PHYSIOLOGICAL ADAPTATIONS OF *AVICENNIA MARINA* TO SEAWATER CONCENTRATIONS IN THE INDUS DELTA, PAKISTAN

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Abstract

Avicennia marina is the most dominant species among mangroves found in the Indus delta, Pakistan, alongwith a few populations of *Aegiceras corniculata, Rhizophora mucronata* and *Ceriops tagal*. Propagules of *Avicennia marina* collected from the Indus delta were grown in pots containing sandy soil that were sub-irrigated with 0, 25, 50, 75 and 100% seawater fortified with nitrogen. Growth and physiological responses recorded at seedling and sapling stages showed a maximum growth in 50% seawater which declined with an increase in salinity. All the other growth parameters followed more or less a similar pattern. Xylem pressure potential showed a strong positive relationship, while osmotic potential, water potential and stomatal conductance a strong negative relationship with the increase in media salinity. Proline concentrations substantially increased in treatments up to 50% seawater showing no change with further increase in salinity. Oxalate concentration decreased with increase in salinity. Sodium and chloride ions increased substantially while calcium, magnesium and potassium decreased with an increase in seawater concentrations.

Introduction

Mangroves are a diverse group of predominantly tropical trees and shrubs growing in the marine intertidal zone (Duke, 1992). They have been variously described as coastal wetlands, tidal forests and mangrove forests (Tomlinson, 1986). These forests are characterized by large variations in salinity, both spatially and seasonally related to regional climate and topographic feature (Gordon, 1993). Thus these species may be exposed to low salinity levels in estuaries to hypersaline conditions higher than seawater (Tomlinson, 1986). The mangrove forests in Sindh extend from Korangi to Seer creek touching the Indian border, whereas in Balochistan they are located in Miani Hor near the Porali river (Ansari, 1987). Preliminary investigations suggest the presence of *Avicennia marina* (98%) followed by eight other mangrove species in Pakistan (Saiful-lah, 1982). Over exploitation, pollution and reduction of fluvial discharge into the Indus Delta has caused extinction of some species as well as threatened the survival of mangrove species in Pakistan (Kogo *et al.*, 1986).

Mangroves could tolerate a large range of salinities under natural conditions (Saurez *et al.*, 1998) but their physiological mechanisms are poorly understood. There is a great deal of variation in the level of salinity required for optimal growth which varies from 10 to 50% seawater (Downton, 1982; Clough, 1984; Naidoo, 1987; Lin & Sternberg, 1992; 1995; Karim & Karim, 1993; Ball & Pidsley, 1995) and a decline in their overall growth is observed with a further increase in salinity. Similarly, decreased stomatal conductance, lower water potential and accumulation of inorganic ions are the result for most plant species from extreme saline environments (Ball & Farquhar, 1984;

Naidoo, 1987). A variety of adaptations to extreme habitats occur in mangroves such as 1) salt exclusion by root ultrafiltration (Hegemeyer, 1997), 2) salt secretion via glands (Fitzgerald, 1992), 3) ion accumulation in leaf cells for osmotic adaptation and osmotic adjustment with compatible osmotica (Popp, 1994) and 4) leaf succulence (Roth, 1992). Experiments were carried out to determine the effects of salinity on the ion accumulation, growth and water relation of *Avicennia marina* growing along the Karachi coast of Pakistan.

Materials and Methods

Propagules of *Avicennia marina* were collected during the summer of 1993 from the Indus delta populations near Karachi, Pakistan. They were immediately transferred to 36 cm diameter plastic pots filled with acid washed beach sand. The pots were arranged in a randomized block design and five plants per treatment were used. Plants were grown in a greenhouse under natural temperature and light. The seedlings were initially watered for two weeks using a sub-irrigation method. After two weeks plants were treated with 0, 25, 50, 75, and 100% seawater related to 0, 0.72, 1.45, 2.17 and 2.9 -MPa concentrations, respectively fortified with 1 mM NH_4NO_3, 1 mM NH_4Cl, 0.1 mM KH_2PO_4 and 0.05 mM Fe-EDTA (Popp & Polania, 1989). Seawater concentrations were gradually increased by 25% (0.72 -MPa) at 2-day intervals to reach the maximum salinity levels of 100% seawater after 10 days. Seawater was completely replaced once a week to avoid build up of salinity in pots and water level was adjusted daily to correct for evaporation. Fresh and dry weight of five replicates of plant shoots and roots, plant height, number of nodes, number of leaves, leaf area and diameter of stem at first internode (at each salinity level) were measured during successive harvests at 6 month and one year intervals. Dry mass was determined after drying for 48 h in a forced-draft oven at 80°C.

Water potential was measured by Wescor HR33T Dew Point Microvoltmeter (Model HR 33T, Wescor Inc, USA) and osmotic potential measured by freezing the leaf disc (five treatments at each salinity level) in liquid nitrogen using the same equipment. Plant water status was evaluated by stem xylem pressure potentials measured with a plant water status console (Arimad-2, Wagtech International Limited, UK) on five shoots from each treatment. Stomatal conductance was measured using an AP_4 porometer (Delta-T devices, UK) on the adaxial surface of fully expanded leaves (5 treatments) at the first node.

For proline and ions measurements five replicates of 0.5 g each were boiled in 10 ml of water for two hours at 100°C using a dry heat bath. This hot water extract was cooled and filtered using Whatman no. 42 filter paper and then used directly to measure proline using Bates *et al.,* (1973) method. The acid soluble, total and water-soluble oxalates were measured by the Karimi & Ungar (1986) method. One ml of hot water extract was diluted with distilled water for ion analysis. Chloride ion content was measured with Beckman specific ion electrode. Ion content of plant organs were analyzed using an atomic absorption spectrometer (Model 360, Perkin Elmer, Germany). The Na^+ and K^+ concentrations of plant tissue was assayed by flame emission and Ca^{2+} and Mg^{2+} concentrations by atomic absorption spectrophotometer.

Table 1. Results of two way ANOVA of characteristics by age of stage of life history (L), and seawater (S) treatments.

Independent variable	L	S	LXS
Fresh weight	11.84*	71.24***	17.9***
Dry weight	16.93**	61.44***	12.14***
Leaf area	464.18***	711.56***	51.20***
Plant height	765.23***	936.45***	101.23***
Xylem tension	11.43**	1.75ns	2.78*

The results of growth and proline content were analyzed with two way ANOVA, and for water relations with a three way ANOVA to determine if significant differences were present among means. A Bonferroni test was carried out for ions to determine if significant ($P < 0.05$) differences occurred between individual treatments (Anon., 1999).

Results

The fresh weight, dry weight, leaf area, plant height of *A. marina* and their interaction were significantly affected by salinity and age (Table 1). Growth was optimum at 50% seawater and declined with a further increase in salinity (Fig. 1). Number of nodes and leaves gradually increased up to the 50% seawater treatment and decreased with increasing salinity (Fig. 2). Stem diameter was highest at 50% seawater (Fig. 3) and leaf area substantially increased in the 50% seawater treatment. There was no significant difference among low (0 and 25%) and high (75 and 100%) seawater treatments.

