Journal of Experimental Botany, Vol. 44, No. 258, pp. 9–16, January 1993

Effects of Salinity Fluctuation on Photosynthetic Gas Exchange and Plant Growth of The Red Mangrove (*Rhizophora mangle* L.)

GUANGHUI LIN[1] and LEONEL da S. L. STERNBERG

Department of Biology, University of Miami, Coral Gables, Florida 33124, USA

Received 30 June 1992; Accepted 14 October 1992

ABSTRACT

The red mangrove (*Rhizophora mangle* L.) in southern Florida occurs frequently in two distinct growth forms, tall and scrub plants, with the scrub form usually found in coastal inland areas having a higher fluctuation of soil water salinity. In the present study, effects of constant and fluctuating salinities on leaf gas exchange and plant growth of red mangrove seedlings were investigated under greenhouse conditions. Both constant and fluctuating salinity treatments significantly affected leaf gas exchange and plant growth of red mangrove seedlings. Seedlings subjected to the fluctuating salinity with the mean of both 100 and 250 mol m^{-3} NaCl showed significantly lower photosynthesis and plant growth than those subjected to the corresponding constant salinity with the same mean. The photosynthetic and growth rates of the seedlings under these fluctuating treatments were as low as, or even lower than those expected if they were growing under the high constant salinity of their respective fluctuation treatments. Seedlings subjected to the fluctuating salinity with the mean of 500 mol m^{-3} NaCl, however, demonstrated slightly higher CO_2 assimilation rate and stomatal conductance, but the same plant growth rates as those under the constant 500 mol m^{-3} NaCl treatment. These results suggest that, in general, fluctuating salinity has significant negative effects on photosynthesis and plant growth relative to constant salinity with the same mean. If this finding can be applicable to field situations, the low photosynthesis and plant growth observed previously in several scrub mangrove forests probably can be attributed in part to the salinity fluctuation of soil water in these mangrove forests.

Key words: Fluctuating salinity, photosynthesis, growth, growth forms, mangroves.

INTRODUCTION

Mangroves are woody plants which form the dominant vegetation in tidal, saline wetlands along tropical and subtropical coasts. Salinity is one of the most outstanding environmental features of mangrove swamps and has long been recognized as an important factor regulating physiological processes, growth, height, survival. and zonation of mangroves (Macnae, 1968; Teas, 1979; Snedaker, 1982; Ball and Farquhar, 1984*a*, *b*; Naidoo, 1985, 1987; Tomlinson, 1986; Hutchings and Saenger, 1987; Ball, 1988*a*; Lin and Sternberg, 1992*b*, *c*). Soil salinity is determined by a number of factors, including tidal inundation, soil type and topography, depth of impervious subsoils, amount and seasonality of rainfall, freshwater discharge of rivers, run-on from adjacent terrestrial areas, run-off and evaporation (Hutchings and Saenger, 1987). Thus salinity regimes under field conditions vary in time and space, with the time-scale and magnitude of fluctuations dependent on the climate and hydrological characteristics of the coastal environment. Naturally, the extent to which a species can cope with fluctuations in salinity will be an important determinant of the distribution and relative importance of that species along salinity gradients (Ball, 1988*a*). The ability to sustain growth over a wide range of salinities is clearly advantageous in fluctuating environments. However, such ability must entail considerable carbon costs to the species since, in general, the broader the range of salinity tolerance of a species, the slower is its growth rate under optimal conditions (Ball, 1988*b*).

The red mangrove (*Rhizophora mangle* L.), a dominant species in mangrove swamps of southern Florida, occurs frequently in two distinct growth forms, tall and scrub

[1] To whom correspondence should be addressed at: Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA.

plants (Lugo and Snedaker, 1974; Lin and Sternberg, 1992*a*). Our previous studies demonstrated that the two growth forms differ significantly in both morphological and physiological characteristics, with lower tree height and photosynthetic rates, but higher leaf $\delta^{13}C$ values or higher water use efficiency for the scrub form (Lin and Sternberg, 1992*a*, *b*). Greenhouse culture experiments and field studies showed that these differences may result from hypersalinity or salinity fluctuation (Lin and Sternberg, 1992*b*, *c*). In southern Florida, scrub red mangrove grows usually in coastal inland areas with higher elevations, and thus higher salinity fluctuation (salinity may change between 0 and 60‰ or higher) due to seasonal changes in rainfall, tidal inundation and soil surface evaporation (Lin and Sternberg, unpublished data). There are few studies on the effects of salinity fluctuation on photosynthesis and plant growth of mangroves under controlled conditions (Ball and Farquhar, 1984*b*), although the effects of salinity gradients on mangrove physiology and growth have been studied by many researchers (Downton, 1982; Farquhar, Ball, von Caemmerer, and Roksandic, 1982; Ball and Farquhar, 1984*a*; Burchett, Field, and Pulkownik, 1984; Clough, 1984; Naidoo, 1985, 1987; Pezeshki, DeLaune, and Patrick, 1990; Lin and Sternberg, 1992*c*).

