Aust. J. Plant Physiol., 1992, **19**, 509–17

Effect of Growth Form, Salinity, Nutrient and Sulfide on Photosynthesis, Carbon Isotope Discrimination and Growth of Red Mangrove (*Rhizophora mangle* L.)

Guanghui Lin[AB] *and Leonel da S. L. Sternberg*[A]

[A] Department of Biology, University of Miami,
Coral Gables, Florida 33124, USA.
[B] Corresponding author.

Abstract

The red mangrove (*Rhizophora mangle* L.), a dominant mangrove species in Florida, frequently occurs in two distinct growth forms, scrub and tall trees. These two growth forms show significant differences in physiology in the field, with lower CO_2 assimilation rate, stomatal conductance, and carbon isotope discrimination or higher transpiration efficiency for the scrub form. To elucidate the possible factors responsible for these physiological differences, we studied the physiological and growth responses of scrub and tall red mangrove seedlings grown hydroponically in the greenhouse under 12 different growth conditions combining three salinities (100, 250, 500 mM NaCl), two nutrient levels (10, 100% strength of full nutrient solution), and two sulfide concentrations (0, 2·0 mM Na_2S). The two growth forms showed similar physiological and growth responses to these treatments, suggesting no genetic control of physiological and growth differences between the growth forms of this species. High salinity, low nutrient level, and high sulfide concentration all significantly decreased CO_2 assimilation, stomatal conductance, and plant growth, but only salinity significantly decreased intercellular CO_2 concentration and leaf carbon isotope discrimination, suggesting that the lower carbon isotope discrimination, or higher transpiration efficiency, observed for scrub mangroves in the field is caused only by high salinity during the dry season. Hypersalinity thus seems to be one of the stressful environmental conditions common to all scrub red mangrove forests studied in southern Florida.

Introduction

One interesting aspect of mangrove swamps is the occurrence of distinct growth forms within many mangrove species, especially those in genera *Aegiceras*, *Avicennia*, *Ceriops*, *Laguncularia*, and *Rhizophora* (Lugo and Snedaker 1974; Rao 1986; Lin and Sternberg 1992*a*). They occur in a tall form with tree height ranging from several to over 30 m when growing in fringe, riverine, overwash or basin habitats, as well as a scrub or dwarf form with canopy height only about 1 m high when grown in other habitats, such as locations with higher elevation (Lugo and Snedaker 1974; Lin and Sternberg 1992*b*). The occurrence of distinct growth forms is also common in other coastal wetland plants such as salt marsh species *Spartina alterniflora* Loisel. and *Juncus roemerianus* Scheele (Valiela *et al.* 1978; Anderson and Treshow 1980; Eleuterius 1984; Gallagher *et al.* 1988; Eleuterius 1989). Controversy has surrounded the cause of the differences between growth forms; whether the mechanism is related to environmental differences or genetic variation is still not clear (Gallagher *et al.* 1988; Lin and Sternberg 1992*a*).

The red mangrove (*Rhizophora mangle* L.), one of the most abundant mangrove species in Florida, is known to occur frequently in both scrub and tall form (Lugo and Snedaker 1974; Lin and Sternberg 1992*a*). Our previous studies showed that these two growth forms differ significantly not only in morphology, but in photosynthetic gas exchange and transpiration efficiency under field conditions (Lin and Sternberg 1992*a*, 1992*b*). Scrub red

0310-7841/92/050509$05.00

mangroves usually showed significantly lower CO_2 assimilation rate and stomatal conductance, but higher transpiration efficiency reflected by their lower carbon isotope discrimination or higher leaf carbon isotope ratios (Lin and Sternberg 1992*a*, 1992*b*). It is not clear whether these differences are attributed to genetic variation or environmental differences. As for environmental differences between the two growth forms, hypersalinity, nutrient limitation and waterlogging are among the factors speculated to be responsible for the occurrence of scrub red mangroves in southern Florida (Davis 1940; Egler 1952; Lugo and Snedaker 1974; Lin and Sternberg 1992*b*).

To elucidate the possible factors responsible for physiological differences between scrub and tall red mangroves, we studied the physiological and growth responses of both scrub and tall red mangrove seedlings grown hydroponically in the greenhouse under different growth conditions combining various salinities, nutrient levels and sulfide concentrations. We measured leaf gas exchange, carbon isotope discrimination and plant growth of these seedlings under greenhouse conditions, and compared them with the results of previous studies under field conditions (Lin and Sternberg 1992*a*, 1992*b*).

