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Salt tolerance in seedlings of the mangrove *Kandelia candel* (L.) Druce, Rhizophoraceae

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Abstract. We investigated the growth and ion content of seedlings of the mangrove *Kandelia candel* (L.) Druce over a range of salinity, using NaCl as the major ion in a modified Hoagland's solution. The mangrove grew well at salinity levels up to 260 mM NaCl; the optimum was 85 mM. Growth was inhibited at salinity levels above 340 mM. *Kandelia candel* behaved like a typical halophyte, showing high levels of inorganic ion accumulation even at low salinities; this caused low osmotic potential in tissues. *Kandelia candel* did not show increased succulence in tissues at high salinities. As salinity increased, Na replaced K to a large extent in all tissues. Chloride was the major balancing anion in all tissues at all salinity levels.

Keywords: Growth; Ion regulation; *Kandelia candel*; Mangrove; NaCl; Osmotic potential; Rhizophoraceae; Salinity.

Introduction

The mangrove *Kandelia candel* (L.) Druce, a member of Rhizophoraceae, grows in the intertidal zone of the north-western coast of Taiwan. This plant and five other mangrove species were once the dominant coastal plant species in western Taiwan (Liu, 1982), but they have been severely damaged by industrial development. To date, two mangrove species (*Bruguiera gymnorrhiza* Lam. and *Ceriops tagal* C. B. Rob.) have become extinct (Hung et al., 1981) and *K. candel* has become the most abundant mangrove species in Taiwan. In 1993 only 85 ha of *K. candel* remained in Taiwan, and the stands are still decreasing (Huang Tsau-Chin, pers. comm.).

Previous investigations (Chiang, 1984; Chiu and Chou, 1991; Chou and Bi, 1990; Chou et al., 1987; Hwang, 1983) of mangroves in Taiwan have focused on distribution of species, anatomy, and ecology; only a few were on physiology. There has been considerable research done on mangroves in the tropics and the western part of the world (Walsh, 1974; Tomlinson, 1986), but little on *K. candel*—possibly a result of the geographical distribution of this species; it is the northern-most population of mangrove, and is found at latitudes up to 30° N (Tomlinson, 1986). It is believed that *K. candel* tolerates lower air temperatures in winter than do other mangrove species.

This plant grows on the banks of tidal rivers, close to the estuary, where the salinity of the water at high tide is similar to that of sea water. *Kandelia candel* does not possess salt glands, bladders, or other salt secreting structures in its leaves or stem (Chiang, 1984). How the growth of this plant and the regulation of salt accumulation in its tissues responds to increased salinity in sediment is not well understood. In this paper, we report on the responses of growth and ion content of *K. candel* seedlings that were exposed to a range of salinities.

Materials and Methods

Plant Material

Mature propagules of *Kandelia candel* (L.) Druce were collected from mature trees growing along the Tamshui River, Taipei, Taiwan, (121°26'E, 25°9'N). A propagule was deemed to be mature if it could be removed from the tree by a gentle pull or if the color of the expanded section at the lower part of the propagule was orange-red. Propagules ranging in length from 23 to 26 cm were used in this study.

Plant Culture

The bottom 5 cm of each propagule was embedded in a pot of sand (10 cm high, 10 cm diameter). Twenty-four pots were placed tubs and submerged in culture solution. The propagules were treated with different concentrations of salinity (Table 1) from the beginning of the experiment. The basic culture solution was a modified Hoagland's solution (Haines and Dunn, 1976) to which NaCl was added (0, 85, 260, 430, 600, and 770 mM) as the major ion. The pH of the culture solutions was adjusted to 6.0. The level of the culture solution in the tubs was maintained each day with de-ionized water, and the solutions were replaced with fresh solutions every 30 days. In all salinity treatments, the propagules produced roots from the bottom 4-cm region after one week of culture, and produced expanded cotyledons after 3 weeks. All plants were grown from

May to September in a naturally illuminated glasshouse with about 60% of the outside photosynthetic photon flux density (PPFD). The day/night mean air temperature in the experimental period was 28/26 ± 2°C.

