Hootsmans and Wiegman, 1998). In this study, we determined the effects of salinity on morphology, biomass accumulation, ion and water relations and gas exchange characteristics of a hitherto poorly studied species. The following questions were addressed: (1) What are the limits and mechanisms of salt tolerance in this species? (2) Are there any potential indicators of salt tolerance, either morphological or physiological? (3) What are the constraints imposed by high salinity on the ecophysiology of this species?

Materials and methods

Plant material and cultural conditions

Rhizomes of *O. paucinervis,* collected from a salt flat near Walvis Bay, Namibia, were cut into 8 cm segments and potted in a 3:1 mixture of sand and vermiculite. Pots were watered with tap water and fertilized weekly with one-fifth strength nutrient solution (Hoagland and Arnon, 1950). After 3 weeks, individual plants of approximately the same size (120 mm in height with three culms) were transferred to 15 cm diameter by 15-cm-depth plastic pots containing the same potting mixture as above. After 3 months, salinity treatments were gradually introduced using dilutions of sea water. Salinity was added at increments of 10% sea water every 3 days until final treatment levels were attained. Plants were subjected to 0.2%, 10%, 20%, 40%, 60% and 80% seawater dilutions (or 0.076, 3.8, 7.6, 15.2, 22.8, and 30.4 parts per thousand), irrigated from below in plastic trays. These sea water solutions were equivalent to osmotic potentials of −0.005, −0.25, −0.5, −1.0, −1.5 and −2.0 MPa, respectively. Salinity of the treatment solutions was monitored daily and distilled water added to compensate for evapotranspirational losses. There were five replications per treatment and all plants were fertilized every 2 weeks with half-strength nutrient solution. Treatment solutions were renewed every 10 d and all pots maintained in an air-conditioned glasshouse at 25 °C, 50% relative humidity and under natural light. Maximum PPFD during the experimental period was 1800 $\mu mol\, m^{-2} s^1$. Plants were subjected to salinity treatments for 11 weeks. The experimental unit for all treatments was one pot.

At the termination of the experiment, measurements were made of the number of culms, leaves and internodes, internode length, and length and width of leaves. At harvest, soil was removed from roots by quickly rinsing under water, and then in iso-osmotic mannitol containing 2.5 $mol\, m^{-3}$ $CaSO_4$ to remove ions from the free space and give a realistic estimate of root ion concentrations. Plants were separated into roots and shoots and fresh mass determined. The material was then oven-dried at 70 °C to constant mass and reweighed. Dried root and shoot samples were milled through a 1 mm screen and stored in plastic vials.

Gas exchange

Leaf gas exchange characteristics were determined 10 weeks after treatment initiation to provide information on the effects of salinity on CO_2 assimilation. Measurements were taken using a Minicuvette System (H. Walz, Effeltrich, Germany) attached to a BINOS CO_2/H_2O differential gas analyzer (Leybold-Heraeus, Hanau, Germany). The terminal portion of a leafy shoot was placed into the assimilation chamber and exposed to direct sunlight. The shoot was allowed to equilibrate for 10 min to the environmental conditions in the chamber prior to measurements. Measurements were taken on each replicate between 1000 and 1200 h in saturating light ($>1000\, \mu mol\, m^{-2} s^{-1}$) and ambient temperature (28–30 °C). Microclimatic conditions in the chamber were set to track ambient conditions. CO_2 and water vapor were analyzed by a differential IRGA (Binos 2, Heraeus, Hanau, Germany) while ambient CO_2 concentration was measured by an absolute IRGA. The temperature of the leaf was measured by means of thermocouples and incident PPFD by a quantum sensor (190 S Li-Cor Inc., Lincoln, Nebraska, USA) mounted adjacent to the leaf in the assimilation chamber.

Chlorophyll fluorescence

Chlorophyll fluorescence was determined with a field portable, pulse amplitude, modulated fluorometer (PAM 2100, Walz, Effeltrich, Germany). All measurements were taken on the lamina, midway between the base and the tip of mature leaves. Quantum yield of

photosystem II (PSII) electron transport ($\Delta F/F_m'$) was calculated as $(F_m'-F)/F_m'$ (Genty et al., 1989), where F is the light-adapted fluorescence and F_m' the maximum light-adapted fluorescence when a saturating light pulse of 7500 μmol m^{-2} s^{-1} PPFD for 700 ms duration is superimposed on the prevailing environmental irradiance level (Schreiber et al., 1995). Electron transport rate (ETR) through PSII was calculated as $0.5 \times 0.84 \times \text{PPFD} \times \Delta F/F_m'$ assuming that 84% of incidental light is absorbed by the leaves and that the photons are equally distributed between PSII and PSI (Schreiber et al., 1995). Measurements of chlorophyll fluorescence were taken at ambient conditions at saturating light on the same day on which gas exchange measurements were made. There were three measurements per replicate. The intrinsic efficiency of light energy conversion of PSII ($F_v/F_m = F_m - F_o/F_m$ where F_o and F_m are the minimal and maximal fluorescence yields of a dark-adapted sample with all PSII reaction centers fully open or closed, respectively) was measured after 30 min dark adaptation with a dark leaf clip (Walz, Effeltrich, Germany). For F_v/F_m, two measurements were taken per replicate at midday.

Salt secretion

After 9 weeks of treatment, three mature leaves in each pot were rinsed with distilled water to remove previously secreted salt from the leaf surface, tagged and blotted dry. After 5 d, secreted salts from each leaf were rinsed off for 10 s with 10 ml of double distilled water and the wash water sealed in air-tight vials. The washed leaves were excised from the plant and leaf areas determined with a leaf area meter. The leaves were then dried to constant mass at 70 °C, weighed, cut into small fragments and extracted with 5 ml boiling water for 30 min.

Ion analyses

Milled root and shoot material was extracted with boiling water (1:20 wt/vol) for 30 min. Concentrations of Na^+ in roots and shoots as well as in the secreted solutions were determined by flame emission, while K^+, Ca^{2+} and Mg^{2+} were determined by atomic absorption spectrophotometry using a Varian Spectra AA-10. Chloride was determined with an Orion Cl^- selective electrode following procedures and precautions recommended by the manufacturers.