In the present study, we determined the effects of salinity fluctuation on leaf gas exchange and plant growth of red mangrove seedlings by manipulating salinity regimes in culture solutions under greenhouse conditions. We tested the hypothesis that a fluctuating salinity treatment has higher negative effect on photosynthesis and plant growth than a constant salinity, even when the two treatments have the same mean salinity throughout the experimental period.

MATERIALS AND METHODS

Plant materials

Propagules of red mangroves were collected on 4 August 1991, from the scrub mangrove forest along the northwestern coast of the Sugarloaf Key, Monroe County, Florida, USA (24°41′ N, 81°33′ W). The mean fresh weight of propagules was 11.3 ± 0.4 g ($n = 10$). The propagules were then cultivated in vermiculite beds and irrigated with tap water in the shade house on the campus of the University of Miami. The irradiance level in the shade house was controlled with shade cloth to be about one-third strength of natural solar radiation, i.e. 200–800 μE m^{-2} s^{-1}. The propagules were kept in the shadehouse until the seedlings had four fully expanded leaves (November 1991).

Experimental procedures

We selected 66 seedlings with similar dimensions from the population of red mangrove seedlings and recorded their initial fresh weight. The mean initial dry weight and standard error of these seedlings was $5{\cdot}3 \pm 0{\cdot}5$ g, determined on another 10 randomly selected seedlings with the same dimensions. The seedlings were then divided randomly into 11 groups, with six seedlings per group. In the greenhouse, each seedling was placed in a plastic pot (1200 cm^3) containing two parts of vermiculite and one part of gravel. Plastic pots containing the seedlings of the same group were placed together in a large plastic container (25 dm^3) containing 20 dm^3 nutrient solution used by Clough (1984) for the culture of mangrove seedlings.

The salinities of culture solutions were controlled by adding different amounts of refined sea salt at the rate of 50 mol m^{-3} NaCl per day to create a total of 11 salinity treatments listed in Table 1. The seedlings in the first five randomly chosen containers received constant salinity treatments with salinity of 0, 100, 250, 500, and 750 mol m^{-3} NaCl, respectively (salinity treatment I–V). The seedlings in another three randomly chosen containers were exposed to the salinity of 0, 100 and 250 mol m^{-3} NaCl during the first two weeks, then to 200, 400 and 750 mol m^{-3} NaCl during the following two weeks, respectively. This change of salinity in culture solutions was repeated every two weeks (salinity treatment VI–VIII). The seedlings in the rest of the three containers received the similar fluctuating salinity treatments as for treatment VI–VIII, except that the change of salinity was monthly instead of biweekly (salinity treatment IX–XI). These two types of fluctuating salinity treatments were chosen based on the fact that salinity fluctuation in the scrub mangrove forest under field conditions may result from tidal inundation occurring biweekly or/and monthly changes in rainfall and soil evaporation (Naidoo, 1989; Lin and Sternberg, personal observation). Nutrient solutions for all treatments were changed every two weeks to ensure a constant and similar nutrient supply for seedling growth.

The seedlings receiving these salinity treatments were grown in the greenhouse where the temperature was maintained close to that outside the greenhouse, with maximum temperature of 34 °C in the hottest month (May 1992) and minimum temperature of about 10 °C in the coldest month (February 1992) during the experimental period. The irradiance level inside the greenhouse was controlled to be about half-strength of natural solar radiation, i.e. 600–1200 μE m^{-2} s^{-1}, and relative humidity was 40–65% during the time of investigation. The seedlings under the treatment of constant 750 mol m^{-3} NaCl (salinity treatment V) all died after receiving the treatment for about one month. The experiment was concluded after the seedlings received their respective treatments for 6 months (from November 1991 to May 1992). There were two seedlings dead in the two treatments (treatment VIII and XI) and one seedling dead in the other two treatments (salinity treatment VII and X) at the end of the experiment.

Gas exchange measurements

Photosynthetic gas exchange was measured on intact leaves with a LI-6250 portable photosynthesis system equipped with 1 dm^3 leaf chamber (LI-COR, Lincoln, Nebraska). Leaf gas exchange was measured only on four seedlings of each container at two different times during the last month of the experiments (May 1992). The first measurements were done two weeks after seedlings under the fluctuating salinity treatments were subjected to the low salinity of their respective fluctuation cycles. The second measurements were done two weeks after they were subjected to the high salinity of their respective fluctuation cycles. Measurements were made hourly from 10.00 a.m. to 3.00 p.m. to ensure constant high radiation (1000–1200 μE m^{-2} s^{-1}) on sunny dates. During gas exchange measurements, leaf temperature was maintained close to the air temperature in the greenhouse. Raw data accumulated with the LI-6250 were used to calculate mean CO_2 assimilation rates, stomatal conductance to water vapour, and intercellular CO_2 concentration (Pezeshki *et al.*, 1990).