Experimental Procedure

Three plants were harvested from each treatment at each of days 30, 60, 90, and 120. Plants were removed from the sand, cleaned in water, rinsed in distilled water, and blotted dry. Plants were separated into leaves, stem, hypocotyl, and roots. Leaf area, stem length, and the fresh and dry weights of all tissues were measured. Plant materials were dried at 60°C for 1 week. Leaf area was measured with a leaf area meter (model Li-3000A, LI-COR, Inc., Lincoln, NE, USA). Mean relative growth rate (RGR) was calculated according to $RGR = (\ln W_2 - \ln W_1)/(t_2 - t_1)$, where W_1 and W_2 are tissue dry weights at the beginning and end of the experimental period, $t_2 - t_1$.

Tissue Ion Analysis

Tissue cation solution was prepared by a dry ashing method according to Kalra and Maynard (1991). Dry tissues were ground, then burned at 470°C for 16 h. The ash residue was dissolved in diluted acids to bring the mineral elements into solution. Na and K were analyzed by flame photometry (Ciba Corning Flame Photometer, Model 410, Halstead, Essex, England), and Ca and Mg by atomic absorption spectrophotometry (Perkin-Elmer Atomic Absorption Spectrophotometer, Model 2380, Norwalk, Connecticut, USA). Cl extract was prepared by hot-water extraction according to Ghosh and Drew (1991) and determined by a digital chloridometer (Buchler Instruments, Model 442-5000, Lenexa, Kansas, USA). We expressed ion concentration on a tissue water basis, instead of tissue dry weight basis, to reflect the activities of ions in tissues.

Table 1. Composition of culture solution.

Solution	Major ions (mM)							
(mM NaCl)	K^+	Na^+	NH_4^+	Mg^{2+}	Ca^{2+}	Cl^-	SO_4^{2-}	PO_4^{3-}
0	6	0	1	1	4	9	1	6
85	6	85	1	1	4	94	1	6
260	6	260	1	1	4	269	1	6
430	6	430	1	1	4	439	1	6
600	6	600	1	1	4	609	1	6
770	6	770	1	1	4	779	1	6

Sap Osmotic Potential Measurement

Mature leaf and mature root sections were used for sap osmotic potential (Ψs) determination. Blot-dried tissues were sealed in a capped vial and frozen at -25°C overnight. The frozen tissues were thawed at room temperature and macerated in the vial, then the sap was used for Ψs determination using a Wescor HR-33T Dew Point Microvoltmeter equipped with a C-52 Sample Chamber (Wescor, Logan, Utah, USA).

Mean values of three replicates of each parameter were compared for all salinity treatments using the SAS general linear model procedure (PROC GLM) one-way analysis of variance and Tukey's Studentized Range test ($P \leq 0.05$; SAS, 1989).

Results

The total dry weights were not significantly different at the end of the experiment, because the hypocotyl dry weights represented 50–85% (from low to high salinities) of the total dry weight. The hypocotyl dry weights among salinity treatments were insignificantly different at the end of the experiment and were insignificantly different throughout the experiment in the same salinity treatment (data not shown), but there were differences in growth of leaves, stem, and roots between salinities. All tissue dry weights, except hypocotyl, were combined to represent total dry weights in the analyses.

Growth of all tissues was significantly inhibited at a salinity of 430 mM NaCl and above (Table 2). Plants grown at a salinity lower than 430 mM NaCl were insignificantly different in leaf area, leaf dry weight, and root dry weight, but the mean values of these parameters were always higher in the 85 mM NaCl treatment than in the 0 and 260 mM NaCl treatments, which indicates that sodium salt can improve the growth of *K. candel.* On the other

Table 2. Growth parameters (mean ± s.e., n = 3) of *Kandelia candel* grown in various concentrations of NaCl for 4 months.