Water potential

At the termination of the experiment, the water potential of terminal shoots was measured in triplicate with a Scholander pressure chamber (Soil Moisture Equipment Corporation, Santa Barbara, CA, USA) using a pressurization rate of 0.2 MPa per min. The pressure chamber was partly lined with moistened paper to reduce evaporation. Predawn (between 5 h 30 min and 6 h 30 min) and midday (between 12 h 30 min and 13 h 30 min) ψ were determined for each of three replicates per treatment. Diurnal course of shoot water potential (from predawn to dusk) was determined for plants maintained at 0.2% and 80% sea water.

Proline

At harvest, subsamples of roots and shoots were excised from each replicate, frozen in liquid nitrogen and freeze-dried. Proline, a compatible organic solute which accumulates in response to salt and drought stress, was extracted from freeze-dried milled samples with 3 ml of 3% sulfosalicylic acid and determined according to the procedure of Bates et al. (1973).

Statistical analyses

All data met the criteria of normality and homogeneity and were analyzed with the Super ANOVA statistical package (Abacus Concepts Inc., CA., 1991). Treatment means were compared using Tukey–Kramer multiple comparisons test at $P<0.05$. For all analyses where multiple measurements were collected on each replicate (gas exchange and chlorophyll fluorescence), data were pooled.

Results

Morphology

Increase in salinity from 0.2% to 20% sea water had no effect on total dry biomass, while further increases to 40%, 60% and 80% sea water significantly decreased biomass ($F_{5,24} = 5.1$, $P<0.003$) by 58%, 66% and 80%, respectively, compared to the 0.2% sea water treatment (Fig. 1 A). Morphological changes induced by salinity included significant reduction in number of leaves ($F_{5,24} = 25.5$, $P<0.001$), internodes ($F_{5,24} = 11.9$, $P<0.0001$), culms ($F_{5,24} = 20.7$, $P<0.0001$), and leaf length:leaf width ratio ($F_{5,24} = 8.85$, $P<0.0001$) as well as decreases in internode length ($F_{5,24} = 34.3$, $P<0.0001$) (Fig. 1B–F).

At sea water concentrations below 40%, leaves were larger, light green in color and relatively soft, while at higher salinities leaves were smaller, dark green and rigid. As salinity increased leaf angle became more acute and in the 60% and 80% sea water treatments leaves were almost vertical. Leaf rolling in response to salinity became apparent about 6 weeks after treatment and was

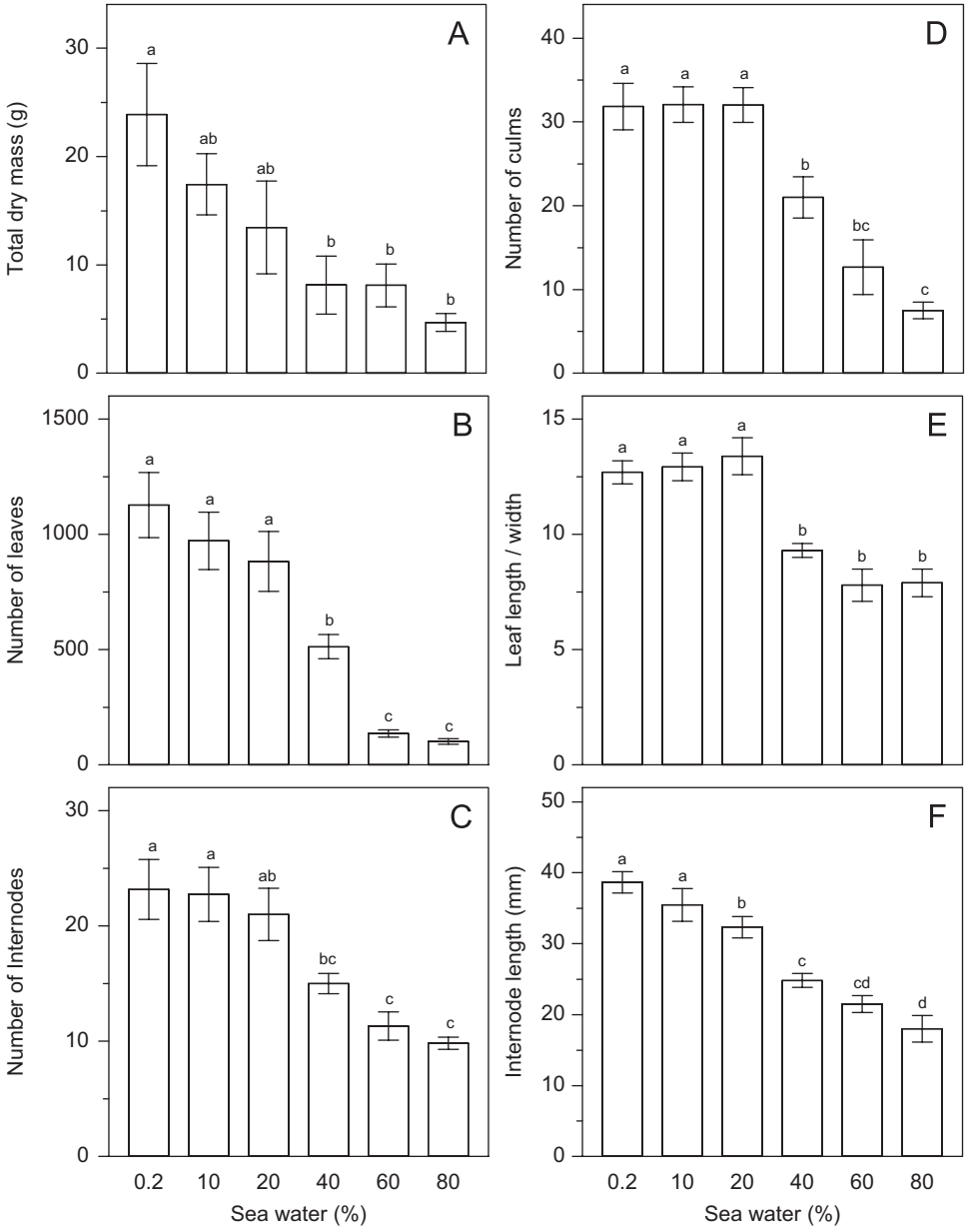

Fig. 1. Effects of salinity on total dry biomass accumulation (A), number of leaves (B), number of internodes (C), number of culms (D), leaf length/width (E), and internode length (F) in *Odyssea paucinervis*. Plants were subjected to salinity treatments for 11 weeks. Means ± S.E. are given, $n = 5$. Means with different letters are significantly different at $P < 0.05$ using Tukey–Kramer multiple comparisons test.

most pronounced in the 60% and 80% sea water treatments. There were significant reductions in the number ($F_{5,24} = 19.43$, $P < 0.0001$) and length ($F_{5,24} = 17.51$, $P < 0.0001$) of inflorescences in 60% and 80% sea water compared to the other treatments (results not presented).