TABLE 1. *Mean salinity and salinity change frequency for three types of salinity treatment for red mangrove seedlings*

Treatment type	Salinity treatment	Mean salinity (mol m^{-3} NaCl)	Salinity change (mol m^{-3} NaCl)	Change frequency
Constant salinity (CS)	I	0	0	NA
	II	100	0	NA
	III	250	0	NA
	IV	500	0	NA
	V	750	0	NA
Biweekly fluctuating salinity (FSI)	VI	100	200(0↔200)	Biweekly
	VII	250	300(100↔400)	Biweekly
	VIII	500	500(250↔750)	Biweekly
Monthly fluctuating salinity (FSII)	IX	100	200(0↔200)	Monthly
	X	250	300(100↔400)	Monthly
	XI	500	500(250↔750)	Monthly

Growth measurements

At the conclusion of the experiment, the numbers of leaves of each seedling were counted and 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 leaves, stem and roots from each seedling was then determined by drying all plant materials in an oven. The net growth in biomass (*NBG*) was calculated as increment in dry weight per plant during the 6 month period (g/plant), and the relative growth rate (*RGR*) was calculated according to the following equation:

$$RGR = (\ln W_2 - \ln W_1/(t_2 - t_1)$$

where W_1, W_2 is the initial and final dry weight of each seedling, respectively, and $(t_2 - t_1)$ is the total number of days during the experimental period (172 d in the present study) (Beadle, 1985). Since it was impossible to measure W_1 for each seedling, the mean value of W_1 ($5{\cdot}6 \pm 0{\cdot}5$) was used here for all seedlings.

Statistical analysis

Effects of salinity treatments on photosynthetic gas exchange, and plant growth were tested by MGLH and STATS programs in SYSTAT (Wilkinson, 1989). The relationship between CO_2 assimilation rate and stomatal conductance was tested by the regression analysis according to the least squares method. The difference in the relationship between CO_2 assimilation rate and stomatal conductance was compared by ANCOVA between different types of salinity treatments (fluctuating versus constant salinity), and between the two different measuring times (at the low salinities versus the high salinity for fluctuating salinity treatments).

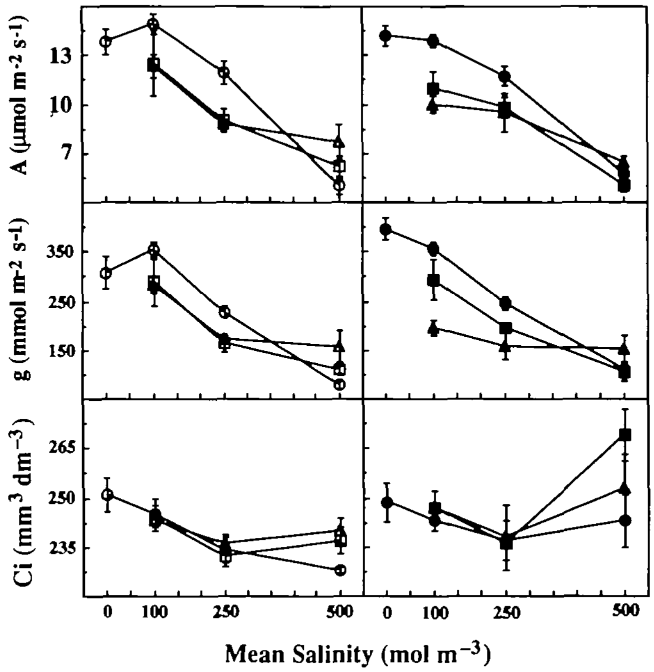

FIG. 1. Effects of three types of salinity treatment (circles: constant salinity, triangles: biweekly fluctuating salinity, and squares: monthly fluctuating salinity) on leaf gas exchange of scrub red mangrove seedlings. Open symbols represent the results from the measurements when the culture solutions were in lower salinity, while closed ones represent the results from the measurements when the culture solutions were in higher salinity for the fluctuating salinity treatments. Error bar represents the standard error with 4 replicates.

RESULTS

Both constant and fluctuating salinity significantly affected leaf gas exchange of red mangrove seedlings (Fig. 1; Table 2). When the mean salinity increased from 100 to 500 mol m^{-3} NaCl, both CO_2 assimilation rate and stomatal conductance decreased significantly in all three types of salinity treatments (Fig. 1). Generally, for the fluctuating salinity treatments, there were no significant differences in leaf gas exchange when measured at the high and low salinity of their fluctuation cycles (Fig. 1; Table 2).