Water potential and osmotic potential in both young and old leaves of seedlings and saplings rapidly became more negative at 25% seawater and after that variations in media salinity had no effect and there was a negative relationship between water potential of leaves and seawater concentrations (Fig. 4 and 5). Stomatal conductance significantly decreased with an increase in salinity and there was a negative relationship between stomatal conductance and salinity concentration (Fig 6). Xylem tension of seedlings and saplings increased slightly with substantial increase in salinity (Fig. 7).

Concentrations of Na and Cl in leaves increased with increasing NaCl concentration in medium while K concentrations in leaves generally decreased with increasing salinity, and Ca and Mg also decreased with the increase in salinity. The ratio of Na/K gradually increased with the increase in salinity (Table 2).

Proline production significantly ($P < 0.001$) increased with increasing concentration of seawater both in young and old leaves. However, young leaves had higher concentration of proline than old ones (Fig. 8). Acid soluble, water soluble and total oxalates significantly ($P < 0.001$) decreased with an increase in salinity (Fig. 9).
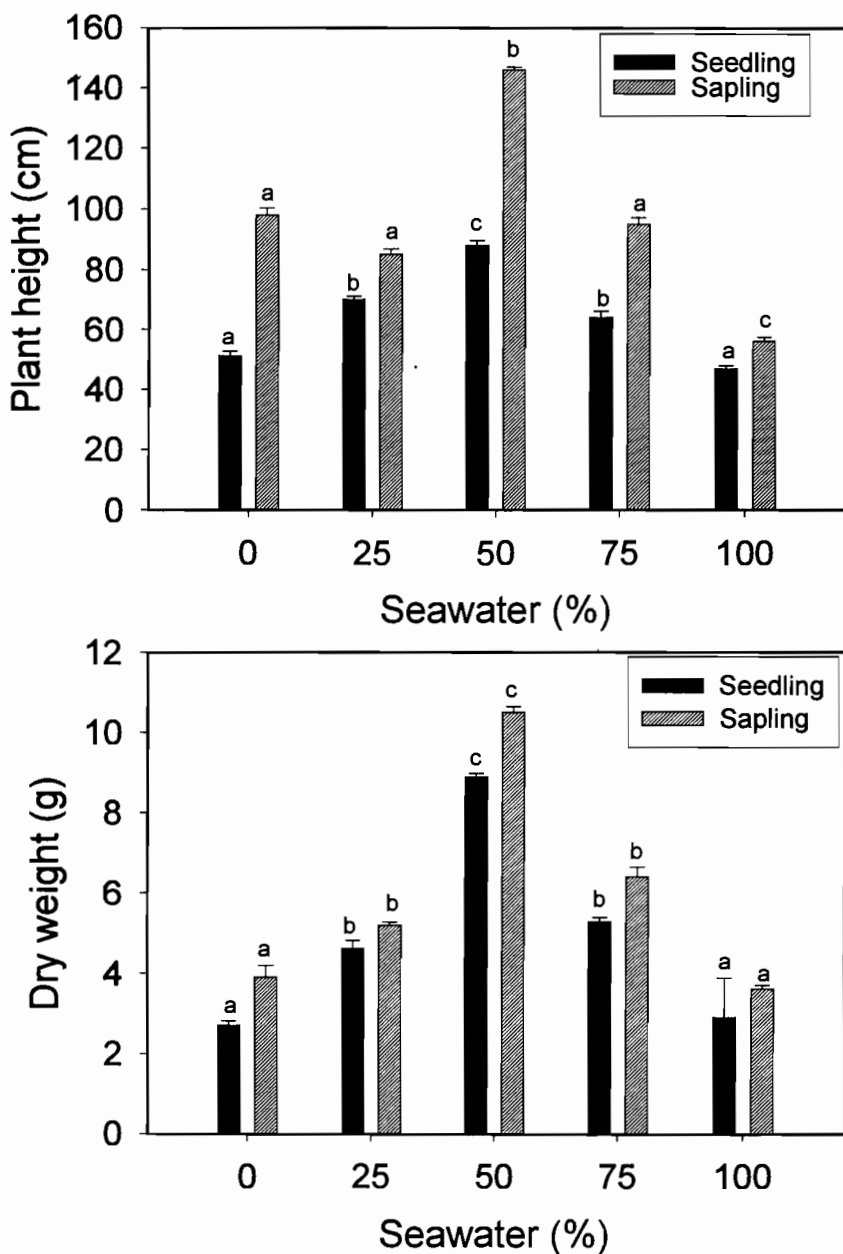
Fig. 1. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on height and dry weight in *Avicennia marina* plants. Bar represent means standard errors. Bars for plant age at different treatment levels with different letters are significantly different (P < 0.05), Bonferroni test.
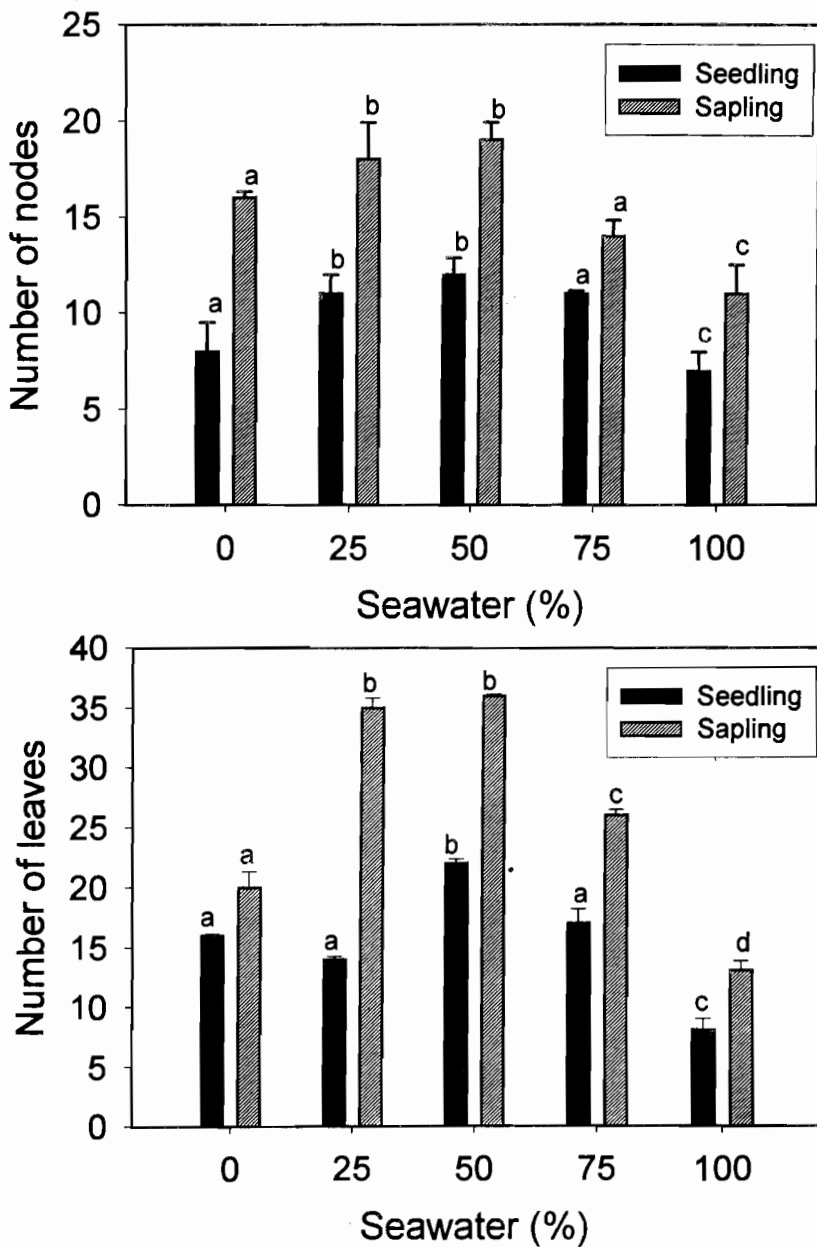
Fig. 2. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the number of nodes and leaves in *Avicennia marina* plants. Bar represent means standard errors. Bars for plant age at different treatment levels with different letters are significantly different (P < 0.05), Bonferroni test.
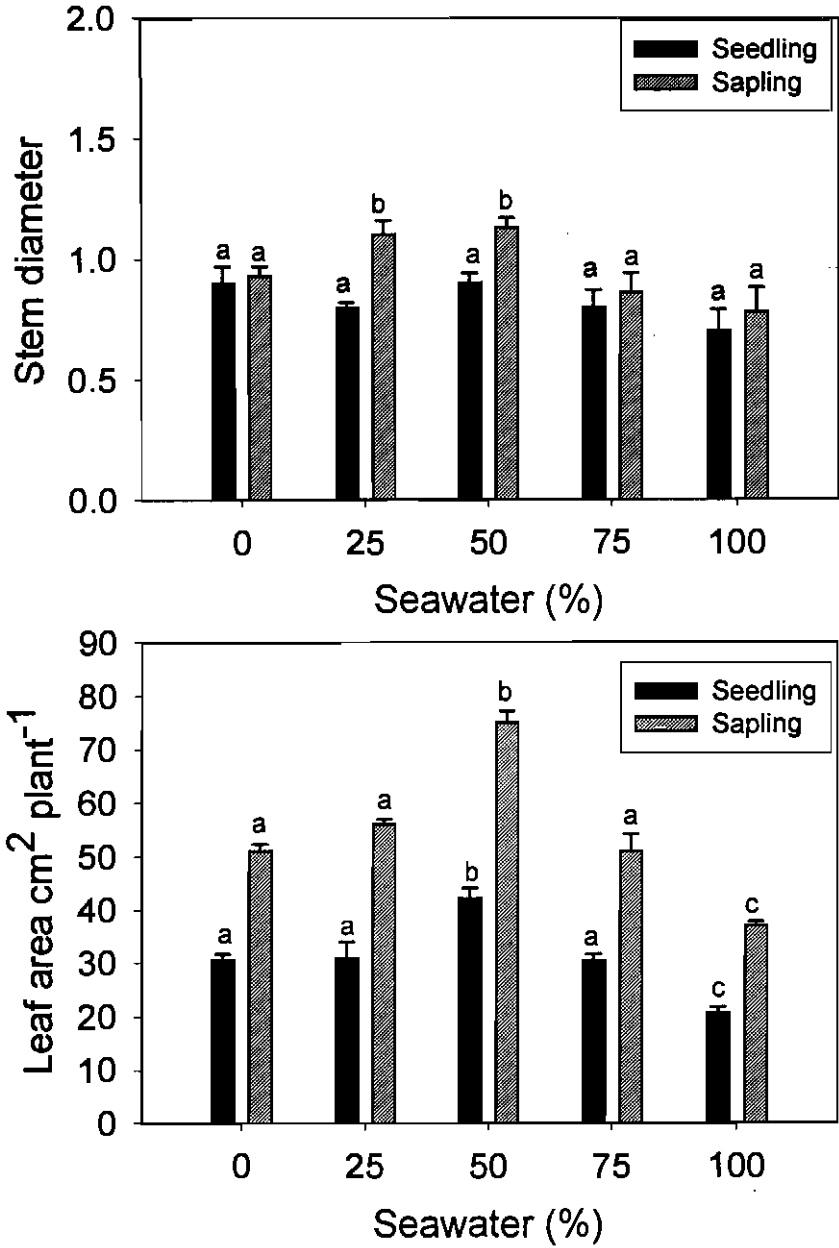
Fig. 3. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the leaf area and stem diameter in *Avicennia marina* plants. Bar represent means standard errors. Bars for plant age at different treatment levels with different letters are significantly different ($P < 0.05$), Bonferroni test.
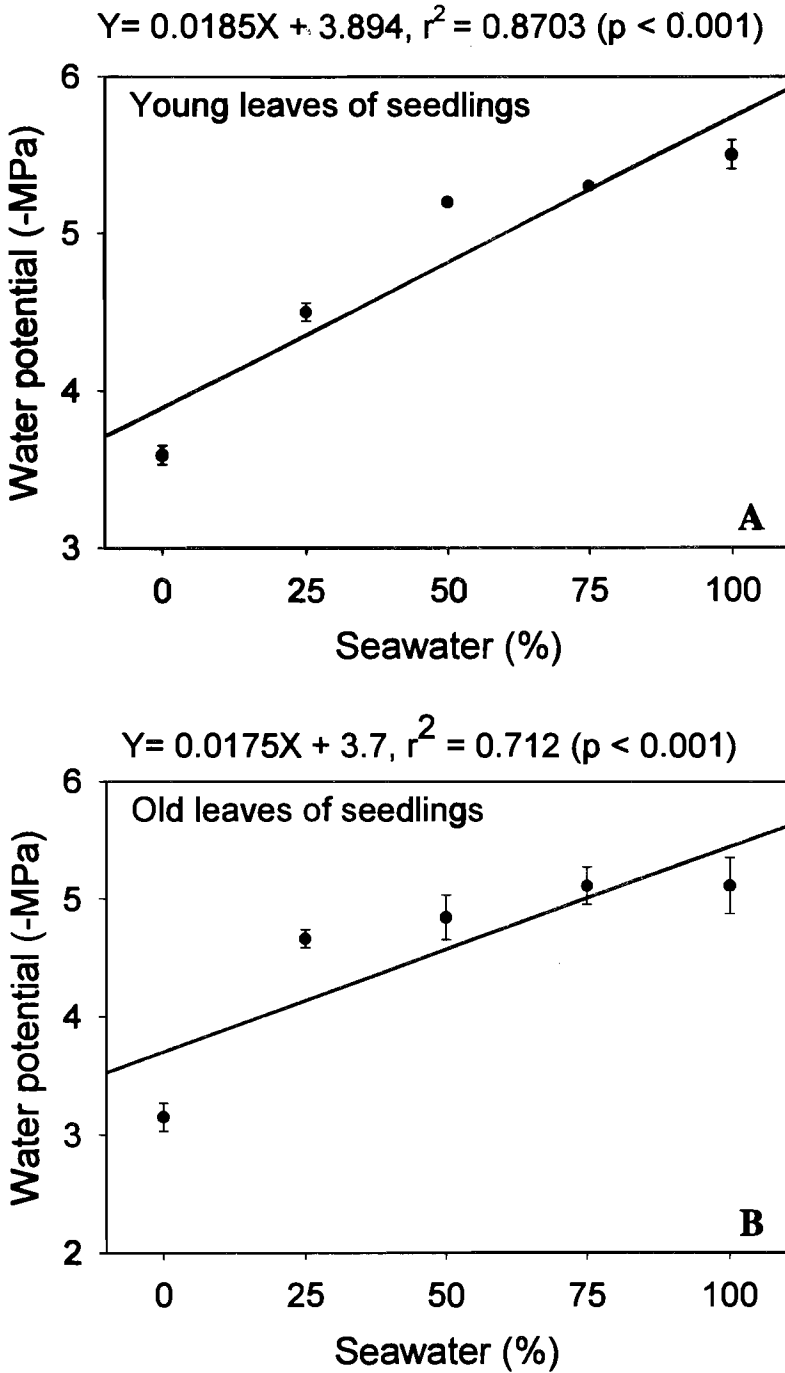
$$Y = 0.0185X + 3.894, \; r^2 = 0.8703 \; (p < 0.001)$$