Gas exchange

Carbon dioxide exchange was unaffected by salinity increase from 0.2% to 20% sea water but decreased progressively with further increase in salinity to 80% ($F_{5,24} = 7.74$, $P < 0.002$). Decreases in CO_2 exchange with salinity increase were associated with parallel decreases in leaf conductance and transpiration (Fig. 2A–C). At 80% sea water, CO_2 exchange was more reduced than transpiration which, lowered water use efficiency in this treatment compared to the others.

Chlorophyll fluorescence

Quantum yield of PSII electron transport (yield), ETR through PSII and intrinsic PSII efficiency were unaffected by salinity increase from 0.2% to 40% sea

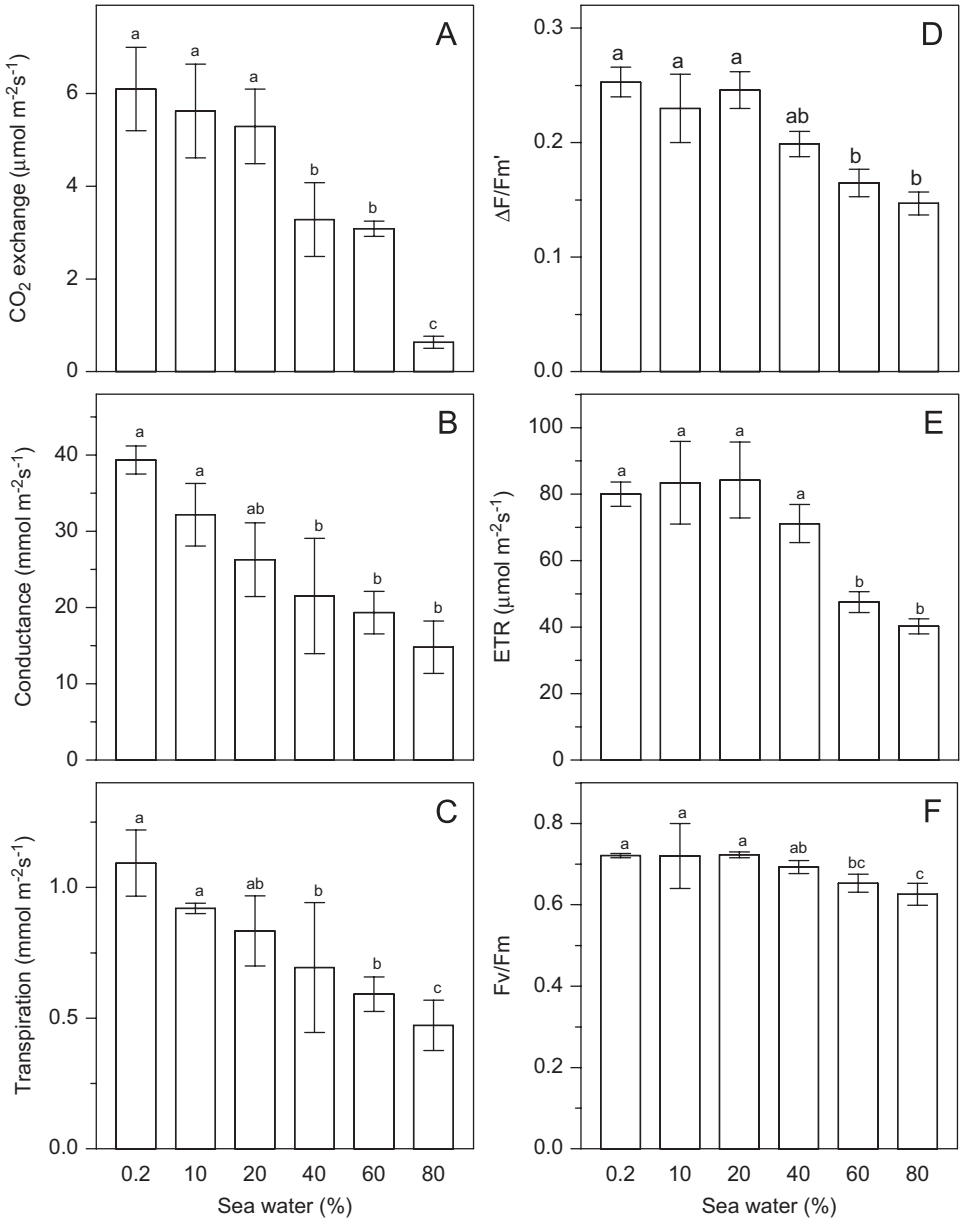

Fig. 2. Effects of salinity on carbon dioxide exchange (A), leaf conductance (B) and transpiration (C), photosystem II quantum yield (D), electron transport rate through PS II (E) and photochemical efficiency of PS II (F) in *Odyssea paucinervis*. Other details as for Fig. 1.

water but decreased significantly with further increase in salinity to 80% (Fig. 2D, E). Midday F_v/F_m values decreased ($F_{5,24} = 6.6$, $P < 0.002$) from 0.72 in the 0.2% sea water treatment to 0.63 in 80% sea water (Fig. 2F).