Materials and Methods

Plant Materials

Propagules of *Rhizophora mangle* were collected on 8 August 1990 from scrub and tall trees growing along the northwestern coast of Sugarloaf Key, Monroe County, Florida (24°41'N,81°33'W). The mean fresh weight of propagules was 11·6 ± 0·5 g for the scrub form, and 12·7 ± 0·4 g for the tall form. The propagules were then cultivated in vermiculite beds and irrigated with tap water in the shade house on the campus of University of Miami, Coral Gables. The irradiance level in the shade house was controlled with cheesecloth to about one-third strength of natural solar irradiation (200–800 μmol m^{-2} s^{-1}). The propagules were kept in the shade house until the seedlings had four leaves (February 1991).

Experimental Procedures

We then collected 36 seedlings with similar dimensions from the population of each growth form, and recorded the initial height and fresh weight of each seedling. Another 10 seedlings were collected from the population of each growth form to determine the mean water content of seedling samples, which was used to calculate initial dry weight of each seedling. The seedlings were then placed in plastic pots (1200 cm^3) containing 2 parts of vermiculite and 1 part of gravel, with one seedling per pot. A randomised block design was used for the experiment; three scrub and three tall mangrove seedlings were selected randomly and placed together in each of 12 plastic containers in the greenhouse for treatments.

In the first 2 weeks, seedlings were allowed to grow in tap water for acclimation to greenhouse conditions, then tap water was replaced by culture solutions with different salinities, nutrient levels and sulfide concentrations according to a factorial design of 3 × 2 × 2. Salinity in the culture solution was adjusted by adding refined sea salt to the solution at a rate of 50 mM NaCl per day to give the final three salinities of 100, 250, 500 mM NaCl (Ball and Farquhar 1984). The nutrient levels in the culture solution were controlled by adding either full nutrient solution used by Clough (1984) for mangrove culture or 10% strength of the full nutrient solution to give high and low nutrient levels, respectively. Sulfide concentrations were increased by adding sodium sulfide (Na_2S) at a rate of 0·2 mM per day to reach the final concentration of 2·0 mM, which is the high level of sulfide concentration in anaerobic soils (Koch and Mendelssohn 1989). Each container was covered with a specially designed cover to prevent evaporation, and the water levels were maintained by the addition of tap water every day. Culture solution was then changed every 2 weeks. Seedlings receiving these salinity treatments were grown in the greenhouse where the temperature was maintained close to that outside the greenhouse, with mean maximum temperature of the hottest month of 37°C and mean minimum temperature of the coldest month close to 10°C during the experiment. The irradiance level inside the greenhouse was about half-strength of natural solar radiation (600–1200 μmol m^{-2} s^{-1}) and relative humidity was 55–75% during the time of investigation. The experiment was concluded after seedlings received the treatments for 6 months (from February to August 1991).

Gas Exchange Measurements

Photosynthetic gas exchange was measured on intact, attached leaves with a LI-6250 portable photosynthesis system equipped with an 1 L leaf chamber (LI-COR, Lincoln, Nebraska). Measurements were made hourly from 1000–1500 hours to ensure constant high radiation (1000–1200 μmol m^{-2} s^{-1}) on three sunny days during the last 2 weeks of the experiment (August 1991). During gas exchange measurements, leaf temperature was maintained close to the air temperature in the greenhouse, which ranged from 28 to 37°C from 1000–1500 hours in August 1991. Raw data accumulated with the LI-6250 were used to calculate mean CO_2 assimilation rates (A), stomatal conductance to water vapour (g), intercellular CO_2 concentration (C_i), and intrinsic transpiration efficiency (A/g).

Carbon Isotopic Analysis

Carbon isotope ratio was measured on all leaves of each seedling as described previously (Lin and Sternberg 1992*b*). $\delta^{13}C$ values were then used to calculate leaf carbon isotope discrimination (Δ) by using the following equation:

$$\Delta = (\delta_a - \delta_p)/(1 + \delta_p) ,$$

where δ_a and δ_p are the carbon isotope ratios of atmospheric CO_2 and plant materials, respectively (Farquhar *et al.* 1989). A mean of $-8{\cdot}0‰$ for δ_a was used in this study (Ehleringer 1990).