At the mean salinity of 100 and 250 mol m^{-3} NaCl, seedlings under the two types of fluctuating salinity treatments showed significantly lower CO_2 assimilation rate and stomatal conductance than those of the corresponding constant salinity treatment, while there were no significant differences in intercellular CO_2 concentration between the fluctuating salinity treatments and the constant salinity treatment (Fig. 1; Table 3). At the mean salinity of 500 mol m^{-3} NaCl, however, there were no significant differences in CO_2 assimilation rate, stomatal conductance, and intercellular CO_2 concentration between the fluctuating salinity treatments and the

TABLE 2. *Statistical results for the effects of salinity treatment (SAL) and time of measurement (MT) on leaf gas exchange (*A*: CO_2 assimilation rate, g: stomatal conductance, and* Ci: *intercellular* CO_2 *concentration) of red mangrove seedlings under three different types of salinity treatment (CS: constant salinity, FSI: biweekly fluctuating salinity, and FSII. monthly fluctuating salinity)*

Treatment type	Factor	DF	*A*	*g*	*Ci*
CS	SAL	3, 24	***	***	*
	MT	1, 24	NS	NS	NS
	SAL × MT	3, 24	NS	NS	NS
FSI	SAL	2, 18	**	*	NS
	MT	1, 18	NS	NS	NS
	SAL × MT	2, 18	NS	NS	NS
FSII	SAL	2, 18	***	***	*
	MT	1, 18	NS	NS	NS
	SAL × MT	2, 18	NS	NS	*

NS: not significant at $P > 0{\cdot}05$; *: significant at $0{\cdot}01 < P < 0{\cdot}05$; **: significant at $0{\cdot}001 < P < 0{\cdot}01$, and ***: significant at $P < 0{\cdot}001$.

constant salinity treatment. Regardless of the mean salinity, there were no significant differences in gas exchange characteristics between biweekly and monthly fluctuating salinity treatments (Fig. 1; Table 3).

There was highly significant correlation between CO_2 assimilation rate and stomatal conductance for red mangrove seedlings (Fig. 2). Seedlings under both fluctuating and constant salinity treatments showed no significant difference in their relationship between CO_2 assimilation rate and stomatal conductance ($P > 0{\cdot}05$, ANCOVA). Similarly, there was no significant difference in their relatinship between measurements at the high and low salinity of their respective fluctuation cycles ($P > 0{\cdot}05$, ANCOVA), although the regression slope for the results from the measurements made when seedlings were in the lower salinities (0·035–0·036) was slightly higher than for those from the measurements made when seedlings were in the higher salinities (0·026–0·031) for fluctuating salinity treatments (Fig. 2).

Seedlings under fluctuating salinity treatments showed significantly lower plant growth than those under the equivalent constant salinity treatment except at the mean salinity of 500 mol m^{-3} NaCl (Fig. 3; Table 3). At the mean salinity of 100 and 250 mol m^{-3} NaCl, leaf number, leaf area and leaf dry weight per plant were all significantly lower for the seedlings under the fluctuating salinity treatments than for those under the corresponding constant salinity treatment (Fig. 3; Table 3). At the mean salinity of 500 mol m^{-3} NaCl, there were no significant differences in leaf area and leaf dry weight per plant

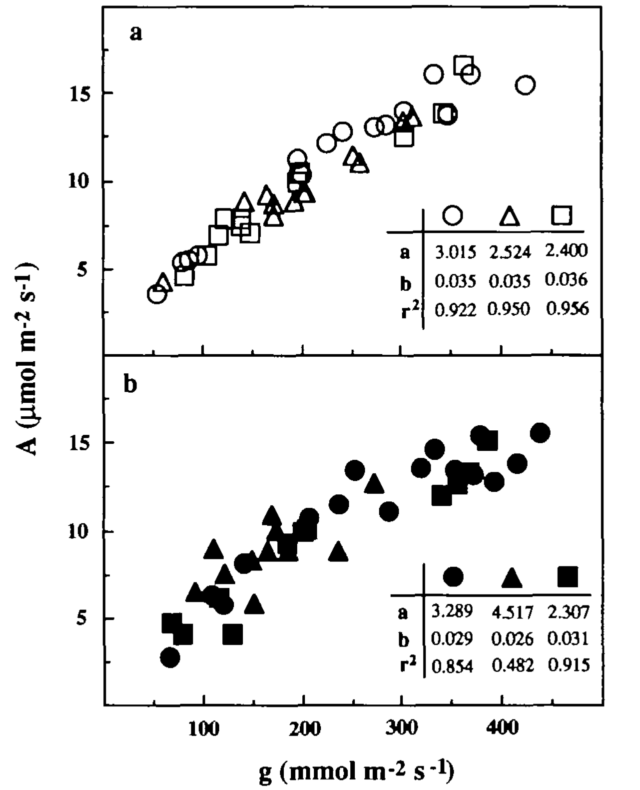

FIG. 2. Relationship between CO_2 assimilation rate (*A*) and stomatal conductance (*g*) for scrub red mangrove seedlings grown under three types of salinity treatment and measured at two different times. See Fig. 1 for the symbols.