Ions in tissues

Increase in substrate salinity significantly increased concentrations of Na^+ and Cl^- in shoots and roots. In roots Na^+ and Cl^- concentrations increased significantly with increase in salinity from 0.2% to 10%. Between 10% and 60% sea water there were no differences between treatments, while further increase to 80% significantly increased root Na^+ ($F_{5,24} = 2.8$, $P < 0.03$) and Cl^- ($F_{5,24} = 3.62$, $P < 0.002$) (Fig. 3A, B). Salinity increase from 0.2% to 20% sea water had no effect on shoot Na^+ or Cl^-, while further increase to 40% and higher significantly increased shoot concentrations of Na^+ ($F_{5,24} = 3.52$, $P < 0.016$) and Cl^- ($F_{5,24} = 7.4$, $P < 0.0003$) (Fig. 3D, E). The concentration of Cl^- in shoots was similar to those for roots but shoot Na^+ concentrations were lower than those in roots. Na^+/K^+ ratios, which were higher in the roots than shoots, generally increased with increase in substrate salinity and ranged from 1.76 to 3.28 in roots and from

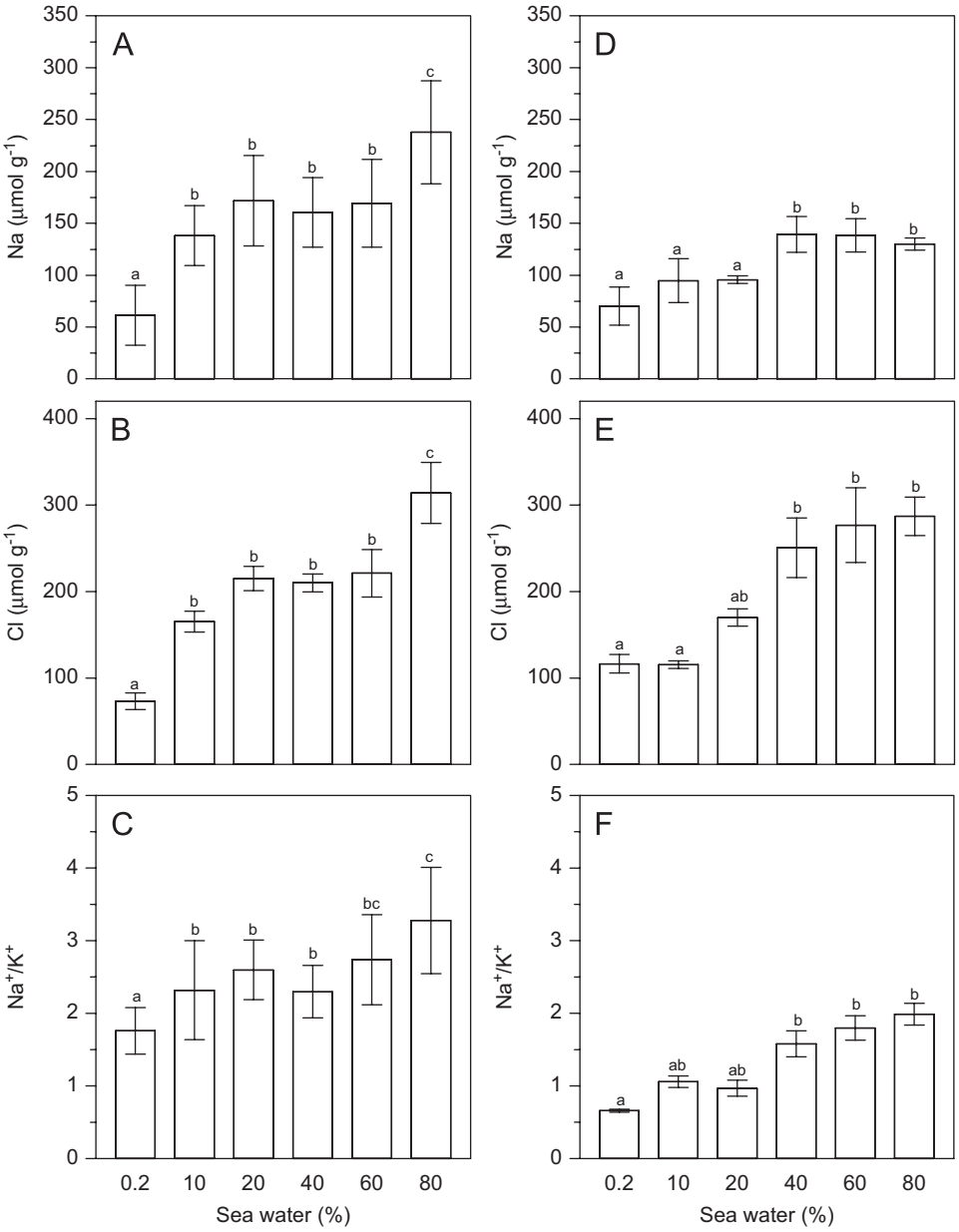

Fig. 3. Effects of salinity on concentrations of Na, Cl and Na/K ratios in roots (A–C) and shoots (D–F) of *Odyssea paucinervis*. Other details as for Fig. 1.

0.66 to 1.99 in shoots (Fig. 3C–F). Concentrations of Ca^{2+} and Mg^{2+} in roots and shoots were considerably lower than those of Na^+ and Cl^- with no differences between treatments, except for root Ca^{2+} which was significantly higher at 40% and above compared to the 0.2% sea water treatment (results not presented).

Salt secretion

The major ions secreted from the leaves were Na^+ and Cl^- with smaller amounts of K^+ (Fig. 4A–C), Ca^{2+} and Mg^{2+} (results not presented). Concentrations of Ca^{2+} and Mg^{2+} were considerably lower than those of Na^+ and Cl^-. Increase in salinity from 0.2% to 40% sea water had no effect on secretion of Na^+ and Cl^-, while further increase to 60% and 80% significantly increased secretion of Na^+ ($F_{5,24} = 27.1$, $P < 0.0001$) and Cl^- ($F_{5,24} = 28.9$, $P < 0.0001$). K^+ (Fig. 4B), Ca^{2+} and Mg^{2+} in the secretion followed trends similar to those of Na^+ and Cl^-, but at lower concentrations. The negative charge of Cl^- in the secretion was balanced predominantly by Na^+, and by K^+, Ca^{2+}, Mg^{2+} and other undetermined cations.