Growth Measurements

At the conclusion of the experiment, height of each seedling was measured, and height growth was calculated as the difference between the final and initial height (Pezeshki *et al.* 1990). The total leaf area of each seedling was determined with a portable leaf area meter (LI-3000, LI-COR, Lincoln, Nebraska). The dry weight of each seedling was then determined by drying all plant materials in an oven, and growth rates were calculated as increment in dry weight per unit time per plant (mg per day per plant).

Statistical Analysis

Effects of growth form, salinity, nutrient, sulfide and their interactions on photosynthetic gas exchange, leaf carbon isotope discrimination and plant growth were tested by MGLH program in SYSTAT (Wilkinson 1989). The relationship between CO_2 assimilation and stomatal conductance, and between leaf carbon isotope discrimination and intercellular CO_2 concentration or intrinsic transpiration efficiency (A/g) was compared between scrub and tall mangroves by ANCOVA.

Results

Growth form had no significant effects on CO_2 assimilation rate (A), stomatal conductance (g), and intercellular CO_2 concentration (C_i) (Table 1), and scrub and tall red

Table 1. Significant levels of effects of growth form, salinity, nutrient and sulfide on leaf gas exchange, carbon isotope discrimination and plant growth of *R. mangle* seedlings

Measured parameters are CO_2 assimilation rate (A), stomatal conductance (g), intercellular CO_2 concentration (C_i), leaf carbon isotope discrimination (Δ), leaf area (LA), growth rate (GR), and height growth (HG). NS, not significant ($P>0{\cdot}05$); *, significant at $P<0{\cdot}05$; **, significant at $P<0{\cdot}01$; ***, significant at $P<0{\cdot}001$

Factor	d.f.	A	g	C_i	Δ	LA	GR	HG
Growth form	1,47	NS	NS	NS	NS	NS	NS	NS
Salinity	2,47	***	***	***	*	***	***	***
Nutrient	1,47	***	***	NS	NS	***	***	***
Sulfide	1,47	***	***	NS	NS	NS	NS	NS
Salinity × nutrient	2,47	**	***	NS	NS	NS	NS	***
Salinity × sulfide	2,47	***	***	*	NS	NS	NS	NS
Nutrient × sulfide	1,47	NS	NS	NS	NS	NS	NS	NS
Salinity × nutrient × sulfide	2,47	NS	NS	NS	NS	NS	NS	NS

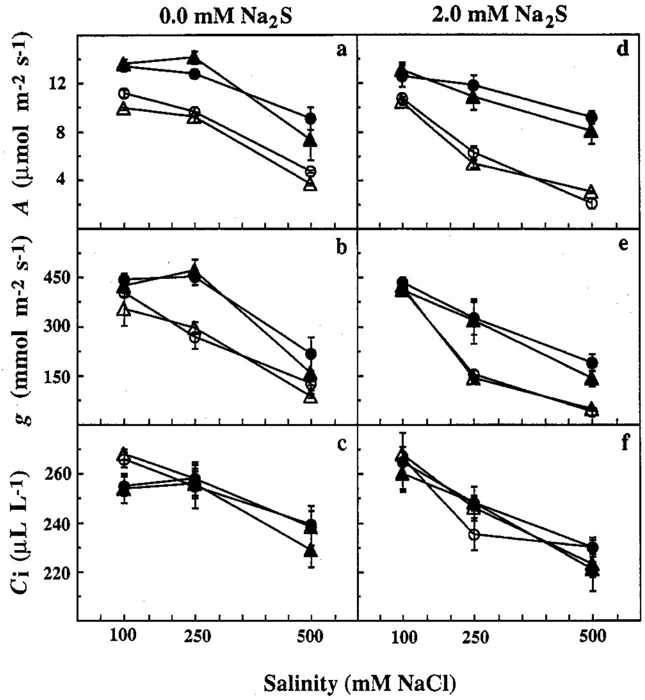

Fig. 1. CO_2 assimilation rate (*A*), stomatal conductance (*g*), and intercellular CO_2 concentration (C_i) of seedlings from scrub (circles) and tall (triangles) red mangroves grown under three different salinities, two nutrient levels (open symbols for 10% and closed symbols for 100% strength of full nutrient solution), and two sulfide concentrations (left side for no sulfide and right side for high sulfide concentration).