$$Y = 0.0175X + 3.7, \; r^2 = 0.712 \; (p < 0.001)$$

Fig. 4. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the water potential of *Avicennia marina* plants. Bar represent means standard errors.
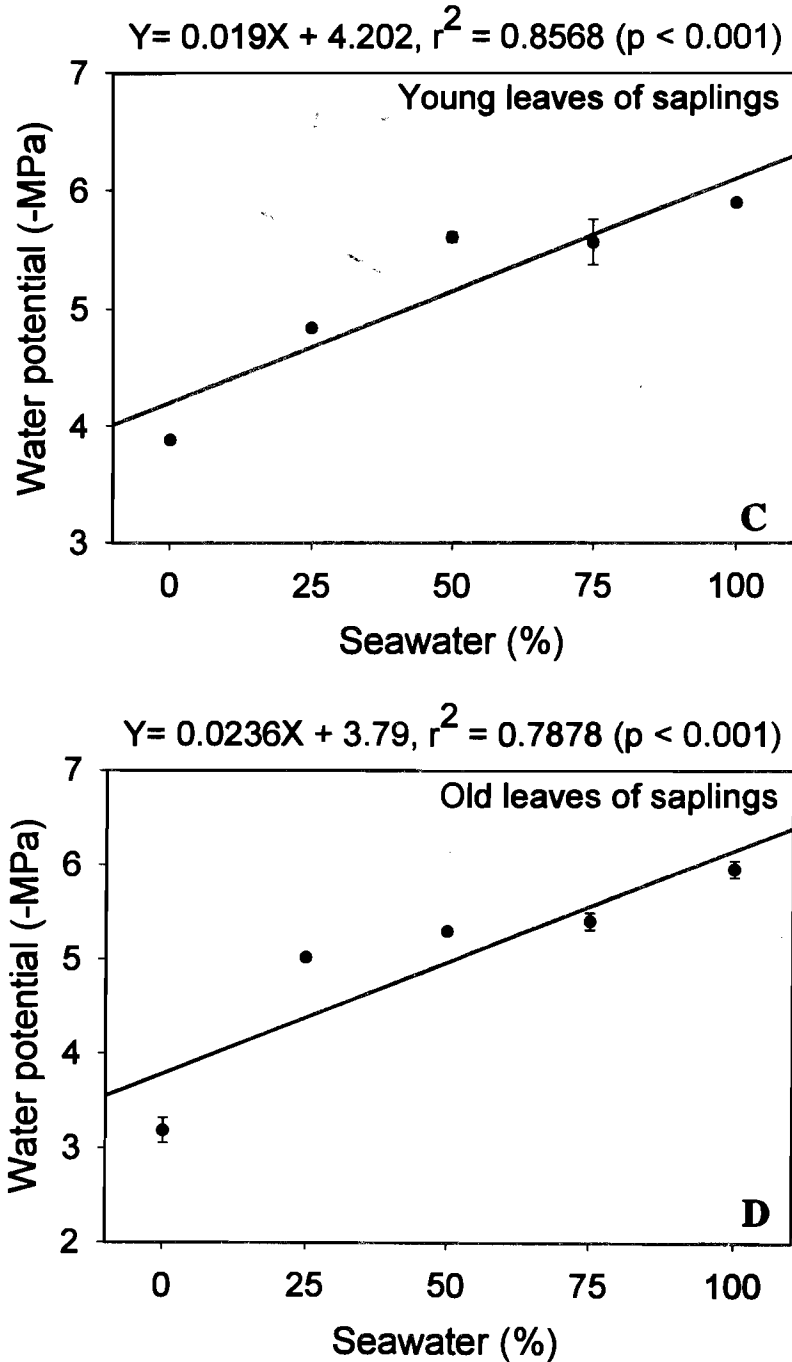
$$Y= 0.019X + 4.202, r^2 = 0.8568 \ (p < 0.001)$$