Analysis of the leaves used for the secretion study showed that Na^+ and Cl^- were the predominant inorganic ions. In the leaves, the concentrations of Na^+ ($F_{5,24} = 31.8$, $P < 0.0001$) and Cl^- ($F_{5,24} = 15.8$,

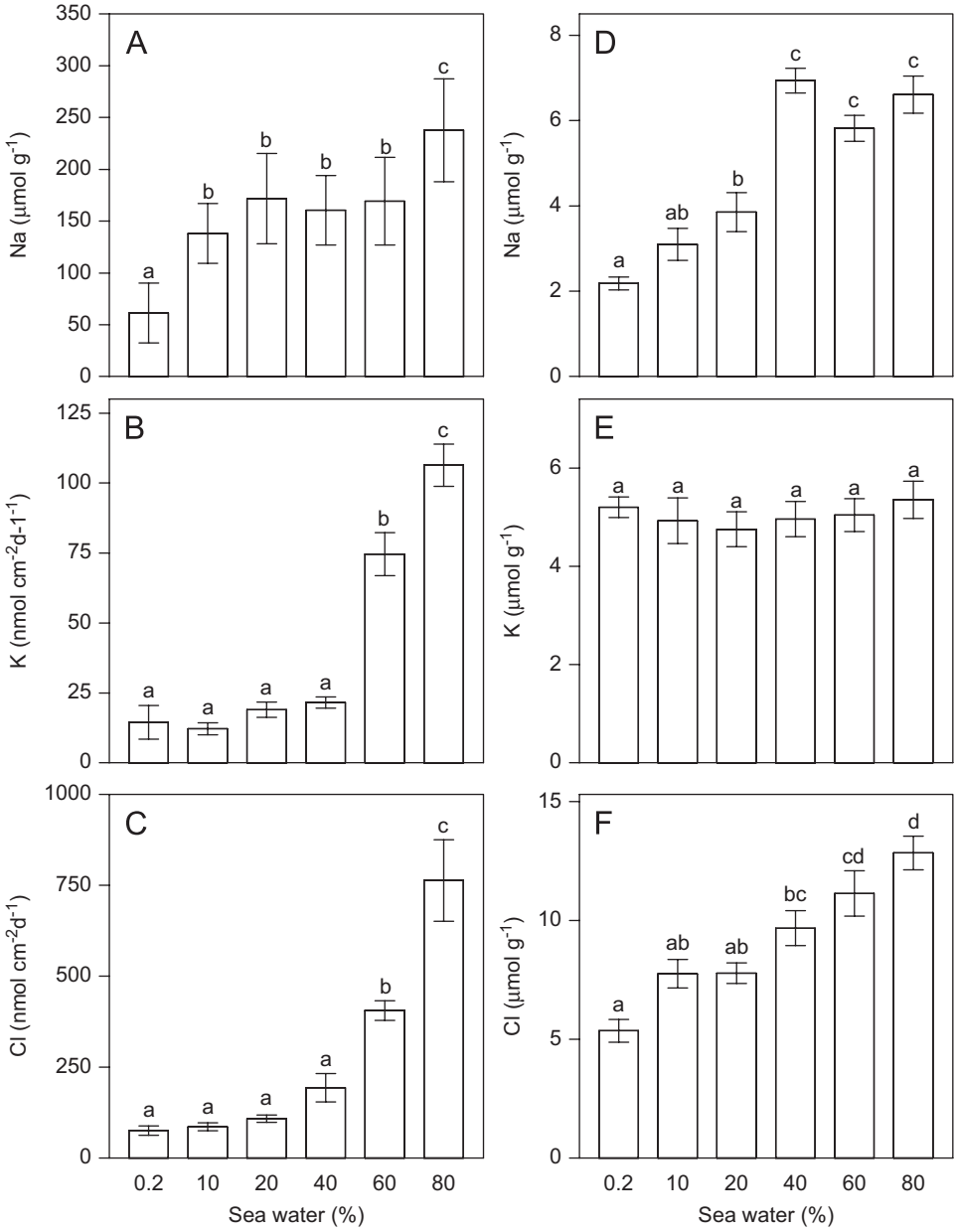

Fig. 4. Effects of salinity on secretion of Na (A), K (B) and Cl (C) and leaf concentrations of Na (D), K (E) and Cl (F) in *Odyssea paucinervis.* Other details as for Fig. 1.

$P<0.0001$) increased significantly with increase in substrate salinity (Fig. 4D, F). There were no differences in leaf concentrations of Na^+ or Cl^- between the 60% and 80% sea water treatments (Fig. 4D, F). In contrast, K^+ concentrations in leaves did not respond to the salinity treatments. The concentrations of Na^+ and Cl^- in leaves (Fig. 4) were much smaller than the corresponding concentrations for shoots (Fig. 3), probably because shoots included leaves and culms.

Water potential

Predawn and midday shoot ψ (Fig. 5A, B) decreased with increase in substrate salinity and ranged from –0.64 to –3.03 MPa at predawn ($F_{5,24} = 24.7$, $P<0.0001$) and from –1.38 to –3.67 at midday ($F_{5,24} = 27.4$, $P<0.0001$). In all treatments shoot ψ was more negative than that of the treatment sea water solution. The diurnal course of shoot ψ in the 0.2% and 80% sea water treatments indicated that the midday minimum was followed by a slow but complete recovery at dusk when ψ values were similar to those at predawn (results not presented).