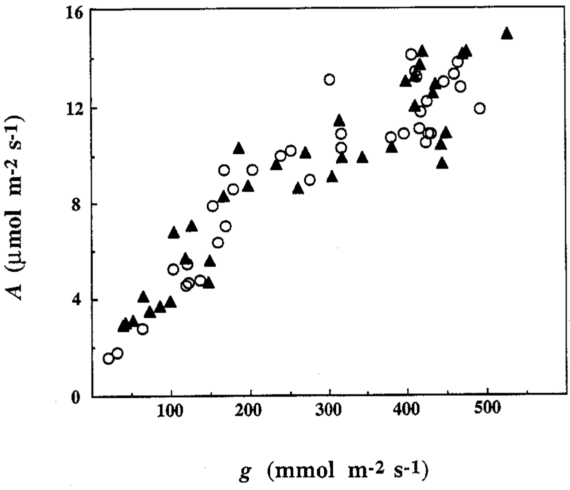

Fig. 2. Relationship between CO_2 assimilation rate (*A*) and stomatal conductance (*g*) for scrub (circles) and tall (triangles) red mangrove seedlings grown in the greenhouse. For scrub mangroves: $A = 3 \cdot 0053 + 0 \cdot 0222\, g$ ($r^2 = 0 \cdot 839$, $P < 0 \cdot 001$), while for tall mangroves: $A = 2 \cdot 8769 + 0 \cdot 0226\, g$ ($r^2 = 0 \cdot 866$, $P < 0 \cdot 001$). There was no significant difference in correlation between scrub and tall mangroves ($P > 0 \cdot 05$, ANCOVA).

mangrove seedlings showed similar responses in leaf gas exchange to salinity, nutrient and sulfide treatments under the same greenhouse conditions (Fig. 1). A and g were significantly affected by salinity, nutrient and sulfide treatments, while C_i was affected only by salinity (Table 1). A, g and C_i all decreased with increasing salinity from 100 mM to 500 mM, except that 250 mM salinity had no significant effects on A, g and C_i when seedlings were grown under high nutrient and no sulfide conditions (Fig. 1). Lower nutrient level (10% of strength of full nutrient solution) decreased both A and g, especially when seedlings were grown under medium and high salinities (250 and 500 mM) and high sulfide concentration (2·0 mM) (Fig. 1*a*, *b*, *d*, *e*). High sulfide concentration had significant effects on A and g only when seedlings were grown under low nutrient level (Fig. 1*a*, *b*, *c*, *d*). Thus, there were synergistic effects between salinity and nutrient treatment, and between salinity and sulfide treatment on A and g, but no synergistic effects between nutrient and sulfide treatment (Table 1). In addition, there was a highly significant correlation between A and g in both scrub and tall red mangrove seedlings, with no significant difference in correlation between scrub and tall mangroves (Fig. 2).

No significant differences in leaf carbon isotope discrimination between scrub and tall mangroves were observed under all growth conditions (Table 1), and both forms of red mangroves had similar responses in Δ to salinity, nutrient and sulfide treatments (Fig. 3). Salinity treatment significantly decreased Δ, while nutrient and sulfide treatment had no such effects, except that low nutrient level decreased leaf Δ when seedlings were grown under salinity of 250 and 500 mM (Table 1, Fig. 3). There were significant correlations between leaf Δ and C_i and between leaf Δ and intrinsic transpiration efficiency (A/g), and no significant difference in correlation was observed between scrub and tall red mangroves (Fig. 4). Note that Δ values reported here were obtained by pooling all leaves on the plants, and thus they integrated C_i over the whole 6 month period, whereas our gas exchange measurements were only for the last 2 weeks of the experiment. In addition, C_i and leaf Δ values reported here were relatively high in comparison with the published values for mangroves (Farquhar *et al.* 1982; Ball and Farquhar 1984; Lin and Sternberg 1992*b*), probably due to the low light level used in the present study.

