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Strong positive growth responses to salinity by *Ceriops tagal*, a commonly occurring mangrove of the Gujarat coast of India

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Abstract

Background and aims	Mangroves of Western Gujarat (India) are subject to die-back. Salinity intolerance is one possible cause, especially in young plants. We therefore quantified the extent to which young plants of one widely occurring mangrove species (*Ceriops tagal*) tolerate high salt in terms of establishment, growth, water status, proline content and mineral accumulation.
Methodology	In a greenhouse study, juvenile plants were established from mature propagules over 40 days in soil containing added NaCl, raising soil water salinity to 0.2, 2.5, 5.1, 7.7, 10.3, 12.6, 15.4, 17.9, 20.5 and 23.0 ppt (w/v). Growth and physiological characteristics were monitored over the subsequent 6 months.
Principal results	Despite a negative relationship between the percentage of young plant establishment and salt concentration (50 % loss at 22.3 ppt), the remaining plants proved highly tolerant. Growth, in dry weight, was significantly promoted by low salinity, which is optimal at 12.6 ppt. Water content, leaf expansion and dry matter accumulation in tissues followed a similar optimum curve with leaf area being doubled at 12.6 ppt NaCl. Salinity >12.6 and <23 ppt inhibited plant growth, but never to below control levels. Root:shoot dry weight ratios were slightly reduced by salinity (maximum 19 %), but the water potential of roots, leaves and stems became more negative as salinity increases while proline increases in all tissues. The concentration of Na increased, whereas concentrations of K, Ca, N and P decreased and that of Mg remained stable.
Conclusions	*Ceriops tagal* has a remarkably high degree of salinity tolerance, and shows an optimal growth when soil water salinity is 12.6 ppt. Salinity tolerance is linked to an adaptive regulation of hydration and ionic content. The cause of localized die-back along the coastal region of Gujarat is thus unlikely to be a primary outcome of salinity stress although amendments with Ca and K, and perhaps proline, may help protect against extreme salinity.

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Introduction

Mangroves are woody plants that inhabit intertidal zones with high salinity (Shan *et al.*, 2008; Parida and Jha, 2010) and can tolerate a wide range of salinities under natural conditions (Suarez *et al.*, 1998). In nature, the growth and physiological tolerance mechanisms of mangroves vary due to a complex physical structure and differences in flooding regime, tidal inundation, rapid influx of extra nutrients and soil type (Clough, 1984; Naidoo, 1987). Mangroves display a range of adaptive responses to their specific habitat, including salt exclusion by root ultrafiltration (Scholander, 1968), salt secretion (elimination of substances not metabolically changed) via glands (Roth, 1992), ion accumulation in leaf cells (Popp, 1994), leaf succulence (Roth, 1992) and accumulation of organic acids as osmotica to counter toxic effects of salinity (Popp, 1984). Like other halophytes, mangroves decrease their water and osmotic potentials to maintain leaf turgor at high salinity (Naidoo, 1987; Khan *et al.*, 2000*a*,*b*). The level of salinity required for optimal growth varies from 10 to 50 % seawater (Downton, 1982; Clough, 1984; Naidoo, 1987; Lin and Sternberg, 1992, 1995; Ball and Pidsley, 1995; Patel NT *et al.*, 2010), and a decline in growth occurs with a further increase in salinity. Lowered water potentials and an associated accumulation of inorganic ions are common patterns observed in mangrove plants in extreme saline habitats (Ball and Farquhar, 1984; Naidoo, 1987; Patel NT *et al.*, 2010) and are seen as a mechanism for maintaining turgor.

Mangroves are common along the coasts of Western Gujarat (India), but the stands are repeatedly decimated and fragmented (Patel, 2009). Little information exists about the salt tolerance of mangroves of the coastal region of Gujarat, and this information is crucial for the success of mangrove restoration efforts in that region. *Ceriops tagal* is one of the most common species in the coastal region of Gujarat. Its range extends from the semi-arid (near-arid) region of Saurashtra to the saline desert of Kutch, adjacent to the border of Pakistan. Ball (1988) reported that *C. tagal* is a salt-tolerant mangrove with the competitive ability to grow in highly saline and poorly inundated locations. Aziz and Khan (2001) and Khan and Aziz (2001) reported that *C. tagal* from Pakistan showed an optimal growth at 50 % seawater salinity. It is assumed that mangroves growing along the coasts of Western Gujarat have tolerance to arid conditions and high salinities (Patel, 2009). Thus, the present study investigated the tolerance of *C. tagal* of Gujarat at increasing salinity levels, by measuring plant establishment from propagules, juvenile plant growth, and water and mineral status. Such studies have been lacking up to now for mangroves of arid regions.

Materials and methods

Study area

The study was performed in a greenhouse of the botanical garden of Saurashtra University at Rajkot (22°18′N latitude, 70°56′E longitude), Gujarat, India. For propagule establishment and growth of young plants, the top 15 cm of black-cotton soil (vertisol), which is predominant in the Saurashtra region of Gujarat, was collected from an agricultural field near Saurashtra University. This soil is a clayey loam, containing 19.6 % sand, 20.3 % silt and 60.1 % clay by weight of dry soil. The available soil water between wilting coefficient and field capacity ranged from 18.3 to 35.0 %. The total organic carbon content was 1.3 % and pH was 7.2. The salinity of the soil was 0.2 ppt (w/v of soil water). Nitrogen, phosphorus, potassium, calcium and sodium concentrations were 0.15, 0.05, 0.03, 0.05 and 0.002 % by weight of dry soil, respectively. This soil is fertile and used for intensive agriculture. Physical and chemical properties of the soil have been reported earlier (Pandya *et al.*, 2004).

Salinization of soil

Surface soil was collected, air dried and passed through a 2-mm mesh. Twelve samples of soil, each of 100 kg, were separately spread, about 50 mm thick, over polyethylene sheets. Sodium chloride (NaCl) amounting to 0, 280, 690, 1410, 1900, 2400, 2900, 3300, 3800, 4200, 4700 and 5170 g was then allocated to each sample and thoroughly mixed to give interstitial soil water salinities of 0.2, 2.5, 5.1, 7.7, 10.3, 12.6, 15.4, 17.9, 20.5, 23.0, 25.6 and 28.2 ppt, measured by electrical conductivity in a soil suspension prepared in distilled water with a 1:2 soil:water ratio following Patel AD *et al.* (2010). The suspension was shaken and allowed to stand overnight. Thereafter, the electrical conductivity of the supernatant solution was determined with a conductivity meter (Systronics, Model No. 304, India). The salinity of untreated control soil was 0.2 ppt. Seawater salinity at Jamnagar coast in Saurashtra varies from 28.8 to 30.7 ppt during the rainy (monsoon) season, which favours the establishment of propagules. Thus, soil salinity in the present investigation was not imposed above 28.2 ppt.