Proline

Proline concentrations increased significantly with increase in substrate salinity in roots ($F_{5,24} = 56.2$,

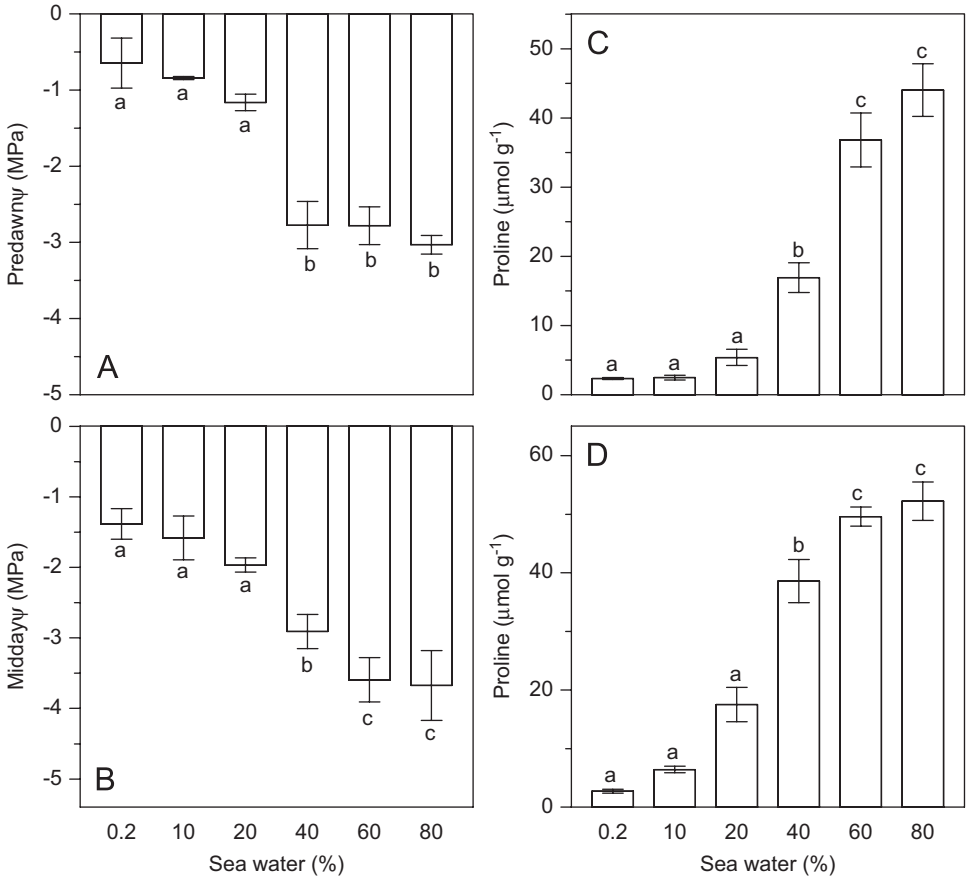

Fig. 5. Effects of salinity on predawn (A) and midday (B) water potential and proline concentrations in roots (C) and shoots (D) of *Odyssea paucinervis*. Other details as for Fig. 1.

$P<0.0001$) and shoots ($F_{5,24} = 79$, $P<0.0001$). In the 80% sea water treatment, proline levels were at least 15-fold greater than those at 0.2% sea water in both roots and shoots (Fig. 5C, D).

Discussion

Morphology

This study has demonstrated that *O. paucinervis* is a highly salt-tolerant species that is able to survive, grow and flower at salinities up to 80% sea water. The morphometric and biomass accumulation data suggest that *O. paucinervis*, like most other monocotyledonous halophytes, exhibits little or no growth stimulation at low salinities (Munns, 1993; Naidoo and Kift, 2006), while higher salinities reduced growth. In the field, this species naturally inhabits brackish and highly saline areas. Progressive suppression of whole plant growth with increase in salinity was associated with several specific structural changes that presumably prevented water balance from becoming detrimental to plant survival (Pezeshki and DeLaune, 1994). These changes included reduction in the number of culms, leaves and internodes, length of internodes and length and width of leaves. These reductions were associated with progressive decrease in shoot ψ as salinity increased. Despite growth reduction at high salinities, plants appeared healthy with no signs of salt injury or mortality, even at 80% sea water for 11 weeks.

Gas exchange and chlorophyll fluorescence

Decreases in CO_2 exchange, quantum yield of PS II, ETR through PS II and F_v/F_m with salinity increase suggested that photosynthetic efficiency was reduced at high salinities. Evidence suggests that salt-induced reduction in chloroplast stromal volume, as well as generation of reactive oxygen species at high salinities, have deleterious effects on cell metabolism, photosynthetic capacity and growth (Borsani et al., 2001; Polle, 1997; Price and Hendry, 1991). Smaller, near vertical, rolled leaves in the higher salinity treatments probably minimized high leaf to air vapor pressure deficits, reduced transpiration and salt loading and contributed to more conservative water use (Björkman and Demming-Adams, 1995). Significant depression in F_v/F_m in

the 60% and 80% sea water treatments, compared to lower salinities, suggested that photoinhibition occurred despite vertical leaf orientation. Recovery in midday reductions in the efficiency of PSII to predawn values at dusk suggests that photoinhibition was due to down-regulation of the photosynthetic apparatus rather than due to photodamage (Christian, 2005).

Ion relations

Lowering of tissue ψ in *O. paucinervis,* as well as in most halophytes with salinity increase, is achieved primarily by inorganic ion uptake, specifically Na^+ and Cl^- (Marcum, 2006). Ion distributional patterns were typical for those of salt-tolerant species where the major portion of the absorbed ions is translocated to the shoots, which act as a sink (Munns, 1993). Accumulation of Na^+ and Cl^- in shoots would cause ionic imbalance (Zhu, 2001) and deleterious effects on cellular metabolism (Serrano et al., 1999). Plant cells respond to salt stress by increasing Na^+ efflux at the plasma cell membrane and Na^+ accumulation in the vacuole (Borsani et al., 2003). Pathways for Na^+ entry into cells have been elucidated (Zhu, 2000) and the cloning of Na^+/H^+ antiporters (Ohta et al., 2002) has demonstrated the importance of vacuolar Na^+ compartmentation in salt tolerance.

Salt tolerance involves not only adaptation to Na^+ influx, but also acquisition of K^+, whose uptake is adversely affected by high external Na^+ concentration, due to the chemical similarity of these two ions. Maintenance of a high K^+ cytosolic concentration with increasing salinity apparently occurs via highly selective pathways at the root–soil interface and is an important determinant of salt tolerance (Maathuis and Amtmann, 1999; Rodriguez-Navarro, 2000). In *O. paucinervis,* Na^+/K^+ ratios generally increased with salinity increase and ranged from 1.76 to 3.28 in roots and 0.66 to 1.99 in shoots, which are similar to those reported in other members of the Poaceae (Flowers et al., 1986). Since leaf K^+ concentrations were maintained at a constant level for all sea water treatments, the increase in Na^+/K^+ ratio was due to an increase in Na^+ concentration only with no apparent negative effect of excess Na^+ on K^+ uptake.