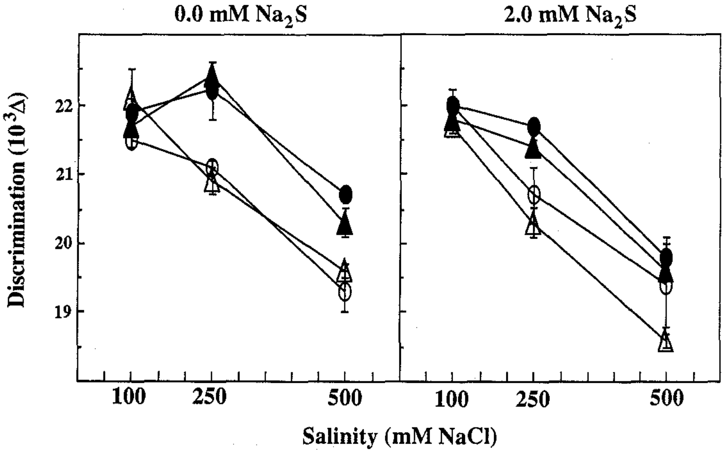

Fig. 3. Leaf carbon isotope discrimination of seedlings from scrub (circles) and tall (triangles) red mangroves grown under three different salinities, two nutrient levels (open symbols for 10% and closed symbols for 100% strength of full nutrient solution), and two sulfide concentrations (left side for no sulfide and right side for high sulfide concentration).

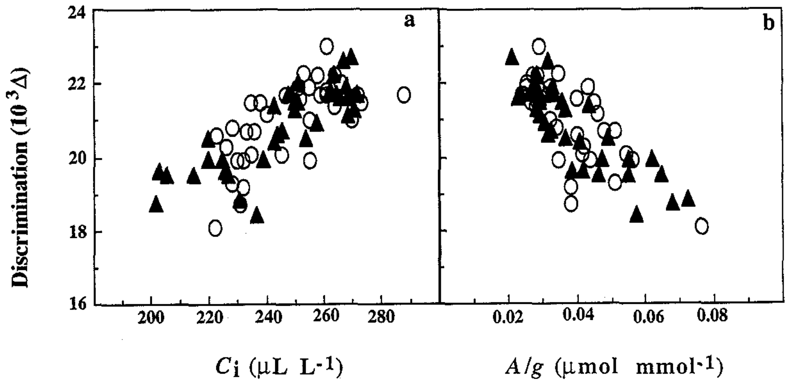

Fig. 4. Relationship between leaf carbon isotope discrimination and intercellular CO_2 concentration (C_i) (*a*), and between leaf carbon isotope discrimination and intrinsic water use efficiency (*A/g*) (*b*) for scrub (circles) and tall (triangles) red mangrove seedlings grown in the greenhouse. For scrub mangroves: $\Delta = 9{\cdot}8658 + 0{\cdot}0449\ C_i$ ($r^2 = 0{\cdot}462$, $P < 0{\cdot}01$) and $\Delta = 23{\cdot}605 + 69{\cdot}284\ A/g$ ($r^2 = 0{\cdot}499$, $P < 0{\cdot}01$), while for tall mangroves: $\Delta = 9{\cdot}9175 + 0{\cdot}0444\ C_i$ ($r^2 = 0{\cdot}666$, $P < 0{\cdot}001$) and $\Delta = 23{\cdot}661 - 71{\cdot}914\ A/g$ ($r^2 = 0{\cdot}723$, $P < 0{\cdot}001$). There was no significant difference in correlation between scrub and tall mangroves ($P > 0{\cdot}05$, ANCOVA).