Plant material

Propagules (turions) of *C. tagal* develop on branches of the plants. Mature propagules were collected on 14 December 2007 from the Jamnagar coast (22°27′N latitude, 70°07′E longitude) of the Saurashtra region of Western Gujarat with the help of Gujarat Forest Depart-

ment. Mature propagules were yellowish green, approx. 6.5 g (fresh weight), 17–20 cm long and 0.8–1.0 cm wide. Young propagules are brighter green, and were avoided because of poor germination.

Plant establishment

For each level of soil salinity, 20 polyethylene bags (20.5 cm wide and 41 cm long) were each filled with 5 kg of soil. About 2.5 L of tap water were added to the soil in each bag until the water level was 2 cm above the soil surface. Bags were kept in an uncontrolled greenhouse under natural temperature and light. Ten propagules were planted (propagules were inserted up to one-third of their length into the soil) in each bag on 15 December 2007. Tap water was added daily to compensate for evapotranspiration loss. Plant establishment was recorded daily over 40 days, establishment being defined as the date when the first pair of leaves unfurled. A linear model was fitted to the cumulative proportion of established plants and the increasing soil salinity using the expression:

$$Sin^{-1}\sqrt{P} = \beta_0 + \beta_1 X$$

where $Sin^{-1}\sqrt{P}$ denotes the proportion of cumulative established plants, X is soil salinity and β_0 and β_1 are coefficients of linear regression. The salt concentration at which plant establishment was reduced to 50 % (SE_{50}) was estimated using the model.

Plant growth

The two plants that established first were left in each bag, the others being removed as they appeared. At high salinities, young plants opened their first pair of leaves between 9 and 30 d later than controls. The full opening of the first pair of leaves defined the establishment of young plants. No further experiments were conducted on plants grown in soils at the two highest salinities (25.6 and 28.2 ppt) because (i) mortality of established plants did not occur at all salinity levels and (ii) Khan and Aziz (2001) and Aziz and Khan (2001) found that plant dry weight of *C. tagal* was maximum in 50 % seawater and higher salinity (100 % seawater) was without effect compared to controls. At the two highest salinities, established plants were therefore expected to grow similarly to control plants. Following 40 days for establishment, the smaller of the two plants was removed, leaving the more vigorous of the pair for further study. Thus, 20 single replicate plants were factorialized with 10 grades of soil salinity (0.2, 2.5, 5.1, 7.7, 10.3, 12.6, 15.4, 17.9, 20.5 and 23.0 ppt). The 200 growth bags were arranged in 20 completely randomized blocks. Plants were watered daily to

maintain the water level above the soil surface and the experiment was terminated after 6 months. The mean daily maximum temperature of the greenhouse decreased from $29.5 \pm 0.6\,°C$ in December 2007 to $28.1 \pm 0.4\,°C$ in February 2008, and increased thereafter to $40.7 \pm 0.4\,°C$ in May 2008. The mean maximum temperature then decreased to $37.6 \pm 0.3\,°C$ until final harvesting on 15 June 2008. Plants were then washed with tap water to remove soil particles and morphological characteristics of each plant recorded, including shoot height, root length (as length of longest root) and leaf area (using outline tracings on graph paper). Fresh and dry weights of leaves, stems and roots were then determined. Water content (%) was calculated from fresh and dry weights. Data recorded for morphological characteristics, dry weight and water content were analysed by multivariate analysis of variance (MANOVA), using SYSTAT version 12 (Badashah and Nath, 2007) to assess the effect of salinity levels on plant growth variables considered simultaneously. A second-order polynomial model was fitted to the data for the examined parameters and increasing soil salinity using the expression:

$$Y = \alpha + \beta_1 X + \beta_2 X^2$$

where Y is the examined parameters, X is soil salinity, α is the Y-intercept, and β_1 and β_2 are constants.

Determination of water potential and proline content

Ten additional plants grown in the soil at each level of salinity were used for water potential and proline determinations 15 days before the termination of the growth experiment. Water potential of leaves, stems and roots was measured using a Dewpoint Potential Meter WP4 (Decagon Devices, Inc., USA) following Patel AD *et al.* (2010). All the measurements were taken between 7.30 and 10.00 a.m. Proline concentrations were estimated following Bates *et al.* (1973), using an extract of 0.5 g of fresh plant material in aqueous sulfosalicylic acid. The extracted proline was reacted with ninhydrin to form a chromophore read at 520 nm absorbance. Data were analysed by one-way ANOVA and linear regression.

Mineral analyses of plant materials

Mineral analyses were performed on leaves, stems and root tissues. Plant parts were pooled into one composite sample per salinity level separately. Plant samples were ground using a mortar and pestle, and three subsamples were analysed. Total nitrogen was determined by the Kjeldahl method and phosphorus content was estimated by the chlorostannous molybdophosphoric blue colour

method in sulphuric acid (Piper, 1944). Concentrations of Ca, Mg, Na and K were determined by Shimadzu double-beam atomic absorption spectrophotometer AA-6800 (Shimadzu Corporation, Kyoto, Japan) after tri-acid (HNO_3:H_2SO_4:$HClO_4$ at a ratio of 10:1:4) digestion. Mineral data (mg g^{-1} dry weight) were analysed by one-way ANOVA and linear regression.

Results

Effect of salinity on plant establishment

Under non-saline control conditions (0.2 ppt salinity), the first pair of leaves started to open 9 days after planting and 94.4 % of the propagules were established

(i.e. showed signs of leaf opening) over 28 days (Fig. 1). Under saline treatments, the appearance of the first pair of unfurled leaves on propagules did not occur until 1–6 days later, with higher salinities causing longer delays. Leaves continued to unfurl for up to 31 days at 5.1 and 7.7 ppt salinity, and for at least 25 days at 28.2 ppt. Total propagule establishment decreased from 94.0 % at 2.5 ppt to 27.6 % at 28.2 ppt. There was a significant reduction in the percentage of plant establishment with increasing soil salinity according to the following expression: $Y = 107.270 - 2.561X$ ($R^2_{adj} = 0.907$, $P < 0.001$), where Y is arcsine (degrees) of proportion of cumulative plant establishment and X is salt concentration.