	Treatment (mM NaCl)					
	0	86	260	430	600	770
Leaf area (cm^2)	80.1±16.3^{ab}	102.8±12.9^{a}	88.0±13.4^{ab}	65.8±3.8^{ab}	40.3±4.7^{bc}	11.5±2.3^{c}
Stem height (cm)	16.0±2.9^{bc}	28.7±2.9^{a}	21.9±2.7^{ab}	13.6±2.2^{bc}	5.4±0.6^{cd}	1.4±0.3^{d}
Leaf specific weight (mg/cm^2)	9.23	7.98	8.98	9.87	9.44	12.2
Dry weight (g)						
Leaves	0.74±0.13^{a}	0.82±0.13^{a}	0.79±0.11^{a}	0.65±0.05^{a}	0.38±0.05^{ab}	0.14±0.03^{ab}
Stems	0.45±0.07^{ab}	0.75±0.12^{a}	0.61±0.08^{ab}	0.34±0.04^{bc}	0.12±0.01^{c}	0.03±0.01^{c}
Roots	1.35±0.09^{a}	1.30±0.20^{a}	1.13±0.04^{ab}	1.23±0.10^{ab}	0.75±0.04^{bc}	0.36±0.02^{c}
Total	2.54±0.22^{a}	2.87±0.45^{a}	2.53±0.10^{a}	2.21±0.11^{ab}	1.25±0.01^{bc}	0.53±0.06^{c}

[1] Different superscripts indicate that differences between salinity treatment are significant according to the Turkey's Studentized Range test ($P \leq 0.05$).

hand, plants grown at 430 mM NaCl and above had lower values for the above-ground tissues, which indicates that these salinities may have been stressful for *K. candel.*

The development of leaves on seedlings of *K. candel* began between the second and third week after the planting. The leaf area and leaf dry weight increased continuously until the third month and then levelled off (data not shown). On the other hand, roots emerged during the first week after the planting, but did not grow quickly until the third month (data not shown). The change of shoot to root ratio over time (Figure 1A) summarizes the difference in growth rate of shoot and root at different stages of development.

Overall, total growth (excluding hypocotyl) was inhibited at 430 mM NaCl and above, and was not inhibited at 260 mM NaCl and below (Table 2). A higher RGR was found during the first and second months than during other periods in all salinity treatments (Figure 1B), which may indicate that the growth of leaves and roots was using the seedling's reserves during the first two months.

Plants grown in high salinity did not show succulence in their tissues; instead, the water content in above-ground tissues slightly decreased with increased culture salinity (Figure 2). Because there were insignificant differences in tissue water content in the same tissue in different months, the results from different months were pooled and

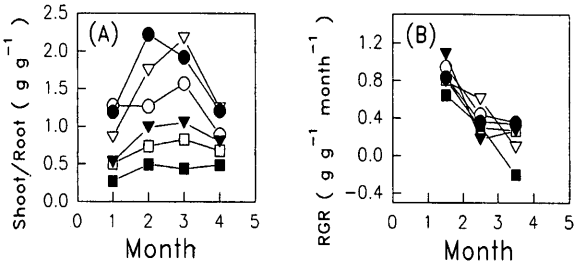

Figure 1. The influence of salinity on A) shoot root ratio and B) RGR of *K. candel* over time. Symbols represent the salinity of the treatments: 0 (hollow-circle), 85 (filled-circle), 260 (hollow-downtriangle), 430 (filled-downtriangle), 600 (hollow-square), and 770 (filled-square) mM NaCl.

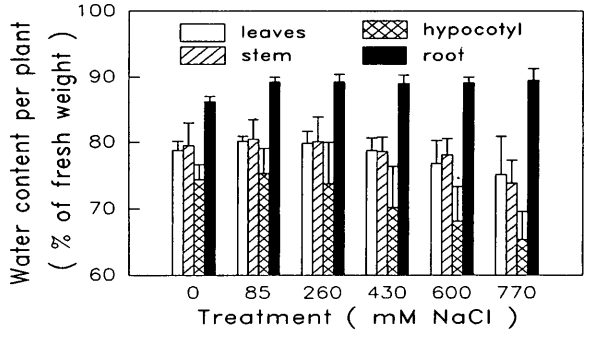

Figure 2. The influence of salinity on tissue water content (% of fresh weight) of *K. candel.* Error bars represent one standard error.