Sequestration of Na^+ within vacuoles requires the accumulation of compatible organic solutes in the cytosol to balance the low osmotic potential in the vacuole, and to reduce oxidative damage by free radicals produced in response to high salinity (Hasegawa et al., 2000). In *O. paucinervis,* the levels of proline, which increased with increasing salinity, were insufficient to contribute to cytoplasmic osmotic adjustment. It is possible that proline is just a stress metabolite that preserves protein structure and activity and reduces enzyme denaturation by inactivating hydroxyl radicals and other reactive chemical species (Saradhi et al., 1995). Moreover, several studies suggest that glycinebetaine, rather than proline, contributes to osmotic adjustment in grasses (Colmer et al., 1995; Marcum, 2006).

Salt secretion by glands, which is an important adaptive mechanism to regulate ion concentration in leaves of many halophytes (Larcher, 1995), is highly efficient in some species (Scholander et al., 1962). Similar to other species (Marcum, 2006; Worku and Chapman, 1998), salt secretion in *O. paucinervis* was highly selective for Na^+ and Cl^- and increased with substrate salinity and tissue concentration of these ions. At higher salinities, leaf ion concentrations remained relatively constant even though ion secretion rates increased. This suggests the existence of an efficient ion exclusion mechanism within roots at high salinities that enabled secretion by glands to keep pace with ion influx. In other species, salt secretion increased with increase in substrate salinity to about 150–200 mM NaCl, after which it declined (Liphschitz and Waisel, 1982). Comparison of salt secretion rates among studies is difficult due to differences in environmental conditions and plant factors, such as age. The highest rate of secretion for *O. paucinervis* was 415 nmol Na^+ cm^{-2} d^{-1} at 80% sea water, which is similar to that reported for *Spartina anglica* (383 nmol Na^+ cm^{-2} d^{-1}) at a salinity of 0.1 M NaCl (Rozema et al., 1981) but lower than that for *Sporobolus virginicus* (700 nmol Na^+ cm^{-2} d^{-1}) at 40% sea water (Naidoo and Naidoo, 1998). At high substrate salinities and increased salt loading in leaves, secretion may be overwhelmed by saturation of carrier molecules and/or ion channels in the membranes of the glands (Ramadan, 2000).

This study has demonstrated that *O. paucinervis* is a highly salt-tolerant species that is adapted to saline environments. The natural distribution of this species in saline or alkaline desert soils and on the fringes of salt pans supports our findings. There appears to be a good relationship between field distribution of the species and its physiological tolerance to salinity under the controlled conditions in this study. Similar to other monocotyledonous halophytes, growth is best at low salinities ($\leqslant$20% sea water) and decreases at higher salinities. Salt tolerance appears to be achieved through an array of stress coping mechanisms including ion exclusion, ion accumulation, salt secretion and suitable osmotic adjustment. Plant indicators of high salinity conditions include suppression of whole plant growth including reduction in the number of culms, leaves and internodes, length of internodes and length and width of leaves. Moreover, at very high salinities, plants are stunted with near-vertical spiny leaves that exhibit low photosynthetic rates and efficiencies. The data reported herein suggest that this species may be a potential

candidate for cultivation as hay and pasture and as a low maintenance ground cover in saline areas.

Acknowledgments

The authors are grateful to R. Jimmy, A. Kaliden, P. Ellapen and A. Jonathan for technical assistance.

References

Apse, M.P., Blumwald, E., 2002. Engineering salt tolerance in plants. Curr. Opin. Biotechnol. 13, 146–150.

Bates, L.S., Waldren, R.P., Teare, I.D., 1973. Rapid determination of free proline for water-stress studies. Plant Soil 39, 205–207.

Björkman, O., Demming-Adams, B., 1995. Regulation of photosynthetic light energy capture, conversion and dissipation in leaves of higher plants. In: Schulze, E.D., Caldwell, M.M. (Eds.), Ecophysiology of Photosynthesis, Ecol. Stud., vol. 100. Springer, Berlin, pp. 17–47.

Borsani, O., Valpuesta, V., Botella, M.A., 2001. Evidence for a role of salicylic acid in the oxidative damage generated by NaCl and osmotic stress in *Arabidopsis* seedlings. Plant Physiol. 126, 1024–1030.

Borsani, O., Valpuesta, V., Botella, M.A., 2003. Developing salt tolerant plants in a new century: a molecular biology approach. Plant Cell Tissue Organ Cult. 73, 101–115.

Christian, R., 2005. Interactive effects of salinity and irradiance on photoprotection in acclimated seedlings of two sympatric mangroves. Trees 19, 596–606.

Clayton, W.D., Renvoize, S.A., 1986. Genera Graminum – Grasses of the World. Her Majesty's Stationery Office, London, p. 389.

Colmer, T.D., Epstein, E., Dvořák, J., 1995. Differential solute regulation in leaf blades of various ages in salt-sensitive wheat and a salt-tolerant wheat × *Lophopyrum elongatum* (Host) A Love amphiploid. Plant Physiol. 108, 1715–1724.

Epimashko, S., Meckel, T., Fischer-Schliebs, E., Lüttge, U., Thiel, G., 2004. Two functionally different vacuoles for static and dynamic purposes in one plant mesophyll leaf cell. Plant J. 37, 294–300.

Flowers, T.J., Hajibagheri, M.A., Clipson, N.J.W., 1986. Halophytes. Quart. Rev. Biol. 61, 313–337.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta 990, 87–92.

Hasegawa, P.M., Bressan, R.A., Zhu, J.K., Bohnert, H.J., 2000. Plant cellular and molecular responses to high salinity. Annu. Rev. Plant Physiol. Plant Mol. Biol. 51, 493–499.