TABLE 3. *Statistical results for the comparisons in the effects of three types of salinity treatment on leaf gas exchange (see Table 2 for relative abbreviations) and plant growth indexes (*LN: *leaf number,* LA: *leaf area,* LDW: *leaf dry weight,* RDW: *root dry weight,* NBG: *net growth in biomass, and* RGR: *relative growth rate) of red mangrove seedlings*

Treatment type	*Mean salinity (mol m^{-3}* NaCl)	*Leaf gas exchange*			*Plant growth*					
		A	*g*	*Ci*	*LN*	*LA*	*LDW*	*RDW*	*NBG*	*RGR*
FSI versus CS	100	**	**	NS	NS	**	***	*	**	**
	250	*	**	NS	*	*	***	***	***	***
	500	NS	NS	NS	*	NS	NS	NS	NS	NS
FSII versus CS	100	*	*	NS	NS	**	***	*	*	*
	250	*	*	NS	*	*	**	***	***	***
	500	NS	NS	NS	**	*	*	NS	NS	NS
FSI versus FSII	100	NS	NS	NS	NS	NS	NS	NS	NS	NS
	250	NS	NS	NS	NS	NS	NS	NS	NS	NS
	500	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS: not significant at $P > 0{\cdot}05$; *: significant at $0{\cdot}01 < P < 0{\cdot}05$; **: significant at $0{\cdot}001 < P < 0{\cdot}01$, and ***: significant at $P < 0{\cdot}001$.

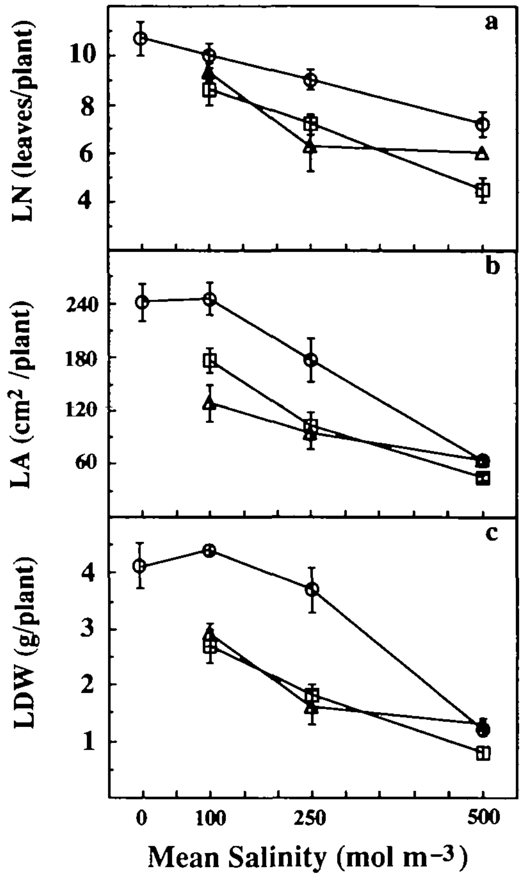

FIG. 3 Total leaf number (*LN*), total leaf area (*LA*) and total leaf dry weight (*LDW*) per plant for scrub red mangrove seedlings under three types of salinity treatment (circles: constant salinity, triangles: biweekly fluctuating salinity, and squares: monthly fluctuating salinity). Error bar represents the standard error with 4–6 replicates.