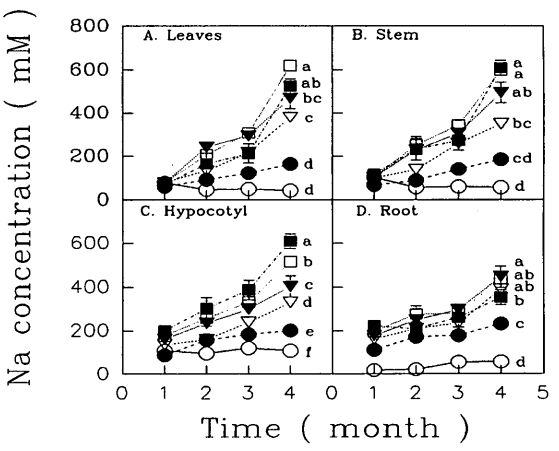

Figure 3. The influence of salinity on Na concentration in A) leaf, B) stem, C) hypocotyl, and D) root tissues of *K. candel* over time (month). Symbols represent the salinity of the treatments: 0 (hollow-circle), 85 (filled-circle), 260 (hollow-downtriangle), 430 (filled-downtriangle), 600 (hollow-square), and 770 (filled-square) mM NaCl. Error bars represent one standard deviation. Different superscripts indicate that differences between salinity treatment at the fourth month are significant according to the Turkey's Studentized Range test ($P \leq 0.05$).

averaged. Root tissues had the highest water content (~90% of fresh weight) and hypocotyl had the lowest (~70% of fresh weight) in all salinities (Figure 2).

The accumulation of Na in tissues was dependent on the salinity of the culture solution (Figure 3). With 0 mM NaCl, the Na concentration in leaves and stem decreased over time. With 86 mM NaCl, the Na concentration increased gradually in all tissues over time and reached a somewhat steady state of 150 to 200 mM during the fourth month, with the highest concentration in roots and the lowest concentration in leaves. The Na concentration in tissues of plants cultured with 260 mM NaCl and greater increased over time. In these higher salinities, the roots had a higher initial Na concentration than the shoots, but this relationship was reversed after the second month of culture.

The accumulation of K in shoots, leaves, and stems depended inversely on the salinity of the culture solution (Figure 4A and 4B). The concentration of K in leaf tissue of plants cultured with 0 mM NaCl remained at ~200 mM (Figure 4A), but the concentration of K in shoots of plants cultured with 86 mM NaCl increased during the first two months then decreased over time. Above 260 mM NaCl, the concentration of K in shoots decreased over time; it was probably replaced in the tissues by Na (Figure 3). The concentration of K in the roots of plants cultured with 0 mM NaCl remained at ~100 mM, which was significantly higher than with other concentrations of NaCl (Figure 4D). No clear pattern of K concentration in hypocotyl was found (Figure 4C).

The accumulation of Ca in tissues (Figure 5) was small compared with that of Na and K (Figures 3 and 4). A higher concentration of Ca accumulated in shoots at 0 mM

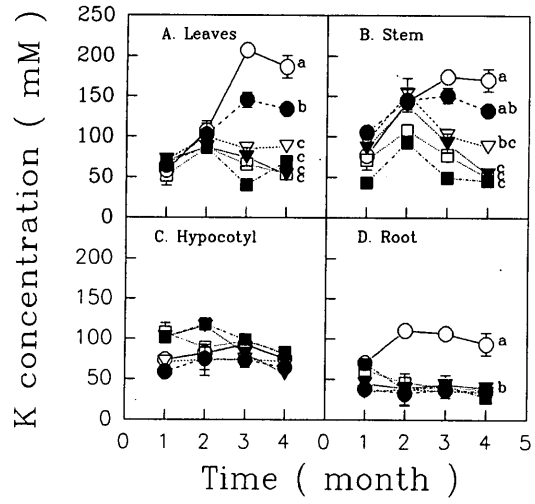

Figure 4. The influence of salinity on K concentration in A) leaf, B) stem, C) hypocotyl, and D) root tissues of *K. candel* over time (month). Symbols, error bars, and superscripts are the same as for Figure 3.