Hoagland, D.R., Arnon, D.I., 1950. The water culture method of growing plants without soil. Calif. Agric. Exp. St. Circ. 347, 1–32.

Hootsmans, M.J.H., Wiegman, F., 1998. Four halophyte species growing under salt stress: their salt life. Aquat. Bot. 62, 81–94.

Huang, J., Hirji, R., Adam, L., Rozwadowski, K.L., Hammerlindl, J.K., Kellar, W.A., Selvaraj, G., 2000. Genetic engineering of glycinebetaine production toward enhancing stress tolerance in plants: metabolic limitations. Plant Physiol. 122, 747–756.

Larcher, W., 1995. Physiological Plant Ecology, third ed. Springer, Berlin.

Leigh, R., 1997. The solute composition of the vacuoles. Adv. Bot. Res. 25, 253–295.

Liphschitz, N., Waisel, Y., 1982. Adaptations of plants to saline environments: salt secretion and glandular structure. In: Sen, D.N., Rajpurohit, K.S. (Eds.), Tasks for Vegetation Science, vol. 2. W. Junk, Hague, pp. 197–214.

Maathuis, F.J.M., Amtmann, A., 1999. K^+ nutrition and Na^+ toxicity: the basis of cellular K^+/Na^+ ratios. Ann. Bot. 84, 123–133.

Marcum, K.B., 2006. Saline tolerance physiology in grasses. In: Khan, M.A., Weber, D.J. (Eds.), Ecophysiology of High Salinity Tolerant Plants. Tasks for Vegetation Science, vol. 40. Springer, Berlin, pp. 157–172.

Munns, R., 1993. Physiological processes limiting plant growth in saline soil: some dogmas and hypotheses. Plant Cell Environ. 16, 15–24.

Munns, R., Greenway, H., Kirst, G.O., 1983. Halotolerant Eukaryotes. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Encyclopedia of Plant Physiology, vol. 12C. Springer, Berlin–Heidelberg–New York, pp. 59–135.

Naidoo, G., Naidoo, Y., 1998. Salt tolerance in *Sporobolus virginicus*: the importance of ion relations and salt secretion. Flora 193, 334–337.

Naidoo, G., Kift, J., 2006. Responses of the saltmarsh rush *Juncus kraussii* to salinity and waterlogging. Aquat. Bot. 84, 217–225.

Ohta, M., Hayashi, Y., Nakashima, A., Hamada, A., Tanaka, A., Nakamura, T., Hayakawa, T., 2002. Introduction of a Na^+/H^+ antiporter gene from *Atriplex gmelini* confers salt tolerance to rice. FEBS Lett. 532, 279–282.

Pezeshki, S.R., DeLaune, R.D., 1994. Variations in responses of two US Gulf Coast populations of *Spartina alterniflora* to hypersensitivity. J. Coastal Res. 2, 89–95.

Polle, A., 1997. Defense against photo-oxidative damage in plants. In: Scandalios, J.G. (Ed.), Oxidative Stress and Molecular Biology of Antioxidant Defenses. Cold Springs Harbour Laboratories, New York, pp. 623–666.

Price, A., Hendry, G., 1991. Iron catalysed oxygen radical formation and its possible contribution to drought damage in nine native grasses and three cereals. Plant Cell Environ. 14, 477–484.

Ramadan, T., 2000. Dynamics of salt secretion by *Sporobolus spicatus* (Vahl) Kunth from sites of differing salinity. Ann. Bot. 87, 259–266.

Rhodes, D., Hanson, A.D., 1993. Quaternary ammonium and tertiary sulfonium compounds in higher plants. Ann. Rev. Plant Physiol. Plant Mol. Biol. 44, 357–384.

Rodriguez-Navarro, A., 2000. Potassium transport in fungi and plants. Biochem. Biophys. Acta 1469, 1–30.

Rozema, J., Gude, H., Pollak, G., 1981. An ecophysiological study of the salt secretion of four halophytes. New Phytol. 89, 201–217.

Saradhi, P.P., Arora, S., Prasad, K.V.S.K., 1995. Proline accumulates in plants exposed to UV radiation and protects against induced peroxidation. Biochem. Biophys. Res. Commun. 290, 1–5.

Scholander, P.F., Hammel, H.T., Hemmingsen, E.A., Garey, W., 1962. Salt balance in mangroves. Plant Physiol. 37, 722–729.

Schreiber, U., Bilger, W., Neubauer, C., 1995. Chlorophyll fluorescence as a nonintrusive indicator of rapid assessment of *in vivo* photosynthesis. In: Schulze, E.D., Caldwell, M.M. (Eds.), Ecophysiology of Photosynthesis, Ecol. Stud., vol. 100. Springer, Berlin–Heidelberg, pp. 49–70.

Serrano, R., Mulet, J., Rios, G., Marquez, J., de Larrinoa, I., Leube, M., Mendizabal, I., Pascual-Ahuir, A., Proft, M., Ros, R., Montesinos, C., 1999. A glimpse of the mechanism of ion homeostasis during salt stress. J. Exp. Bot. 50, 1023–1036.

Somaru, R., Naidoo, Y., Naidoo, G., 2002. Morphology and ultrastructure of the leaf salt glands of *Odyssea paucinervis* (Staph) (Poaceae). Flora 197, 67–75.

Ungar, I.A., 1982. Germination ecology of halophytes. In: Sen, D.N., Rajpurohit, K.S. (Eds.), Contributions to the Ecology of Halophytes, Tasks for Vegetation Science, vol. 2. Junk Publication, Hague, pp. 143–154.

Worku, W., Chapman, G.P., 1998. The salt secretion physiology of the Chloridoid grass, *Cynodon dactylon* (L) Pers and its implications. Sinet Ethiop. J. Sci. 21, 1–16.

Yeo, A., 1998. Molecular biology of salt tolerance in the context of whole-plant physiology. J. Exp. Bot. 49, 915–929.

Zhu, J.K., 2000. Genetic analysis of plant salt tolerance using *Arabidopsis*. Plant Physiol. 124, 941–948.

Zhu, J.K., 2001. Plant salt tolerance. Trends Plants Sci. 6, 66–71.