$$Y= 0.0236X + 3.79, r^2 = 0.7878 \ (p < 0.001)$$

Fig. 4. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the water potential of *Avicennia marina* plants. Bar represent means standard errors.
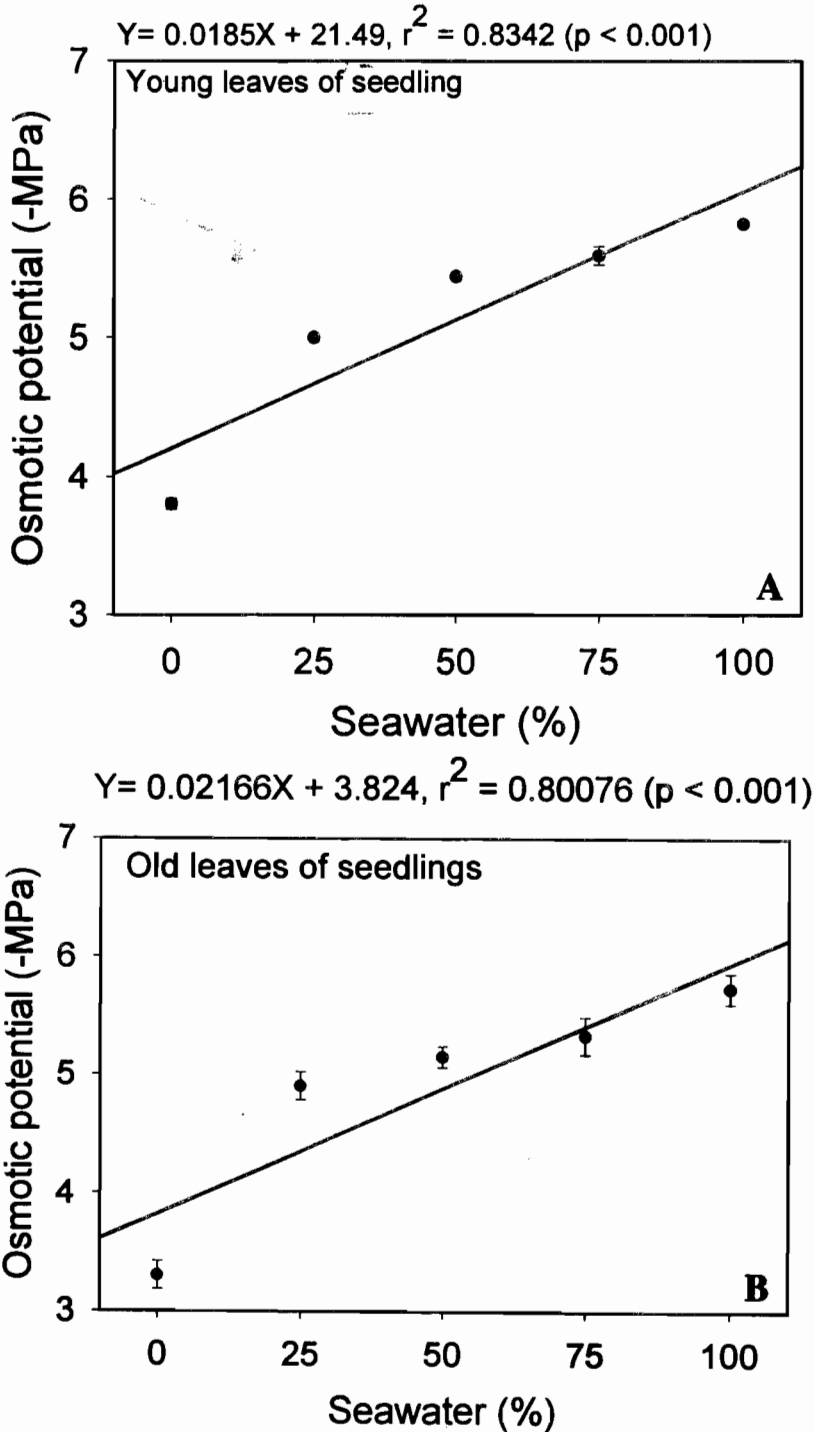
Fig. 5 Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the osmotic potential in *Avicennia marina* plants. Bar represent means standard errors.

$$Y = 0.0236X + 3.791, r^2 = 0.7878 \ (p < 0.001)$$
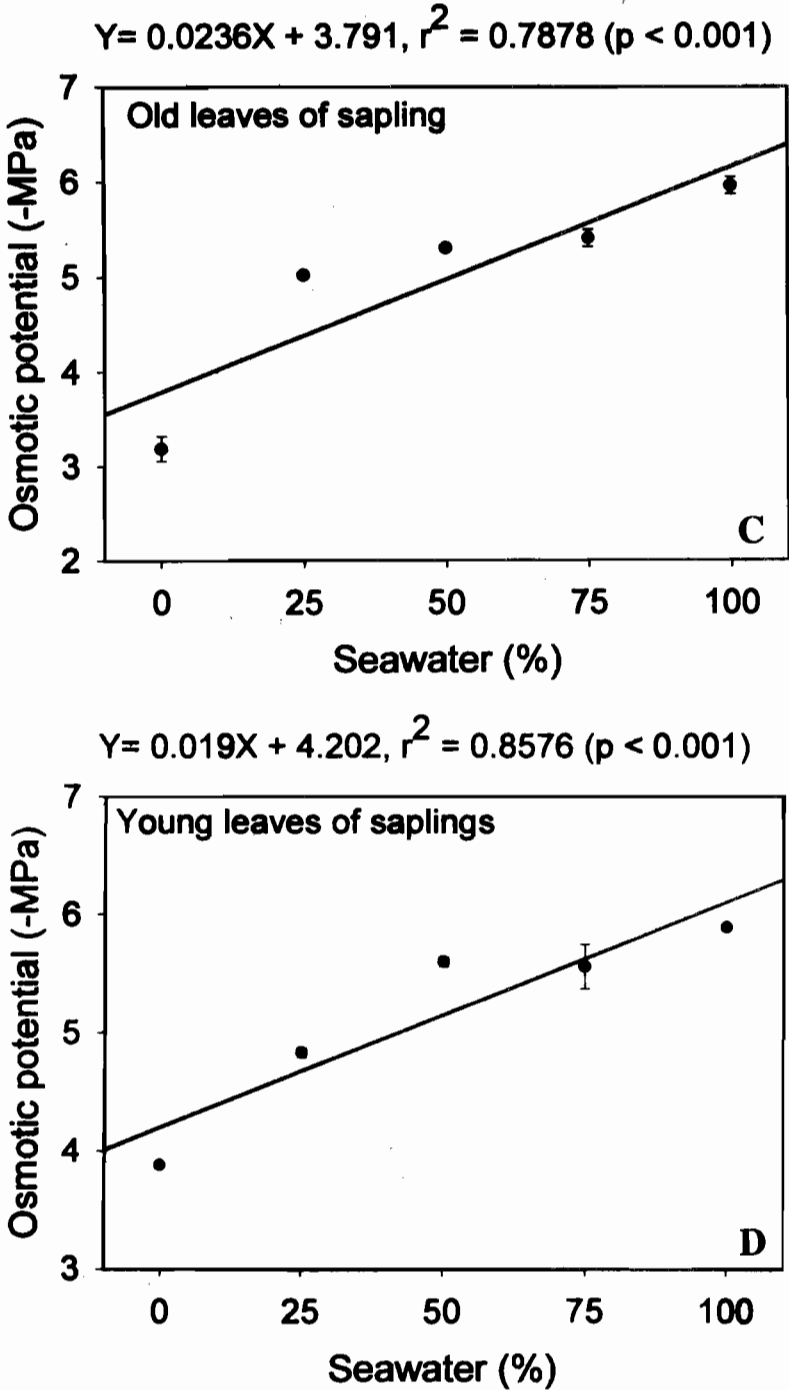