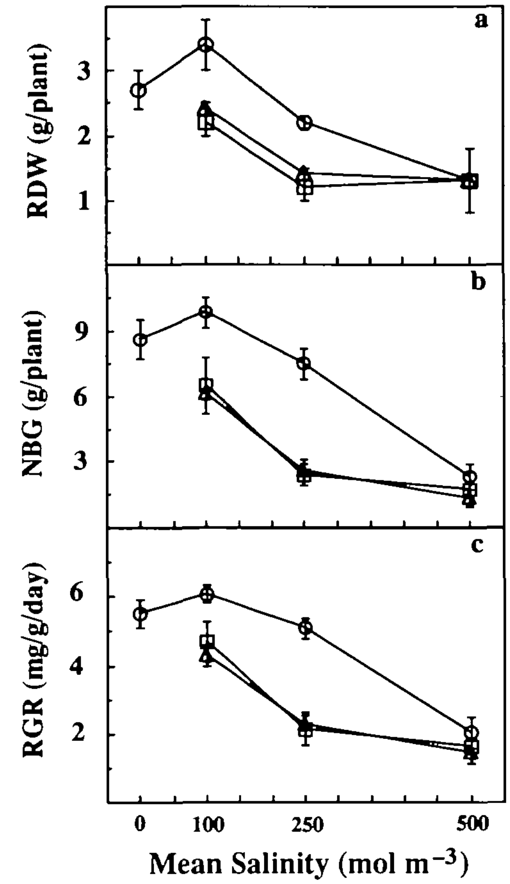

FIG. 4. Total root dry weight (*RDW*), net growth in biomass (*NBG*), and relative growth rate (*RGR*) of scrub red mangrove seedlings under three types of salinity treatment (see Fig. 3 for the symbols representing the treatment types). Error bar represents the standard error with 4–6 replicates.

between the biweekly fluctuating salinity treatments and the constant salinity treatments, but the seedlings under the monthly fluctuating salinity treatment had lower leaf number, leaf area and leaf dry weight per plant than the constant salinity treatment (Fig. 3; Table 3). Similarly, seedlings under the fluctuating salinity treatments had significantly lower root dry weight, net growth in biomass and relative growth rate than those under the constant salinity treatment at the mean salinity of 100 and 250 mol m^{-3} NaCl, while at the mean salinity of 500 mol m^{-3} NaCl seedlings both fluctuating and constant salinity treatments did not differ significantly in these growth characteristics (Fig. 4; Table 3). Again, there were no significant differences in these growth parameters between biweekly and monthly fluctuating treatments (Fig. 4; Table 3).

CO_2 assimilation rates, leaf areas, net growth in biomass and relative growth rates for seedlings subjected to fluctuating salinities in the salinity treatment VI, VII, IX, X were as low as or lower than those expected if they were growing at the constant high salinity of their respective fluctuation cycles (Fig. 5). This comparison could not be made for seedlings with a salinity fluctuating from 250 to 750 mol m^{-3} NaCl (salinity treatments VIII and XI) since seedlings in the constant salinity treatment of 750 mol m^{-3} NaCl did not survive.

DISCUSSION

Inhibition of photosynthesis and plant growth by high salinity has been previously observed in many mangrove species (Downton, 1982; Ball and Farquhar, 1984*a*, *b*; Burchett *et al.*, 1984; Clough, 1984; Naidoo, 1985, 1987; Lin and Sternberg, 1992*c*). In most of these previous studies, however, salinities were all constant throughout the experiments, except in the study of Ball and Farquhar (1984*b*), who studied the photosynthetic responses of the grey mangrove (*Avicennia marina*) to gradual and progressive change in salinity from 50 to 500 and then back to 50 mol m^{-3} NaCl. Under field conditions, the salinity of soil water utilized by mangroves usually shows considerable fluctuation, except in fringe mangrove forests where plants mostly use ocean water with relatively constant salinity throughout the year (Naidoo, 1989; Lin