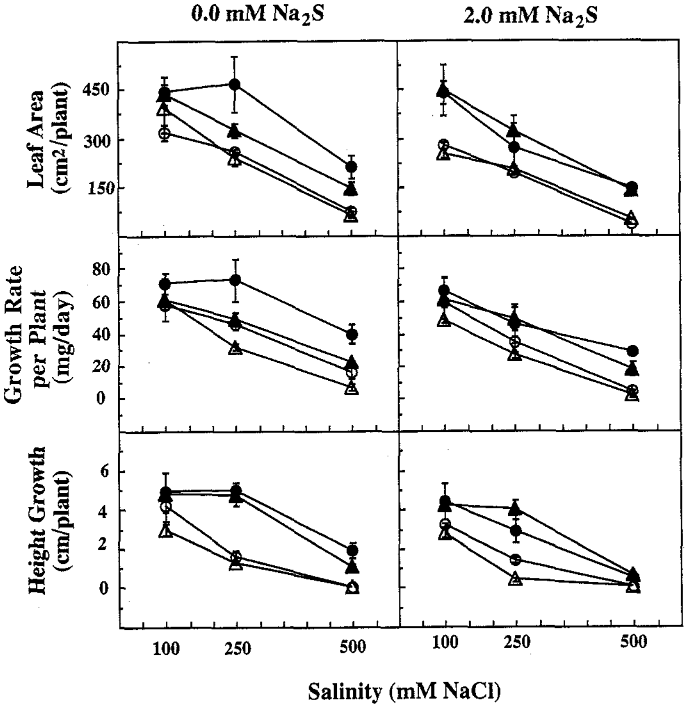

Fig. 5. Total leaf area, growth rate, and height growth of seedlings from scrub (circles) and tall (triangles) red mangroves grown under three different salinities, two nutrient levels (open symbols for 10% and closed symbols for 100% strength of full nutrient solution), and two sulfide concentrations (left side for no sulfide and right side for high sulfide concentration).

Growth form also did not affect leaf area, growth rate and height growth of red mangrove seedlings under all growth conditions (Table 1), except that tall mangroves showed lower leaf area and growth rate than scrub mangroves when grown under high nutrient level and salinities of 250 and 500 mM (Fig. 5). High salinity always decreased leaf area, growth rate and height growth, while low nutrient level reduced plant growth only when seedlings were grown under higher salinities (Table 1, Fig. 5). High sulfide concentration, however, did not significantly affect leaf area, growth rate and height growth of red mangroves (Table 1, Fig. 5).

Discussion

Under the greenhouse conditions, seedlings from two growth forms of red mangroves (scrub and tall) have similar leaf gas exchange characteristics such as CO_2 assimilation rate, stomatal conductance and intercellular CO_2 concentration (Fig. 1), as well as the relation between CO_2 assimilation rate and stomatal conductance (Fig. 2), an indicator of conservative water use in mangroves (Ball 1988). Consistently, they have similar leaf carbon isotope discrimination (Fig. 3), indicating the similar long-term transpiration efficiency (Farquhar *et al.* 1989). Scrub and tall red mangroves also have similar growth rate and height growth under the same growth conditions (Fig. 5). Therefore, it is unlikely that genetic differences can be responsible for the physiological differences between the two growth forms observed previously for this species under field conditions (Lin and Sternberg 1992*a*, 1992*b*). Thus, differences in environmental conditions between scrub and tall mangrove forests are the major factors responsible for these physiological differences. Most studies on growth forms of salt marsh species also showed that the differences between the two distinct growth forms resulted from environmental differences along tidal zones (Mooring *et al.* 1971; Valiela and Teal 1974; Shea *et al.* 1975; Mendelssohn 1979; Howes *et al.* 1981), although a few researchers suggested that they are genetically distinct ecotypes (Mooring *et al.* 1971; Gallagher *et al.* 1988; Eleuterius 1989).

In salt marsh species, salinity, nitrogen level, sulfide concentration and drainage are among the environmental variables suggested as causal factors of the growth form differences (cf. Gallagher *et al.* 1988). Similarly, hypersalinity, nutrient limitation and peat compactment are considered to be responsible for the occurrence of scrub mangroves in southern Florida (Davis 1940; Egler 1952; Craighead 1971; Lugo and Snedaker 1974; Lin and Sternberg 1992*a*, 1992*b*). Effects of peat compactment on physiology and growth of red mangroves was not studied here due to the difficulties of simulating the extent of compactment under our greenhouse conditions. Although low nutrient level or nutrient limitation significantly decreased leaf gas exchange and plant growth (Figs 1, 5), it did not affect leaf carbon isotope discrimination, and thus transpiration efficiency (Fig. 3). Our field studies, however, demonstrated that scrub mangroves showed not only lower gas exchange, but also lower leaf carbon isotope discrimination or higher long-term transpiration efficiency (Lin and Sternberg 1992*a*, 1992*b*). In addition, foliage nutrient contents of scrub red mangroves were not significantly different from those of tall mangroves at the same study site (Lin and Sternberg, unpublished data). Therefore, nutrient limitation cannot account for all physiological differences between the two growth forms of red mangroves under field conditions.