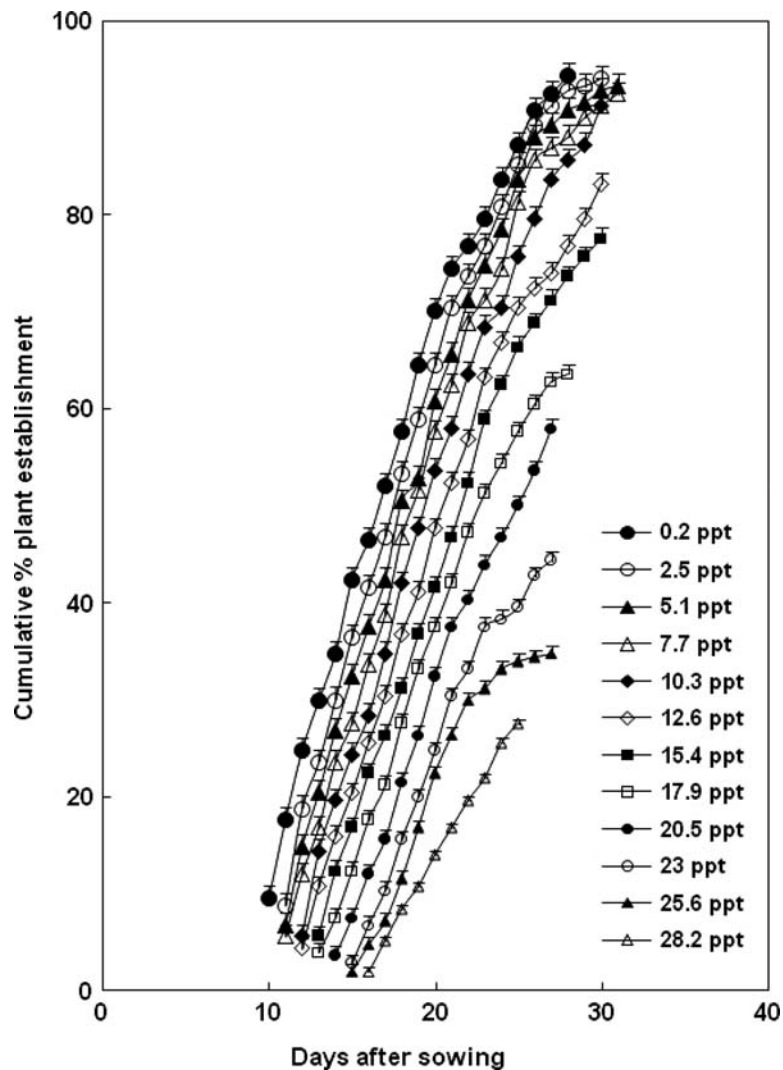**Fig. 1** **Cumulative establishment of propagules of *C. tagal* over 40 days after planting in response to increasing soil salinity.** Error bars represent the SE, *n* = 200. Units of salinity are those measured in the soil water. The salinity of soil not receiving NaCl addition was 0.2 ppt. Percentage establishment indicates the percentage of 10 propagules (planted in each bag) that produced open leaves.

Total dry weight (biomass) of plants

The MANOVA showed a low value of Wilk's lambda (e.g. 0.08 with an associated d.f. of 90, 1237), while a high value for each of Pillai Trace (e.g. 1.47 with an associated d.f. of 90, 1701) and Hotelling–Lawley Trace (e.g. 6.24 with an associated d.f. of 90, 1613) demonstrated a statistically significant ($P < 0.001$) effect of salinity on the examined growth variables when considered simultaneously. Salinity significantly ($P < 0.001$) promoted the total dry weight (shoots + roots; Fig. 2). Total dry weight increased up to 12.6 ppt salinity, but declined with further increases in salinity although dry weights did not fall below control values even at the highest salt concentration (23.0 ppt). The optimum dry weights were at moderate salinities (5.1–12.6 ppt). There was a quadratic relationship between the salt concentration in soil and the dry weight of the whole plant ($Y = 2551.30 + 117.25X - 4.83X^2$, $r^2 = 0.291$, $P < 0.001$).

Stem and root elongation, and leaf expansion

Salinity significantly stimulated ($P < 0.001$) stem and root elongation, although final lengths declined at concentrations over 12.6 ppt to levels similar to those of controls (Fig. 3A and B). Actual stem heights were considerably greater than root lengths under all treatments. There was a quadratic relationship between shoot height ($r^2 = 0.412$, $P < 0.001$) or root length ($r^2 = 0.227$, $P < 0.001$) and salt concentration. A positive
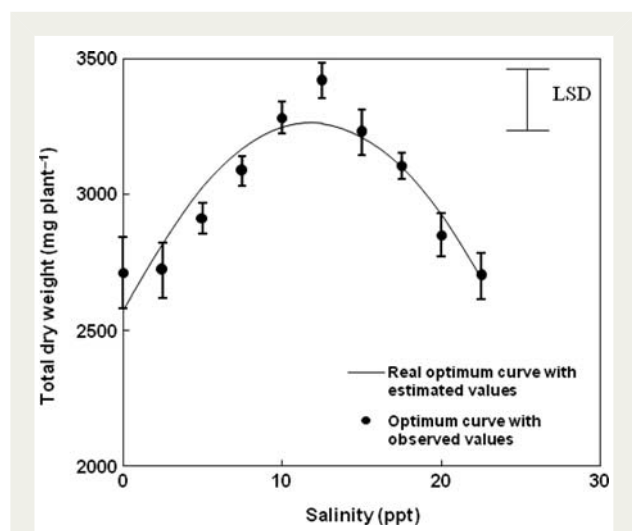

Fig. 2 Effect of increasing soil salinity on total dry weight of *C. tagal* plants after 6 months growth from propagules. A fitted quadratic polynomial curve ($Y = 2243.60 + 354.02X - 30.89X^2$, $r^2 = 0.858$, $P < 0.001$) is shown. The data points show treatment means $\pm$ SE. $n = 20$. The large bar represents LSD at $P < 0.05$.

relationship was obtained between stem height ($r^2 = 0.176$, $P < 0.001$) or root length ($r^2 = 0.107$, $P < 0.001$) and total dry weight of plants. Leaf area was doubled by increasing salinity to 12.6 ppt ($P < 0.001$) but was decreased by higher salinities, although never to below that of control plants (Fig. 3C). A quadratic relationship was obtained between leaf area and salt concentration in soil ($r^2 = 0.537$, $P < 0.001$). There was a positive relationship between leaf area and total dry weight of plants ($r^2 = 0.227$, $P < 0.001$).