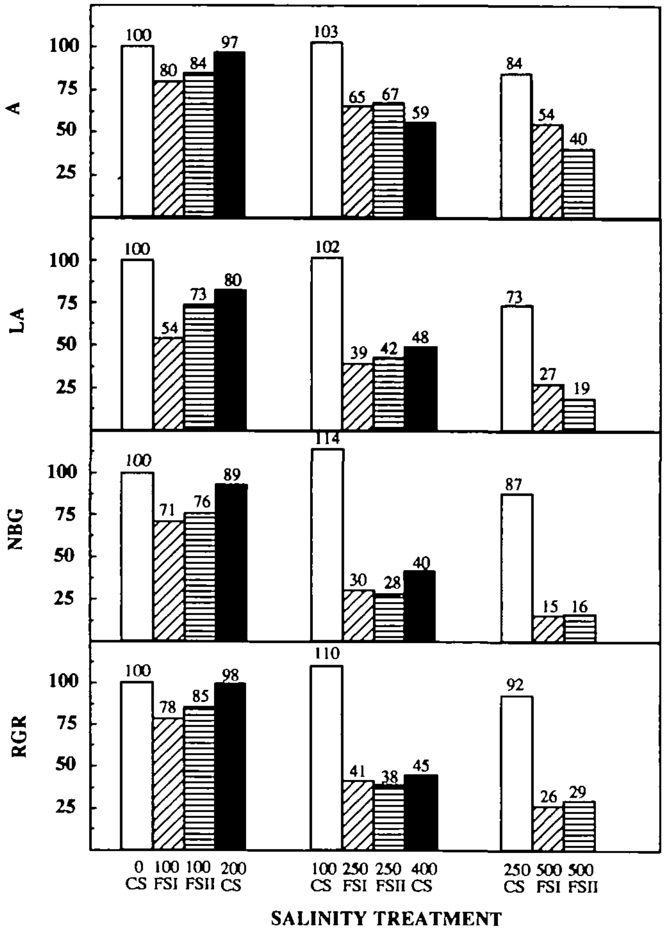

FIG. 5. Comparisons of CO_2 assimilation rate (*A*), leaf area per plant (*LA*), net growth in biomass (*NBG*) and relative growth rate (*RGR*) between red mangrove seedlings subjected to the two types of fluctuating salinity (FSI: biweekly fluctuating salinity; FSII: monthly fluctuating salinity) and those subjected to constant salinity equivalent to the low and high salinity of each respective fluctuating salinity treatment (CS). The number on the top of each bar was the percentage of a given measurement relative to the respective measurement on seedlings subjected to constant salinity of 0 mol m^{-3} NaCl (general control, treatment 1). The data for the constant salinity of 200 and 400 mol m^{-3} NaCl were calculated from the straight line between the two nearby treatments in Figs 1, 3, 4.

and Sternberg, 1992*b*). Such fluctuation in salinity results from different climatic factors and hydrological characteristics of coastal environments, including seasonal changes in rainfall, evaporation, tidal inundation, and elevation, or their interactions (Hutchings and Saenger, 1987; Ball, 1988*a*, *b*; Naidoo, 1989). In southern Florida, for example, salinity of soil water under the canopy of a scrub mangrove forest with a higher elevation than a fringe forest demonstrated greater fluctuation (usually with salinity changing between 0 and 60‰ or higher), relative to that in the fringe mangrove forest (Lin and Sternberg, unpublished data). Salinity change in the field can be gradual or abrupt, depending on the frequency of tidal flooding and the pattern of precipitation.

Results from the present study support our hypothesis that fluctuating salinity has a higher negative effect on photosynthesis and plant growth of mangrove seedlings than a constant salinity with the same mean. Red mangrove seedlings under the fluctuating salinity treatments showed significantly lower photosynthesis and plant growth than those under the constant salinity treatments with the same mean salinity (Figs 1, 3, 4). One exception, which will be discussed later, is that CO_2 assimilation rates and stomatal conductance for the seedlings under the fluctuating salinity treatments with the mean salinity of 500 mol m^{-3} NaCl were slightly higher than for those under the constant salinity treatment of 500 mol m^{-3} NaCl (Figs 1, 3, 4). Both biweekly fluctuating and monthly fluctuating salinity treatments showed similar effects on leaf gas exchange and plant growth of red mangrove seedlings (Table 3). A significant correlation between CO_2 assimilation rate and stomatal conductance (Fig. 2) indicates that salinity treatments, either constant or fluctuating, significantly affect stomatal conductance, resulting in the changes in carbon assimilation and thus plant growth (Ball, 1988*a*, *b*). In addition, CO_2 assimilation rate and stomatal conductance changes were correlated in the same way regardless of the salinity treatment types (Fig. 2). This may lead to the similar intercellular CO_2 concentrations for the three types of salinity treatments (Fig. 1).

There may be three possible contrasting ways in which mangroves may respond to a fluctuating salinity (Fig. 6). In the first type of response (Type I), mangroves change physiological performance and thus growth with change of salinity during the treatment. Hence, carbon assimilation and growth rates are greater when they are subjected to low salinity and shift to lower values when they are subjected to high salinity, or vice versa. If this type of response occurs, mangroves subjected to the fluctuating salinity treatment should show significant differences in leaf gas exchange and growth between the low and high salinity period. In Type II response, mangroves always maintain constant photosynthesis and growth regardless of the salinity levels in a fluctuating salinity treatment, with the carbon assimilation rate and growth rates similar to what is expected for seedlings growing at a constant salinity equal to the mean salinity of their fluctuating salinity treatments. In the third type of response (Type III), carbon assimilation and growth rates for seedlings under a fluctuating salinity treatment are as low as or lower than what is expected for seedlings growing at a constant salinity equal to the high salinity of their respective fluctuation cycles.