Similarly, high sulfide concentration, a result of waterlogging conditions in mangrove soils (McKee and Mendelssohn 1987), also cannot explain the physiological differences between the two growth forms of red mangroves in the field. High sulfide concentration (2·0 mM) did not decrease plant growth, and leaf carbon isotope discrimination or increase transpiration efficiency of red mangroves (Table 1, Figs 3, 5), although it reduced leaf gas exchange (Fig. 1). Furthermore, scrub mangroves in southern Florida occur frequently in areas with higher elevation than most tall mangroves (Lin and Sternberg 1992*b*), thus sulfide concentrations in the soils under scrub mangroves could be much lower (McKee and Mendelssohn 1987).

In contrast, high salinity not only reduced leaf gas exchange (Fig. 1) and thus plant growth (Fig. 5), but also significantly decreased leaf carbon isotope discrimination, or increased transpiration efficiency (Fig. 3). Leaf carbon isotope discrimination of red mangroves grown in 500 mM NaCl (similar salt concentration to sea water) was about 3‰ lower than those grown in 100 mM NaCl, and comparable with that of tall red mangroves grown in sea water (Lin and Sternberg 1992*b*). If the trends observed here can be extrapolated to higher salinity, lower leaf carbon isotope discrimination in scrub red mangroves relative to tall mangroves observed previously under field conditions must be caused by salinity higher than sea water during the dry seasons when salt water of soils in scrub mangrove forests are undergoing evaporation. Previous studies demonstrated that high salinity can reduce stomatal opening, causing a decrease in intercellular CO_2 concentration, and thus results in low carbon isotope discrimination but higher transpiration efficiency (Farquhar *et al.* 1982; Brugnoli and Lauteri 1991), although some halophytes may not have such response in C_i with changing salinity (Farquhar *et al.* 1982; Guy *et al.* 1988). We observed similar results in the present study (Figs 1, 3) as well as in the previous studies (Lin and Sternberg 1992*a*, 1992*b*). We also observed a significant correlation between leaf carbon isotope discrimination and intercellular CO_2 concentration, as well as intrinsic transpiration efficiency (A/g) (Fig. 4), confirming that changes in leaf carbon isotope discrimination result from variation in C_i, and thus can be used as an indicator of long-term transpiration efficiency (Farquhar *et al.* 1989). Therefore, hypersalinity in soil water during the dry seasons may have significant effects on mangrove physiological processes and plant growth, and therefore seems to be one of the stressful environmental conditions common to all scrub mangrove forests studied in southern Florida (Lin and Sternberg 1992*a*, 1992*b*).

Acknowledgments

We thank Mr Tim Banks for technical assistance on isotope analyses and Ms Yuan Ke for her assistance in conducting the greenhouse experiments. This work was partly supported by National Science Foundation of USA grant number 8908240 to L. da S. L. Sternberg. This is publication No. 393 from the program in Ecology, Behavior and Evolution of the Department of Biology, University of Miami, Coral Gables, Florida, USA.

References

Anderson, C. M., and Treshow, M. (1980). A review of environmental and genetic factors that affect height in *Spartina alterniflora* Loisel. (salt marsh cord grass). *Estuaries* **3**, 168–76.

Ball, M. C. (1988). Ecophysiology of mangroves. *Trees* **2**, 129–42.

Ball, M. C., and Farquhar, G. D. (1984). Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina* to long term salinity and humidity conditions. *Plant Physiology* **74**, 1–6.

Brugnoli, E., and Lauteri, M. (1991). Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt-tolerant (*Gossypium hirsutum* L.) and salt-sensitive (*Phaseolus vulgaris* L.) C_3 non-halophytes. *Plant Physiology* **95**, 628–35.

Clough, B. F. (1984). Growth and salt balance of the mangrove *Avicennia marina* (Forsk.) Vierh and *Rhizophora stylosa* Griff. in relation to salinity. *Australian Journal of Plant Physiology* **11**, 419–30.

Craighead, F. C. (1971). 'The Trees of South Florida. Vol. 1. The Natural Environments and their Succession.' (University of Miami Press: Coral Gables.)

Davis, J. H. (1940). The ecology and geologic role of mangroves in Florida. Papers from the Tortugas Lab. 32, 303–412. Carnegie Institute of Washington Publication No. 517.

Egler, F. E. (1952). Southeast saline Everglades vegetation, Florida, and its management. *Vegetatio* **3**, 213–65.

Ehleringer, J. R. (1990). Correlations between carbon isotope discrimination and leaf conductance to water vapor in common beans. *Plant Physiology* **93**, 1422–5.