Dry weight of tissues

The dry weight of leaves, stems, shoots (leaves + stems) and roots was significantly promoted ($P < 0.001$) by salinity up to 12.6 ppt, but, at higher salinity, declined to values similar to those of controls (Figs 3D–F and 4A). There was a quadratic relationship between the salt concentration and dry weight ($r^2 = 0.146, 0.229, 0.278, 0.141$, $P < 0.001$) for leaves, stems, shoots and roots, respectively. A positive relationship was obtained for dry weight of leaves ($r^2 = 0.340$, $P < 0.001$), stems ($r^2 = 0.921$, $P < 0.001$) and roots ($r^2 = 0.104$, $P < 0.001$) with total dry weight of plants. The root:shoot dry weight ratio was 0.06 for plants grown in control soil (Fig. 4B) and did not change with increasing soil salinity.

Water content and water potential of tissues

Water content (%) increased significantly ($P < 0.001$) in leaves, stems and roots up to 12.6 ppt salinity, but declined with further increases in salinity while always remaining above the control values (Fig. 5A). A quadratic relationship was obtained between soil salinity and water content of leaves ($r^2 = 0.219$, $P < 0.001$), stems ($r^2 = 0.211$, $P < 0.001$) and roots ($r^2 = 0.128$, $P < 0.001$). Tissues differed significantly ($P < 0.001$) in their water content. Moreover, the maximum water content was in leaves and the minimum in stems. Water potentials became more negative ($P < 0.001$) as soil salinity increased (Fig. 5B), but never dropped below ~3.4 MPa. There was a negative relationship between soil salinity and the water potential of leaves ($r^2 = 0.891$, $P < 0.001$), stems ($r^2 = 0.869$, $P < 0.001$) and roots ($r^2 = 0.824$, $P < 0.001$). Tissues differed ($P < 0.001$) in their water potential, with leaves the most negative and roots the least.

Proline content of tissues

Proline concentrations (on a fresh weight basis) increased ($P < 0.001$) in leaves, stems and root tissues linearly with soil salinity (Fig. 5C). Stems contained slightly more proline than leaves, with roots containing about half the concentration of leaves. There was a
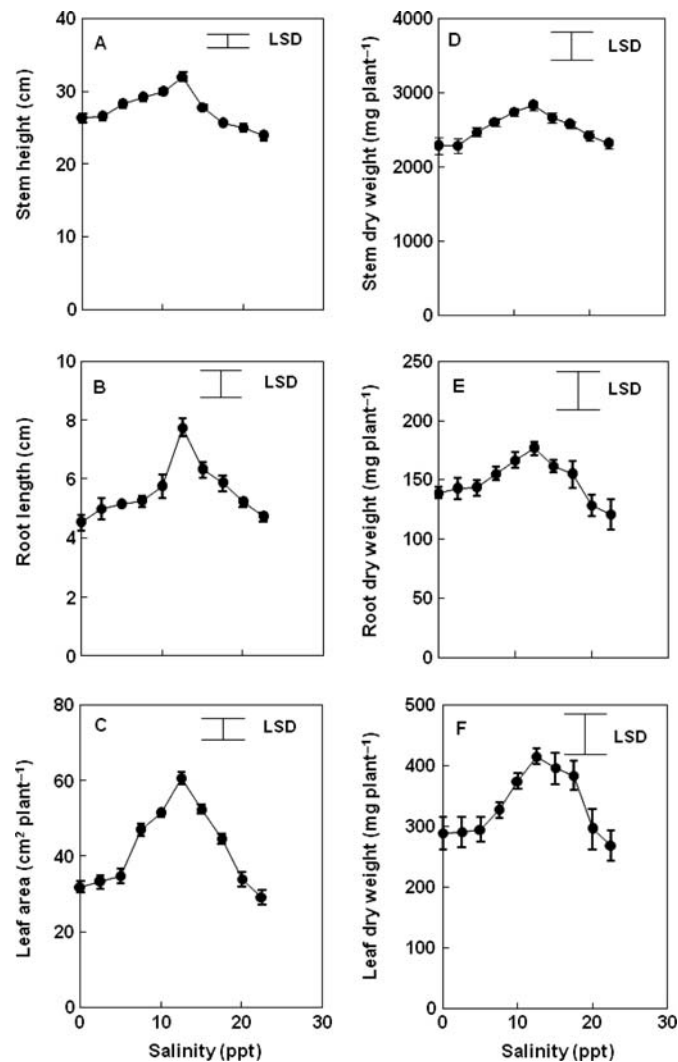
Fig. 3 Effect of increasing soil salinity on size of *C. tagal* plants after 6 months growth from propagules. (A) Stem height, (B) length of longest root, (C) leaf area, (D) stem dry weight, (E) root dry weight and (F) leaf dry weight. The large bar represents LSD at $P \leq 0.05$. Bars on symbols represent the SE, $n = 20$. Some error bars are smaller than the symbols.

positive relationship between salt and proline concentrations of leaves ($r^2 = 0.871$, $P < 0.001$), stems ($r^2 = 0.863$, $P < 0.001$) or roots ($r^2 = 0.850$, $P < 0.001$). A significant inverse relationship was obtained between water potential (more negative values) and the proline content of leaves ($r^2 = 0.865$, $P < 0.001$), stems ($r^2 = 0.811$, $P < 0.001$) and roots ($r^2 = 0.748$, $P < 0.001$).