$$Y = 0.019X + 4.202, r^2 = 0.8576 \ (p < 0.001)$$

Fig. 5 Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the osmotic potential in *Avicennia marina* plants. Bar represent means standard errors.
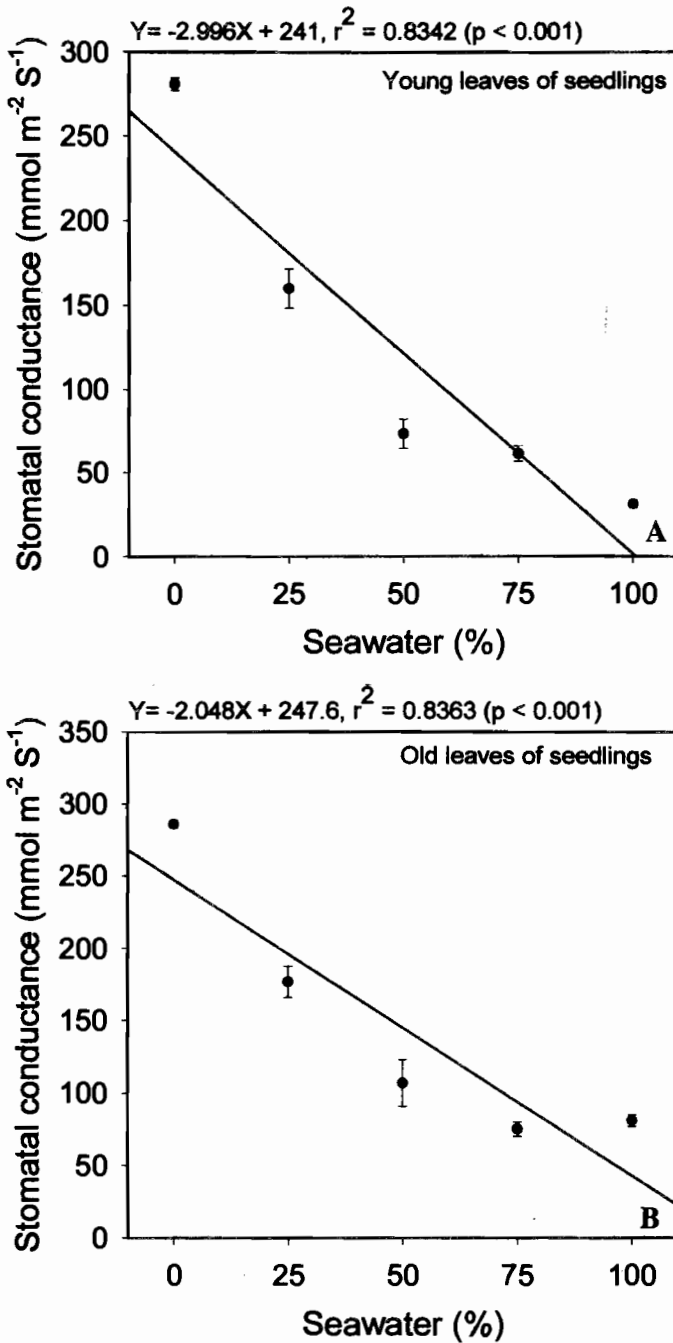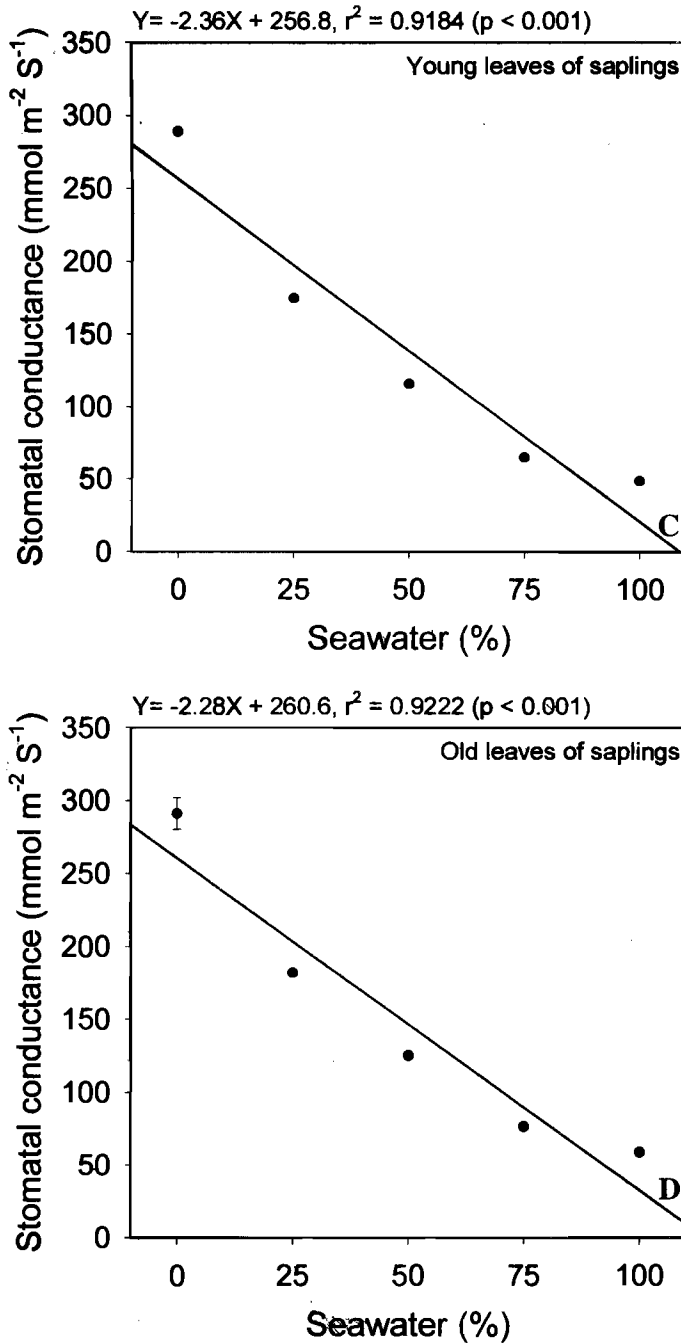
Fig. 6. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the stomatal conductance in *Avicennia marina* plants. Bar represent means standard errors.