Eleuterius, L. N. (1984). Autoecology of the black needlerush, *Juncus roemerianus*. *Gulf Research Report* **7**, 339–50.

Eleuterius, L. N. (1989). Natural selection and genetic adaptation to hypersalinity in *Juncus roemerianus* Scheele. *Aquatic Botany* **36**, 45–53.

Farquhar, G. D., Ball, M. C., Caemmerer, S. von, and Roksandic, Z. (1982). Effects of salinity and humidity on $\delta^{13}C$ values of halophytes – evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric CO_2 under different environmental conditions. *Oecologia* **52**, 121–4.

Farquhar, G. D., Ehleringer, J. R., and Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 503–37.

Gallagher, J. L., Somers, G. F., Grant, D. M., and Selisker, D. M. (1988). Persistent differences in the two forms of *Spartina alterniflora*: a common garden experiment. *Ecology* **69**, 1005–8.

Guy, R. D., Reid, D. M., and Krouse, H. R. (1988). Stable isotope ratios as an index of water-use efficiency in C_3 halophytes – possible relationship to strategies for osmotic adjustment. In 'Stable Isotopes in Ecological Research'. (Eds P. W. Rundel, J. R. Ehleringer and K. A. Nagy.) pp. 55–75. (Springer-Verlag: New York.)

Howes, B. L., Howarth, R. W., Teal, J. M., and Valiela, I. (1981). Oxidation-reduction potentials in a salt marsh: spatial patterns and interactions with primary production. *Limnology and Oceanography* **26**, 350–60.

Koch, M. S., and Mendelssohn, I. A. (1989). Sulphide as a soil phytotoxin: differential responses in two marsh species. *Journal of Ecology* **77**, 565–78.

Lin, G., and Sternberg, L. da S. L. (1992*a*). Differences in morphology, carbon isotope ratios, and photosynthesis between scrub and fringe mangroves in Florida, USA. *Aquatic Botany* **42**, 303–31.

Lin, G., and Sternberg, L. da S. L. (1992*b*). Comparative study of water uptake and photosynthetic gas exchange between scrub and fringe red mangroves (*Rhizophora mangle* L.). *Oecologia* **90**, 399–403.

Lugo, S. E., and Snedaker, S. C. (1974). The ecology of mangroves. *Annual Review of Ecology and Systematics* **5**, 39–64.

McKee, K. L., and Mendelssohn, I. A. (1987). Root metabolism in the black mangrove (*Avicennia germinans* (L.) L.): response to hypoxia. *Environmental and Experimental Botany* **27**, 147–56.

Mendelssohn, I. A. (1979). The influence of nitrogen level, form, and application method on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuaries* **2**, 106–12.

Mooring, M. T., Cooper, A. W., and Seneca, E. D. (1971). Seed germination response and evidence for height ecophenes in *Spartina alterniflora* from North Carolina. *American Journal of Botany* **58**, 48–55.

Pezeshki, S. R., DeLaune, R. D., and Patrick, W. H. Jr (1990). Differential response of selected mangroves to soil flooding and salinity: gas exchange and biomass partitioning. *Canadian Journal of Forest Research* **20**, 869–74.

Rao, A. N. (1986). Mangrove ecosystems of Asia and the Pacific. In 'Mangroves of Asia and the Pacific: Status and Management'. Technical Report of the UNDP/UNESCO Research and Training Pilot Programme on Mangrove Ecosystems in Asia and the Pacific (RAS/79/002). pp. 1–47. (LMC Press: Manila.)

Shea, M. L., Warren, R. S., and Niering, W. A. (1975). Biochemical and transplantation studies of the growth form of *Spartina alterniflora* on Connecticut salt marsh. *Ecology* **56**, 461–6.

Valiela, I., and Teal, J. M. (1974). Nutrient limitation in salt marsh vegetation. In 'Ecology of Halophytes'. (Eds R. J. Reimold and W. H. Queen.) pp. 547–63. (Academic Press: New York.)

Valiela, I., Teal, J. M., and Deuser, W. G. (1978). The nature of growth forms in the salt marsh grass *Spartina alterniflora*. *American Naturalist* **112**, 461–70.

Wilkinson, L. (1989). 'SYSTAT: The System for Statistics.' (SYSTAT, Inc.: Evanston, IL.)

Manuscript received 28 February 1992, accepted 18 May 1992