Mineral accumulation

The concentration of Na on a dry weight basis was greater than that of K, P, Ca and Mg in all tissues of plants under both control and saline conditions (Table 1). Sodium increased significantly ($P < 0.001$) in

leaves, stems and roots with increased soil salinity, giving a statistically significant positive relationship ($P < 0.01$). K in leaves, stems and roots decreased ($P < 0.01$) with increasing salinity, giving a negative relationship between tissue K and salt in the soil ($P < 0.01$). The Na:K ratio increased ($P < 0.001$) with salinity in all three tissues. There was a positive relationship between the Na:K ratio in tissues and salt concentration ($P < 0.01$).

Concentrations of N, P and Ca decreased significantly ($P < 0.01$) in leaves, stems and roots in response to increasing salt concentration in soil. A negative relationship was obtained between N, P and Ca concentration in tissues and salt concentration ($P < 0.01$). The Ca:Na ratio
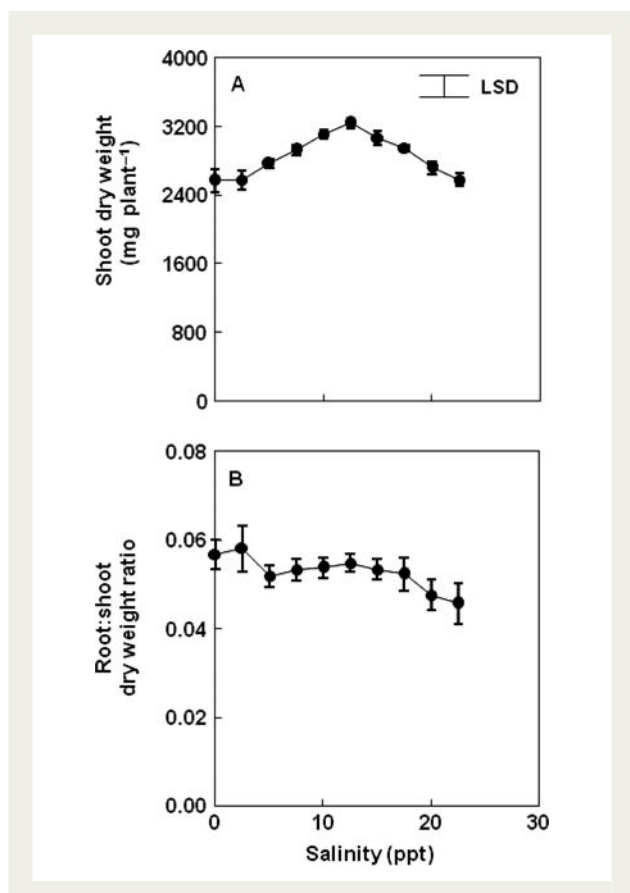
Fig. 4 **Effect of increasing soil salinity on (A) dry weight of shoot (leaf + stem) and (B) root:shoot dry weight ratios of *C. tagal* plants after 6 months growth from propagules.** The large bar represents the LSD at $P \leq 0.05$. Effect of salinity on root:shoot dry weight ratio was not statistically significant. Bars on symbols represent the SE, $n = 20$. Some error bars are smaller than the symbols.

in tissues decreased ($P < 0.001$) with increasing salinity of soil. A negative relationship ($P < 0.01$) was obtained between the Ca:Na ratio in tissues and salt concentration of soil. The concentration of Mg in tissues did not change with increasing salt concentration.

Discussion

It is well established that salinity can reduce and/or delay germination of halophyte seeds (Khan and Ungar, 1984; Ungar, 1996; Katembe *et al.*, 1998; Li *et al.*, 2002; Patel NT *et al.*, 2010). Similarly, with *C. tagal* propagules, salinity over the range 2.5–28.2 ppt delayed propagule establishment and reduced the final percentage of plant establishment to below the control value of 94.4 %. The establishment percentage of *C. tagal* was reduced to 50 % (SE$_{50}$) at a salinity of

22.3 ppt, whereas a 50 % reduction in seed germination (SG$_{50}$) for *Cassia montana*, a halophyte tree in the coastal region of Saurashtra, was already obtained at 6.0 dS m^{-1} (3.8 ppt; Patel and Pandey, 2007). This confirms the high tolerance of the mangrove to salinity. *Ceriops tagal* is characterized by reduced but still considerable establishment of propagules under saline conditions. The capacity of *C. tagal* to invade upper estuarine habitats may thus be dependent on the tolerance shown to salt at this very early developmental stage (Harradine, 1982; Krauss *et al.*, 1998). Adaptation of viviparous propagules to saline environments starts when they are still attached to the mother tree, by continuously absorbing salt from the tree or by a desalinating process (Joshi *et al.*, 1972; Zheng *et al.*, 1999). The tolerance of *C. tagal* also extended to young plants. At all tested salinity levels (0.2–28.2 ppt), no mortality was recorded once the first leaves appeared. Ye *et al.* (2005) reported that for Hong Kong *Avicennia marina* seedlings, the establishment percentage was 100 % at salinities ranging from 0 to 35 ppt.

Growth of young *C. tagal* plants was stimulated by low salinity and was optimal at 12.6 ppt. Similar results have also been reported for other halophytes (Naidoo and Raghunanan, 1990; Ayala and O'Leary, 1995; Khan *et al.*, 2000a; Patel and Pandey, 2007; Patel NT *et al.*, 2010). Soil salinity at 12.6 ppt approximately equals 41 % rainy season seawater of the Jamnagar coast. Similarly, optimum growth of seedlings was obtained at 50 % seawater for *A. marina* from Sunderban (Karim and Karim, 1993), for *A. marina, C. tagal* and *Rhizophora mucronata* from Pakistan (Khan and Aziz, 2001), and for *Sonneratia alba* from Australia (Ball and Pidsley, 1995). Other studies have reported lower optimal ~25 % seawater for *A. marina* and *Rhizophora stylosa* (Downton, 1982; Clough, 1984; Naidoo, 1987; Burchett *et al.*, 1989). This suggests that *C. tagal* growing along the semi-arid and arid coasts of Gujarat has considerable salinity tolerance. As a result, plants of *C. tagal* along the Gujarat coasts in India have approximately a similar salinity tolerance to those of the Karachi coast in Pakistan. Under natural conditions in Gujarat, propagules of *C. tagal* establish during the rainy season when the salinity level of seawater is somewhat diluted.