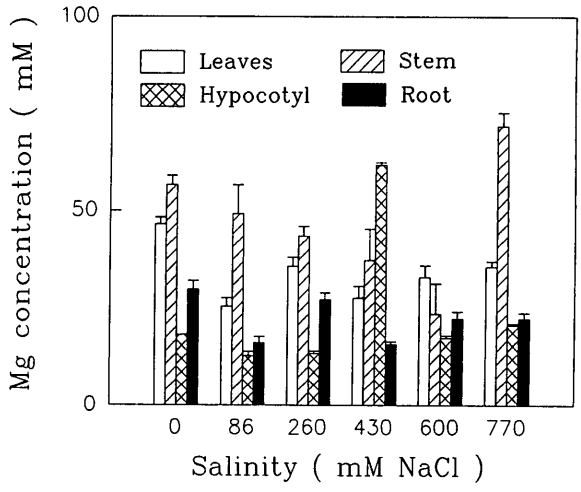

Figure 6. The influence of salinity on Mg concentration in tissues of 4-month-old *K. candel* seedling. Error bars represent one standard deviation.

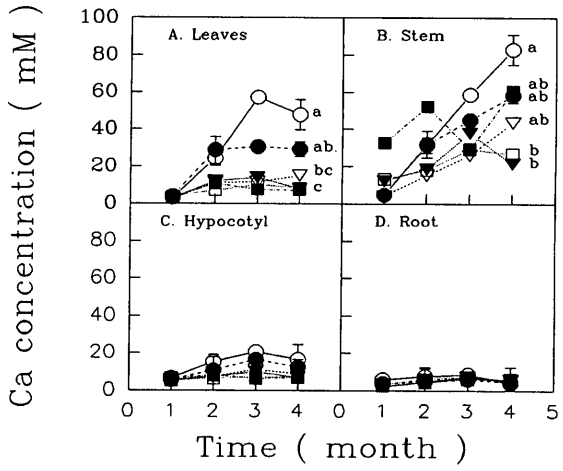

Figure 5. The influence of salinity on Ca concentration in A) leaf, B) stem, C) hypocotyl, and D) root tissues of *K. candel* over time (month). Symbols, error bars, and superscripts are the same as for Figure 3.

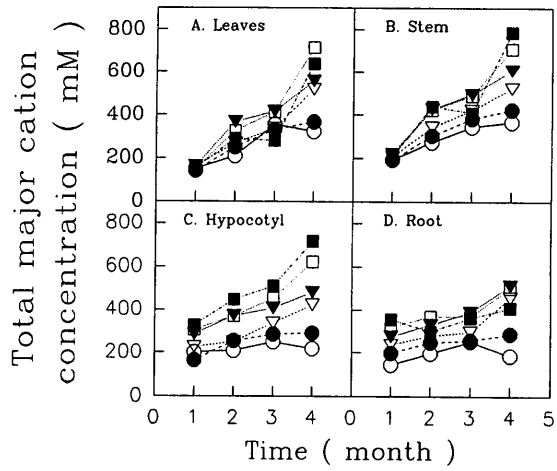

Figure 7. The influence of salinity on total cation concentration in A) leaf, B) stem, C) hypocotyl, and D) root tissues of *K. candel* over time (month). Symbols, error bars, and superscripts are the same as for Figure 3.

NaCl (Figures 5A and 5B), but not in hypocotyl (Figure 5C) or root (Figure 5D). Absorption of Ca in *K. candel* was apparently inhibited by high concentrations of NaCl.

The accumulation of Mg in tissues was not affected by salinity, though a higher Mg content was found in shoots; only the data from the fourth month are shown (Figure 6).