Fig. 6. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the stomatal conductance in *Avicennia marina* plants. Bar represent means standard errors.
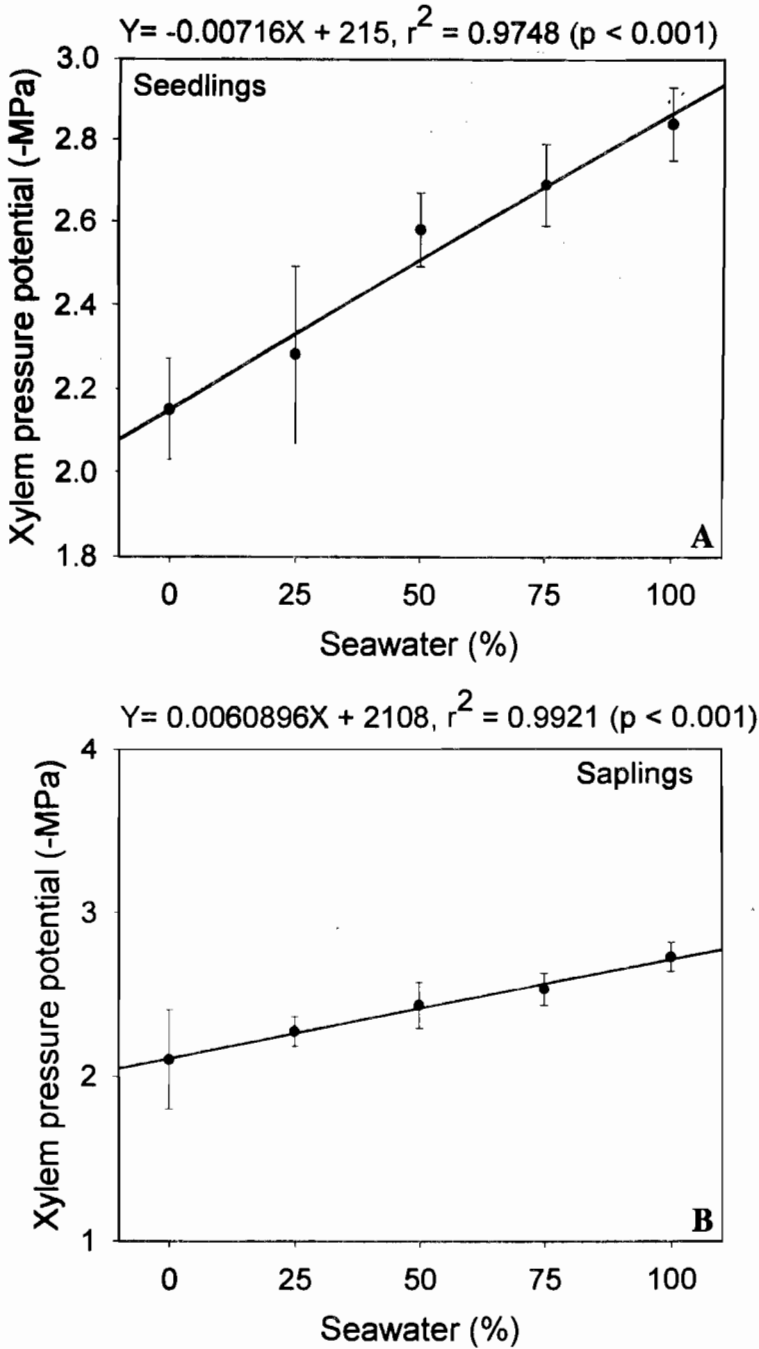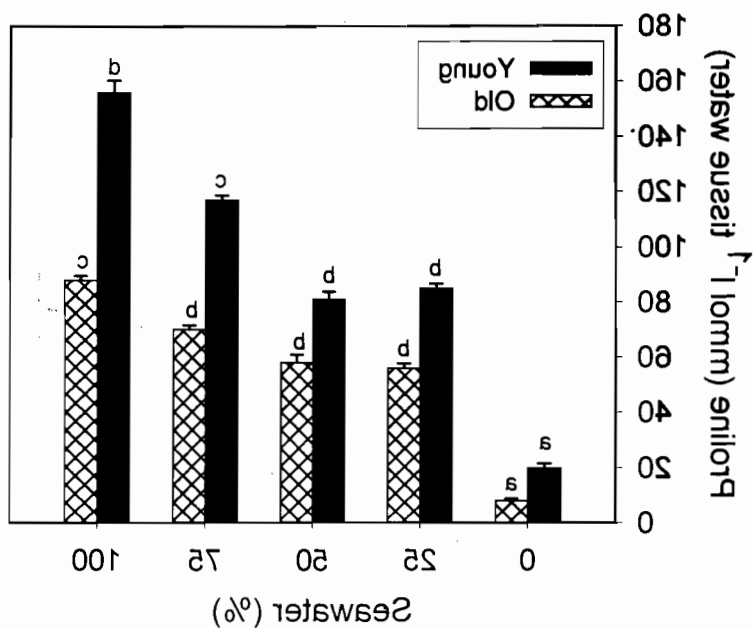
Fig. 7. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the xylem tension in *Avicennia marina* plants. Bar represent means standard errors.

Table 2. Ion concentration (mmol l^{-1} plant water) in *Avicennia marina* harvested twelve months after the highest salinity reached.

Sea water (%)	Na^+	K^+	Ca^{++}	Mg^{++}	Cl^-	Na/K
0	28.4^a ± 1.2	27.1^a ± 3.3	44.0^b ± 1.2	61.0^{ab} ± 4.9	38.63^a ± 2.1	1.11^a ± 0.66
25	193.03^b ± 4.2	25.55^a ± 4.1	40.0^b ± 3.3	72.0^b ± 10.5	201.0^b ± 1.8	6.56^b ± 1.01
50	240.3^e ± 3.7	18.26^b ± 1.58	53.0^c ± 3.2	93.0^c ± 6.7	384.2^c ± 3.3	13.33^c ± 1.54
75	373.0^d ± 7.2	12.38^c ± 2.1	38.0^b ± 3.6	68.0^b ± 8.7	478.2^c ± 1.84	31.12^d ± 1.12
100	533.3^e ± 4.8	9.1^d ± 1.8	29.0^a ± 6.8	54.0^a ± 4.9	583.6^d ± 5.3	59.23^e ± 0.56

Values having different letters are significantly different at 0.5% level by Bonferroni's test.