High soil salinity affects plant growth due to low water potential, ion toxicities, nutrient deficiencies or a combination of these (Khan *et al.*, 2000a). Patel and Pandey (2007) reported that seedlings of *C. montana* grow optimally at 7.9 dS m^{-1} (5.1 ppt) salinity. Evidently, *C. tagal* can be grouped among such highly salt-tolerant plants. The water content of its tissues increased until 12.6 ppt and then declined with increasing salinity while never dehydrating to below control levels. A similar
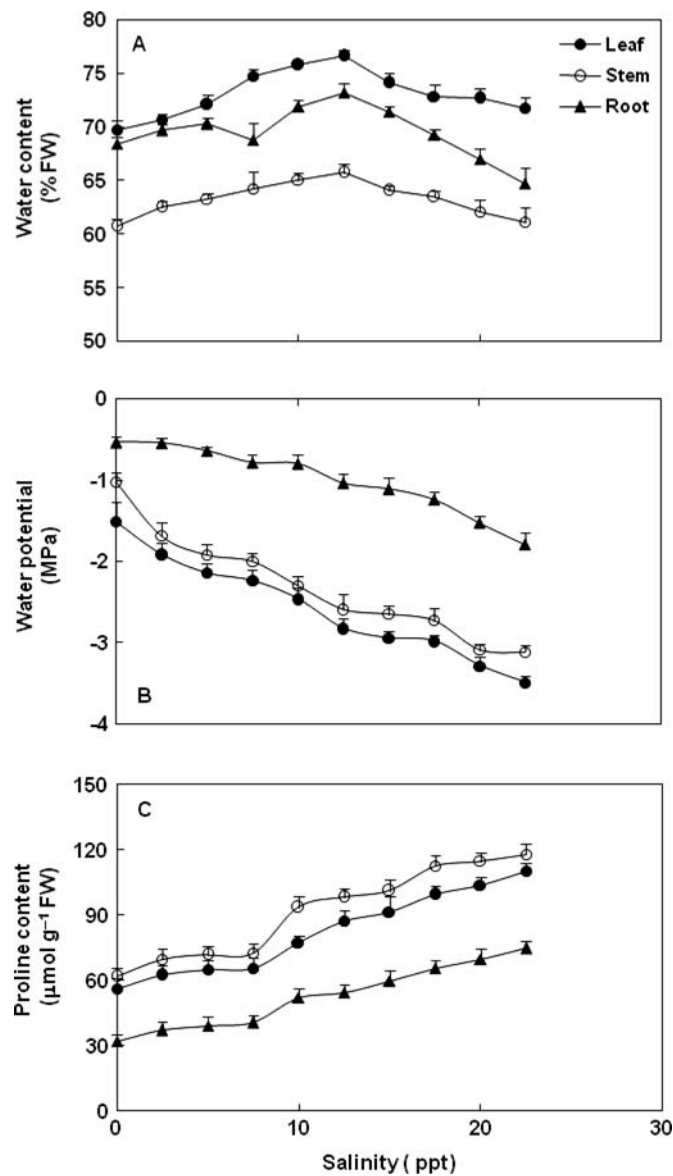
Fig. 5 Effect of increasing soil salinity on (A) water content, (B) water potential and (C) proline content of *C. tagal* plants after 6 months growth from propagules. Water content was determined at final harvest. Water potential and proline concentrations were measured 15 days before harvest. Error bars represent the SE, $n = 20$ for water content and $n = 5$ for water potential and proline content.

result was reported for *Suaeda fruticosa* (Khan *et al.*, 2000a) and *Aegiceras corniculatum* (Patel and Pandey, 2009). Halophytes are known to adjust their tissue water potentials to below those of the soil water (Ungar, 1991). *Ceriops tagal* showed a progressive decrease in the water potential of leaves and stems with an increase in salinity, indicating that it adopts an osmoconforming strategy, as previously described for this species by Khan and Aziz (2001).

Ceriops tagal has the ability to exclude salts via root ultrafiltration (Hagemeyer, 1997). In the present experiment, a high Na concentration was maintained in tissues with an increase in salinity. It was presumably achieved by compartmentalizing Na^+ into vacuoles, as has been found in mangroves and other halophytes (Flowers *et al.*, 1977; Li *et al.*, 2008). High internal salt concentrations benefit mangrove plants by lowering the internal water potential, thereby driving water

Table 1 Effect of soil salinity on nutrient concentration of tissues (leaf, stem and root) of *C. tagal* as indicated by mean ± SEM and estimated linear regression coefficients