Kandelia candel was able to regulate and accumulate high cation contents in tissues when grown at low salinity. When the concentration of major cations was summed together, we found that *K. candel* seedlings cultured with 0 and 86 mM NaCl salinities maintained a cation concentration of ~350 mM in shoots and ~250 mM in roots (Figure 7), and that the cation concentration of plants cultured with 260 mM NaCl or greater increased over time (Figure 7). The increased tissue ion concentration in high salinity cultures may have caused higher leaf specific weight (Table 2), but did not increase the tissue water content (Figure 2).

Chloride was the major anion accumulated in *K. candel* seedlings, even in 0 mM NaCl cultures (Figure 8). The accumulation pattern of Cl in tissues of *K. candel* seedlings was similar to that of total cations (Figure 8).

The levels of Ψs in the leaf and root tissues were lower than that of the culture solution (Figure 9). They were ~1 MPa lower in leaf than in root—possibly because of the greater ion concentration in leaves (Figure 7).

Discussion

The seedling grew well in cultures containing 0 to 260 mM NaCl (Table 2); the optimum salinity was 86 mM

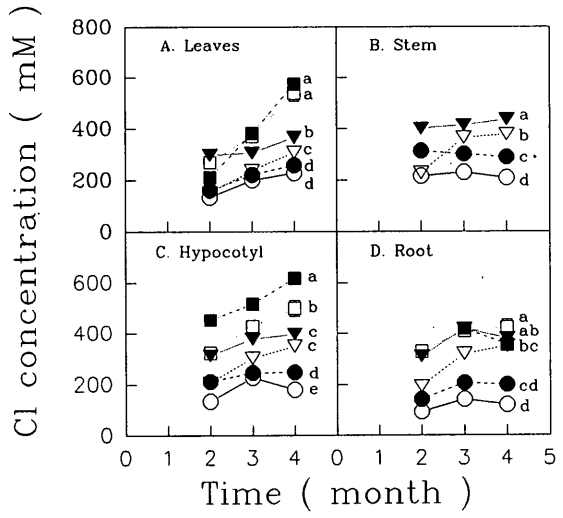

Figure 8. The influence of salinity on Cl concentration in A) leaf, B) stem, C) hypocotyl, and D) root tissues of *K. candel* over time (month). Symbols, error bars, and superscripts are the same as for Figure 3.

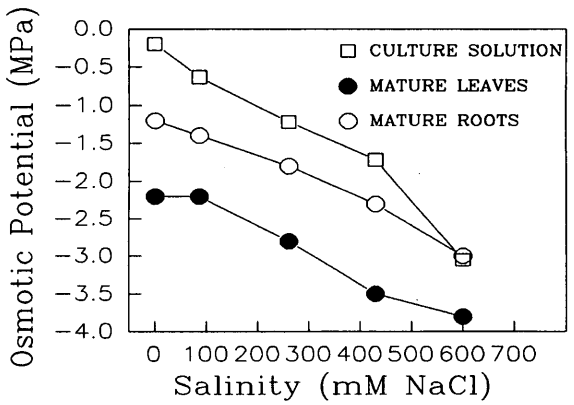

Figure 9. The effect of salinity on leaf and root osmotic potential of *K. candel.*

NaCl. This growth pattern—stimulation in low salinity and inhibition in high salinity—is similar to that of other mangroves (Flowers et al., 1977; Ball, 1988). The optimal growth salinity for *Avicennia marina* (Downton, 1982; Clough, 1984) and *Rhizophora stylosa* (Clough, 1984) was between 10% and 25% of the salinity of seawater, equivalent to 50–120 mM Na.

Most mangroves grow best in moderately saline solutions (Clough, 1984; Werner and Stelzer, 1990). It has been proposed that the ability to maintain turgor by accumulating salts in the tissues stimulates the growth of halophytes in low salinity environments (Flowers et al., 1977). *Kandelia candel*, like most halophytes, accumulates high concentrations of inorganic ions in its tissues even when cultured at 0 mM NaCl salinity (Figure 7). Na and Cl were the major ions in plants cultured at non-zero NaCl salinity (Figures 3 and 8), and K was the major cation at 0 mM NaCl (Figure 4). There was no significant difference in the osmotic potentials of leaves and roots in the 0 and 86 mM NaCl treatments (Figure 9).