Fig. 8. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the proline content in *Avicennia marina* plants. Bar represent means standard errors. Bars for plant age at different treatment levels with different letters are significantly different (P < 0.05), Bonferroni test.
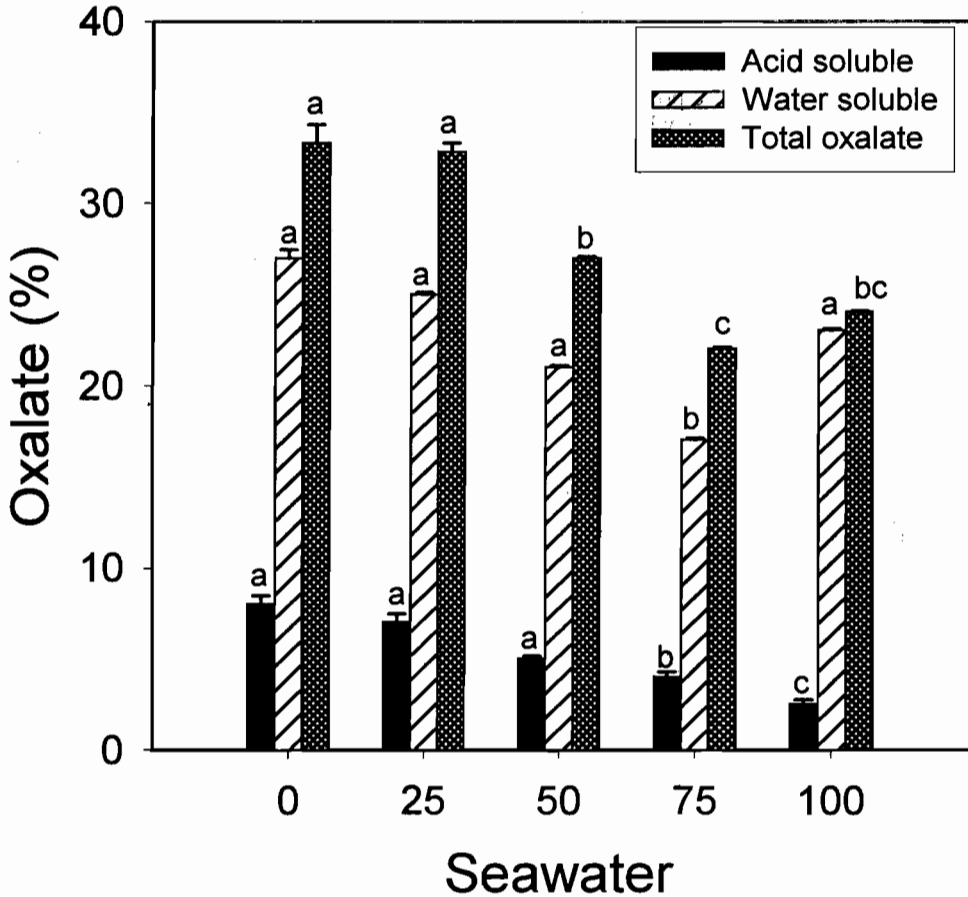
Fig. 9. Effect of NaCl (0, 25, 50, 75 and 100% seawater) on the oxalate content in *Avicennia marina* plants. Bar represent means standard errors. Bars for plant age at different treatment levels with different letters are significantly different (P < 0.05), Bonferroni test.

Discussion

Mangroves usually grow under low salinity regimes and high salinity in the medium causes reduction in their growth that is similar to that of other halophytes (Greenway & Munns, 1980). In the present study growth was promoted at low salinity level (50% seawater). Plant height, fresh and dry weights, leaf area, number of leaves and number of nodes increased at 50% seawater and a decline in growth parameters was noted in the 75% and 100% seawater treatments. Most of the studies reported that mangroves thrive best at concentrations ranging from 10-25% seawater (Downton, 1982; Clough, 1984; Naidoo, 1987; Lin & Sternberg, 1992; 1995; Karim & Karim, 1993; Ball & Pidsley, 1995). However, best growth of Sunderban *A. marina* (Karim & Karim, 1993) and Australian *Sonneratia alba* (Ball & Pidsley, 1995) was reported at 50% seawater. It appears that *A. marina* behaves like a true halophyte, characterized by enhanced growth under high saline conditions (Flowers *et al.*, 1986) and it is more

tolerant in semi arid areas of Pakistan in comparison to the mangroves of Australia, Central America and South Africa which live in more mesic conditions.

One of the most significant characteristics of all halophytes is their capacity to adjust their tissue osmotic potentials to a level that is lower than that of the soil osmotic potential in the habitat in which they are growing (Berger, 1978). Mangroves lower tissue osmotic potential through the net accumulation of solutes in response to salinity or water deficits (Turner & Jones, 1980; Saurez *et al.*, 1998). Some halophytes e.g., *Salicornia europaea* when exposed to salinity develop a more negative water and osmotic potential. Small perturbations in salinity have little affect on them and therefore they are called osmoregulators (Karimi, 1984). Other halophytes like *Atriplex triangularis* which show progressive increase in water and osmotic potential are called osmoconformors. They make osmotic adjustments in tissues to maintain the movement of water into the tissues (Karimi, 1984; Khan *et al.*, 1999, 2000abc). *Avicennia marina* showed a rapid decrease in tissue water and osmotic potential with the introduction of salinity (25% seawater) both in seedlings and saplings. Further increase in salinity had little effect, indicating that it follows an osmoregulator strategy to maintain its osmotic balance.

Stomatal conductance in *A. marina* substantially decreased with an increase in salinity. The decline in stomatal conductance in salt tolerant species under both drought and salinity stress causes an increase in water use efficiency (Sharma, 1977; Werner & Stelzer, 1990; Gordon, 1993). Lowered conductance decreases the rate of carbon dioxide uptake (Apaholo & Jarvis, 1993) and rate of transpiration and causes an increase in xylem tension (Ball & Farquhar, 1984).

Avicennia marina can shed salts via leaf glands when supplied with salinity in the growth medium (Fitzgerald *et al.*, 1992). High internal salt concentrations provide potential benefits to plants growing under conditions where soil osmotic potential is more negative than that of seawater because of high soil salinity (Ungar, 1991). It contributes to lowering the internal water potential required to permit water uptake. Na^+ and Cl- may be accumulated in leaf tissues to provide osmotic adjustment and the turgor to maintain growth (Yeo, 1983; Downton, 1982). *Avicennia marina* maintained high Na^+ and Cl^- concentrations in leaves with the increase in salinity and there was a decrease in the concentration of other cations. The Na^+ and Cl^- concentrations of leaf samples from salt secreting mangroves were close to that of seawater (Popp, 1984; Popp & Polania, 1993). Similar results were obtained in our experiments for *A. marina* at 100% seawater concentration. The Na/K ratio increases in salt tolerant species with increasing salinity in the external medium (Tattini *et al.*, 1995), because mass transport of sodium takes place from root to shoot via the transpiration stream. In *A. marina*, the Na/K rate increased as salinity increased suggesting an increase in transportation of Na^+ ions from root to shoot.

The accumulation of compatible solutes is a common response to salinity or drought stress in higher plants (Brown & Simpson, 1972). These compounds are not toxic to cytoplasmic enzyme functions at high concentrations (Storey *et al.*, 1977), thus helping in osmotic adjustment. Glycinebetaine is known to occur extensively in different *Avicennia* species and it acts as a compatible osmoticum to overcome toxic effects of Na^+ and Cl^- (Popp & Polania, 1989). *Avicennia marina* accumulates abundant Na^+ and Cl^- and proline also increased significantly under salt stress. However, this increase in proline concentration is not sufficient to balance the large amount of salts present in the cell vacuoles. Popp & Albert (1995) reported that *A. marina* accumulates large amount of glycinebetaine to maintain osmotic balance. Soluble oxalate concentrations decreased with an increase in salinity, indicating that it has a small role in osmoregulation. Low concentrations of oxalates in leaves may also make them unpalat-

able, as oxalates are known to pose problems to grazing animals since they are toxic to them (Sharma, 1982).

Our results suggest that *A. marina* is a highly salt tolerant species with the ability to grow in salinities that were higher than seawater concentration. The osmoregulator strategy in *A. marina* confers a protection from sudden changes in media salinity which is common in sub-tropical regions of the world. Proline concentration increased many fold but the concentration was not sufficient to play a significant role is the osmotic balance of the cell.

Acknowledgements

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