Tissue	Salinity (ppt)	N (mg g^{-1} d.m.)	P (mg g^{-1} d.m.)	K (mg g^{-1} d.m.)	Na (mg g^{-1} d.m.)	Ca (mg g^{-1} d.m.)	Mg (mg g^{-1} d.m.)	Na:K ratio	Ca:Na ratio
Leaf	0.2	25.0 ± 1.5	2.3 ± 0.1	6.9 ± 0.3	5.9 ± 0.9	5.1 ± 0.3	1.5 ± 0.0	0.9 ± 0.1	0.9 ± 0.0
	2.5	24.0 ± 1.3	2.2 ± 0.1	6.6 ± 0.1	6.0 ± 0.8	5.1 ± 0.1	1.5 ± 0.1	0.9 ± 0.1	0.9 ± 0.1
	5.1	23.0 ± 1.2	2.2 ± 0.1	6.5 ± 0.3	9.0 ± 0.6	4.9 ± 0.4	1.4 ± 0.0	1.4 ± 0.1	0.5 ± 0.0
	7.7	22.0 ± 1.7	2.2 ± 0.1	6.5 ± 0.3	10.2 ± 0.8	4.7 ± 0.1	1.4 ± 0.0	1.6 ± 0.0	0.5 ± 0.0
	10.3	22.0 ± 1.2	2.2 ± 0.2	6.3 ± 0.2	10.9 ± 0.9	4.6 ± 0.2	1.4 ± 0.0	1.7 ± 0.1	0.4 ± 0.0
	12.6	20.0 ± 1.7	2.1 ± 0.2	6.1 ± 0.3	11.3 ± 1.1	4.5 ± 0.1	1.4 ± 0.0	1.8 ± 0.0	0.4 ± 0.0
	15.4	20.0 ± 1.2	1.8 ± 0.1	6.0 ± 0.1	11.6 ± 0.6	4.3 ± 0.2	1.3 ± 0.1	1.9 ± 0.1	0.4 ± 0.0
	17.9	19.0 ± 1.2	1.7 ± 0.2	5.8 ± 0.2	11.6 ± 0.9	4.1 ± 0.2	1.3 ± 0.0	2.0 ± 0.2	0.4 ± 0.0
	20.5	18.0 ± 1.0	1.5 ± 0.2	5.6 ± 0.2	12.1 ± 0.8	4.1 ± 0.2	1.3 ± 0.1	2.2 ± 0.1	0.3 ± 0.0
	23	18.0 ± 0.7	1.5 ± 0.1	5.6 ± 0.1	12.5 ± 0.3	4.0 ± 0.1	1.3 ± 0.0	2.3 ± 0.1	0.3 ± 0.0
	α	24.712	2.38	6.847	6.838	5.136	NS	0.971	0.763
	β	−0.202	−0.023	−0.037	0.284	−0.034	NS	0.039	−0.023
	r^2	0.601	0.609	0.614	0.77	0.624	NS	0.852	0.721
	F-value	3.569[a]	4.958[a]	3.697[a]	27.393[b]	3.965[a]	NS	24.109[b]	42.803[b]
	LSD$_{0.05}$	4	0.4	0.7	1.4	0.6	NS	0.3	0.1
Stem	0.2	23.0 ± 1.0	2.0 ± 0.1	4.4 ± 0.1	9.9 ± 0.4	4.7 ± 0.1	1.3 ± 0.0	2.3 ± 0.1	0.5 ± 0.0
	2.5	22.0 ± 1.3	2.0 ± 0.3	4.4 ± 0.1	10.5 ± 0.2	4.7 ± 0.1	1.3 ± 0.0	2.4 ± 0.2	0.4 ± 0.0
	5.1	21.0 ± 1.0	2.0 ± 0.2	4.3 ± 0.0	10.9 ± 0.2	4.5 ± 0.2	1.3 ± 0.0	2.5 ± 0.1	0.4 ± 0.0
	7.7	21.0 ± 0.9	1.9 ± 0.2	4.3 ± 0.1	11.1 ± 0.1	4.4 ± 0.1	1.3 ± 0.0	2.6 ± 0.2	0.4 ± 0.0
	10.3	20.0 ± 1.2	1.9 ± 0.1	4.3 ± 0.1	11.5 ± 0.3	4.2 ± 0.1	1.3 ± 0.0	2.7 ± 0.2	0.4 ± 0.0
	12.6	20.0 ± 0.6	1.9 ± 0.1	4.3 ± 0.0	11.7 ± 0.2	4.2 ± 0.1	1.3 ± 0.1	2.7 ± 0.1	0.4 ± 0.0
	15.4	19.0 ± 1.1	1.7 ± 0.1	4.2 ± 0.1	11.8 ± 0.2	4.1 ± 0.3	1.2 ± 0.1	2.8 ± 0.1	0.3 ± 0.0
	17.9	18.0 ± 1.1	1.4 ± 0.2	4.1 ± 0.1	12.1 ± 0.1	4.0 ± 0.1	1.2 ± 0.1	2.9 ± 0.1	0.3 ± 0.0
	20.5	18.0 ± 0.9	1.3 ± 0.1	4.0 ± 0.1	12.4 ± 0.3	3.9 ± 0.1	1.2 ± 0.1	3.1 ± 0.1	0.3 ± 0.0
	23	17.0 ± 1.0	1.3 ± 0.1	3.9 ± 0.1	12.6 ± 0.1	3.9 ± 0.1	1.2 ± 0.1	3.2 ± 0.1	0.3 ± 0.0
	α	22.717	2.124	4.447	10.209	4.685	NS	2.279	0.455
	β	−0.156	−0.022	−0.013	0.107	−0.024	NS	0.025	−0.007
	r^2	0.6	0.546	0.572	0.921	0.612	NS	0.865	0.844
	F-value	3.524[a]	3.887[a]	3.822[a]	43.740[b]	3.795[a]	NS	20.926[b]	16.877[b]
	LSD$_{0.05}$	3.1	0.4	0.3	1.1	0.5	NS	0.4	0

Continued

Table 1 *Continued*

Tissue	Salinity (ppt)	N (mg g^{-1} d.m.)	P (mg g^{-1} d.m.)	K (mg g^{-1} d.m.)	Na (mg g^{-1} d.m.)	Ca (mg g^{-1} d.m.)	Mg (mg g^{-1} d.m.)	Na:K ratio	Ca:Na ratio
Root	0.2	21.0 ± 1.2	1.3 ± 0.1	3.1 ± 0.2	11.4 ± 0.3	4.2 ± 0.1	1.2 ± 0.0	3.3 ± 0.4	0.4 ± 0.0
	2.5	20.0 ± 0.6	1.3 ± 0.1	3.0 ± 0.1	11.5 ± 0.1	4.2 ± 0.2	1.2 ± 0.1	3.4 ± 0.0	0.4 ± 0.0
	5.1	19.0 ± 1.0	1.2 ± 0.2	2.9 ± 0.1	12.3 ± 0.3	4.1 ± 0.1	1.2 ± 0.1	3.6 ± 0.2	0.3 ± 0.0
	7.7	19.0 ± 1.2	1.2 ± 0.1	2.9 ± 0.1	12.4 ± 0.3	3.9 ± 0.1	1.1 ± 0.1	3.8 ± 0.2	0.3 ± 0.0
	10.3	18.0 ± 0.6	1.1 ± 0.1	2.7 ± 0.2	13.5 ± 0.3	3.9 ± 0.3	1.1 ± 0.0	4.2 ± 0.4	0.3 ± 0.0
	12.6	18.0 ± 0.9	1.1 ± 0.1	2.6 ± 0.1	14.1 ± 0.2	3.8 ± 0.1	1.0 ± 0.1	4.4 ± 0.1	0.3 ± 0.0
	15.4	17.0 ± 0.8	1.0 ± 0.0	2.6 ± 0.1	14.6 ± 0.2	3.7 ± 0.1	1.0 ± 0.1	4.8 ± 0.3	0.3 ± 0.0
	17.9	17.0 ± 0.6	0.9 ± 0.1	2.4 ± 0.1	14.9 ± 0.3	3.6 ± 0.2	1.0 ± 0.1	5.4 ± 0.4	0.2 ± 0.0
	20.5	16.0 ± 1.0	0.9 ± 0.1	2.3 ± 0.1	15.1 ± 0.2	3.4 ± 0.1	1.0 ± 0.1	6.0 ± 0.4	0.2 ± 0.0
	23	16.0 ± 0.8	0.8 ± 0.0	2.3 ± 0.2	15.3 ± 0.1	3.4 ± 0.2	1.0 ± 0.1	6.1 ± 0.3	0.2 ± 0.0
	α	20.534	1.335	3.134	11.382	4.272	NS	2.992	0.369
	β	−0.135	−0.015	−0.025	0.188	−0.025	NS	0.084	−0.007
	r^2	0.589	0.605	0.642	0.949	0.6	NS	0.856	0.882
	F-value	3.500[a]	3.630[a]	4.614[a]	120.856[b]	3.758[a]	NS	14.149[b]	23.545[b]
	LSD$_{0.05}$	2.7	0.3	0.4	1.1	0.5	NS	0.9	0