High concentrations of ions (Figure 7) accumulating in tissues of *K. candel* grown in high salinities may have caused a reduction of growth (Table 2). *Kandelia candel* does not have specialized salt secretion glands on leaf and stem (Chiang, 1984), it can be classified as a salt 'non-secretor' (Scholander et al., 1962). High levels of ion contents in *K. candel* cause the levels of Ψs in leaves and roots to be lower than that in the growing solutions (Figure 9), which may avoid severe water deficit in the tissues, but continuous accumulation of ions in *K. candel* grown in high salinities (Figures 7 and 8) may cause salt stress. Concentrations of cations in the plant greater than 180 mM may inhibit biochemical processes, e.g. enzyme activities (Flowers, 1972; Greenway and Osmond, 1972) and protein synthesis (Gibson et al., 1984). It has been demonstrated that most cations in the cells of halophytes are compartmentalized in the vacuole (Storey et al., 1983a; 1983b), and that organic solutes, e.g. proline (Stewart and Lee, 1974), glycinebetaine (Storey and Wyn Jones, 1975), and other low molecular weight carbohydrates (Popp, 1984), are in the cytoplasm as an alternate osmoticum. It is impossible to determine the actual ion compartments in *K. candel* from our data, but it is likely that as in other mangroves, most ions were compartmentalized in the vacuole and compatible organic solutes accumulated in the cytoplasm for osmotic adjustment (Popp et al., 1993). Besides the possible influence on biochemical processes, the cost of maintaining osmoregulation and compatible solute production under high ion content conditions (Yeo, 1983) may limit the growth of mangroves in high salinity solutions.

Popp et al. (1993) found a positive correlation between leaf water content (succulency) and tissue Cl content in mangroves grown in the field, but not for those grown in glasshouse conditions. It has been suggested that the survival of dicotyledonous halophytes in saline environments is achieved by using the ions in the environment and is associated with succulence in tissues (Flowers et al., 1986; Tomlinson, 1986). The succulence of *K. candel*, however, did not increase (Figure 2) when it was grown at high salinity, and in fact the water content of hypocotyl decreased in those grown in 430 mM NaCl and above. Whether succulence in halophytes grown in high salinity is necessary for increasing turgor, and thus increasing growth, is still an open question (Munns, 1993).

Different phases of tissue growth in *K. candel* seedlings were identified. Plants produced roots from the 4-cm region of the lower part of the hypocotyl within one week, but did not produce expanded cotyledons until the third week. Shoots grew faster than roots during the first three months of growth, but then the growth rate of roots increased while the growth of shoots leveled off. This caused a decrease of shoot to root ratio (Figure 1A). In general, RGR was high for all salinity treatment in the first two months (Figure 1B), but then decreased in all salinity treatments. Plants in this stage of growth use reserves in seeds or hypocotyl for the growth of new tissues until the leaves and roots are mature enough to provide resources for growth.

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水筆仔紅樹林 (紅樹科) 幼苗耐鹽之研究

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本文研究不同鹽度對水筆仔紅樹林幼苗生長與離子含量之影響。以 NaCl 爲主要鹽分離子並配以修飾之 Hoagland 營養液進行四個月之生長實驗。適合水筆仔生長之鹽度爲介於 0 和 260 mM NaCl 間，但以 85 mM 之狀況較不加 NaCl 者爲佳。鹽度高於 340 mM NaCl 時，對水筆仔幼苗之生長有抑制作用。水筆仔即使生長於低鹽度環境下，也會在組織中累積高濃度之離子；此爲鹽生植物之共通性。高濃度離子累積之結果，造成組織滲透勢之下降，有助於水筆仔生長於高鹽度環境中。但生長於高鹽度下之水筆仔組織沒有肉質化之現象。水筆仔組織中 Na 含量會因培養液之鹽度增加逐漸取代 K 而增高。 Cl 是水筆仔組織中之主要陰離子。

關鍵詞：水筆仔；生長；紅樹林；紅樹科；氯化鈉；滲透勢；離子調節；鹽度。