Relationships are significant at $P < 0.01$.
NS, non-significant.
[a]F-values are significant at $P < 0.01$.
[b]F-values are significant at $P < 0.001$.

uptake from soil with high salinity and low soil water potential. Yeo (1983) has suggested that Na^+ and Cl^- accumulated in leaf tissue provide osmotic adjustment and turgor to maintain growth. This would explain the remarkable ability of *C. tagal* to expand its leaves more vigorously and improve its tissue hydration at modest salinity levels, and avoid dehydrating to below control levels when higher salinities were imposed.

In the present study, the decrease of K^+ concentration with increasing soil salinity suggests that Na^+ inhibited the K^+ uptake. The Na:K ratio increased in leaves and stems with an increase in salinity, indicating an increase in transportation of Na^+ from root to shoot. Tattini *et al.* (1995) reported that the Na:K ratio increases in salt-tolerant species with increasing salinity in the external medium, because mass transport of sodium takes place from root to shoot via the transpiration stream.

Because of its zwitterionic, high-hydrophilic non-toxic character, proline can act as a 'compatible solute' and its accumulation is a common response to salinity and related stresses (Stewart and Lee, 1974; Storey *et al.*, 1977), allowing it to function at high concentrations to effect osmotic adjustment, stabilization of macromolecules and regulate cellular redox status (Storey *et al.*, 1977; Yamada *et al.*, 2005). The increase of proline concentrations in *C. tagal* with increasing Na concentration indicates that higher proline accumulation may help alleviate NaCl stress in *C. tagal*, although the increase may be too small to influence osmotic balance significantly. Proline accumulation was greater in shoots than in roots. This confirms the observation of Munns (2002) that organic solutes are often lower in roots than shoots. Popp and Albert (1995) reported that *C. tagal* accumulates cyclitols along with Na^+ and Cl^- to maintain osmotic balance.

In general, salinity reduces N accumulation in plants (Feigin, 1985), and we observed a steady reduction in above- and below-ground tissues as salt application increases, with the greatest reduction (28 %) being in leaves. The effect may be ascribed to chloride toxicity (Torres and Bingham, 1973). Similarly, decreases in P concentration were also seen, but both the decline in N and P occurred at low and medium salinities where growth was stimulated, indicating a strong regulation that avoided debilitatingly large declines at modest levels of salinity.

Salinity also decreased Ca^{2+}, suggesting that Na^+ reduced internal concentrations in roots and shoots that might have slowed the growth as optimal levels of salt were exceeded. Uptake of Ca^{2+} may decrease because of ion interactions, precipitation and increase in ionic strength (Janzen and Chang, 1987). It is evidenced that in salt-stressed roots of cotton, Na^+ displaced membrane-associated Ca, which was believed to be primarily at the plasma membrane (Cramer *et al.*, 1985). In addition, NaCl salinity displaced membrane-associated Ca on protoplasts of corn (Lynch *et al.*, 1987) and plasma membrane vesicles of melon (Yermiyahu *et al.*, 1994). One consequence of the displacement of membrane-associated Ca^{2+} by Na^+ is the immediate increase in K^+ efflux across the plasma membrane of salt-stressed cotton roots (Cramer *et al.*, 1985). This effect may be related to the rapid depolarization of the membrane potential upon salinization (Cramer, 1997). In the present study, the increased efflux of K^+ might be one of the reasons for the significant decrease in K concentration in tissues of *C. tagal* in response to NaCl salinity. Shabala *et al.* (2003) reported that in addition to significant Na^+ uptake into the root epidermis of barley, the onset of salt stress caused rapid and prolonged efflux of H^+, K^+ and NH_4^+. But not all key nutrient ions were depressed by salinity. Magnesium concentrations stood out as being very stable and this may be a key feature supporting faster growth at low and moderate salinities, and protecting *C. tagal* from Mg^{2+} decreasing to below control levels at high salinities. As is well known, Mg^{2+} has central roles in chlorophyll structure, as an enzyme cofactor and in exporting photosynthate (Marschner and Cakmak, 1989). The mechanism behind this magnesium homeostasis is unknown.

Conclusions and forward look

High percentages of propagules established successfully under salinity stress, 50 % establishment being achieved at 22.3 ppt NaCl. Subsequent stem and root elongation, and especially leaf expansion, were increased substantially at low and moderate salinities ($\leq$12.6 ppt) while greater salinity failed to slow growth to below control values. Dry matter accumulation in tissues of plants behaved similarly. These findings demonstrate that *C. tagal* is a highly salt-tolerant mangrove at this key early stage in its life cycle. The tolerance is linked to a proportionate regulation of tissue water potentials, which were seen to decrease with an increase in salinity, thereby helping to maintain normal tissue hydration (the osmoconforming strategy). An increased accumulation of proline may also have contributed to this stabilization. A significant increase in Na and a decrease in K, N, P and Ca in tissues may inhibit the growth of the plants in the more extreme saline habitats.

Future work could usefully examine the ability of exogenous proline, and Ca and K to ameliorate the injurious effects of high concentrations of NaCl, although the high tolerance to low and moderate salinities that we demonstrated here strongly suggests that mangrove

die-back on the Gujarat coast may have other causes which now merit further investigation.

Sources of funding

Contributions by authors

N.T.P. and A.N.P. contributed to a similar extent to the experimental work and to writing the paper. A.G. performed the statistical analyses.

Conflict of interest statement

None declared.

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