Our results suggest that Type I response is not present in the red mangrove since CO_2 assimilation rate and stomatal conductance for red mangrove seedlings measured when they were subjected to low salinity of their fluctuation cycles were not significantly different from those measured when they were subjected to high salinity

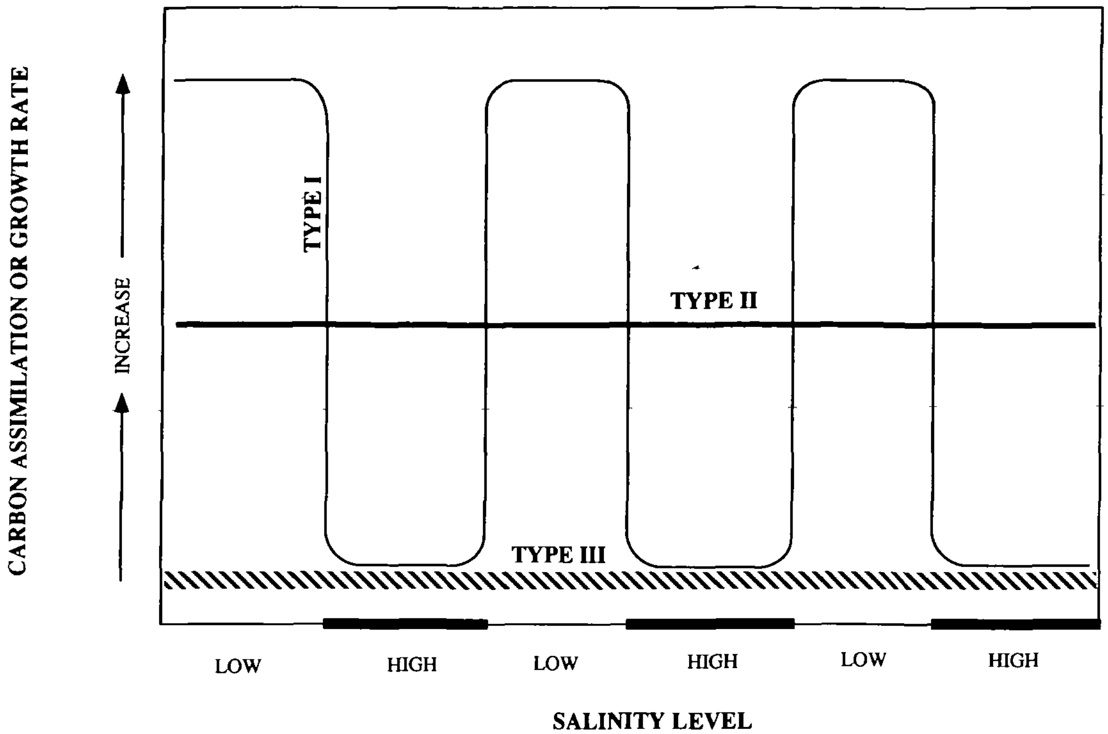

FIG. 6. Three hypothesized types of photosynthetic and growth responses in mangroves to fluctuating salinity (thin solid line: Type I response; thick solid line. Type II response; thick dash line: Type III response). See text for detailed explanation for each type of response.

of the fluctuation cycles (Fig. 1; Table 2). This finding contrasted with the results by Ball and Farquhar (1986*b*), who found that photosynthesis decreased when salinity increased gradually from 50 to 500 mol m^{-3} NaCl, but recovered substantially when salinity returned gradually from 500 to 50 mol m^{-3} NaCl. The absence of the Type I response in the red mangrove for our study may result from the sudden alternation in salinity between the two levels.

The seedlings under the fluctuating salinity treatments having a mean salinity of 500 mol m^{-3} NaCl showed the second type of response to the salinity changes, since their CO_2 assimilation rates and growth rates were similar to those of seedlings growing at a constant salinity of 500 mol m^{-3} NaCl (Figs 1, 3, 4). The seedlings under the fluctuating salinity treatments with the mean salinity of 100 and 250 mol m^{-3} NaCl demonstrated Type III responses in leaf gas exchange and growth to salinity changes, since they had carbon assimilation rates and plant growth rates almost the same as, or even slightly lower than would be expected for the seedlings exposed to the constant high salinity of their respective fluctuation cycles (Fig. 5).

The results from our present study did not provide any evidence for the mechanism controlling the differences in the effects of salinity fluctuation on leaf gas exchange and plant growth between the fluctuating salinity treatment with the mean salinity of 500 mol m^{-3} NaCl and those with the mean salinity of 100 or 250 mol m^{-3} NaCl. One possible explanation is that, under our greenhouse conditions, seedlings grown at a constant salinity of 500 mol m^{-3} NaCl (similar salinity for typical ocean water) are extremely stressed, and maintain very low photosynthesis and thus extremely low growth rate (Figs 1, 4). Therefore, the differences in carbon assimilation and plant growth between the fluctuating salinity treatment with the mean salinity of 500 mol m^{-3} NaCl and the constant 500 mol m^{-3} NaCl salinity treatment are not as evident as those in the fluctuating salinity treatment with the mean salinity of 100 or 250 mol m^{-3} NaCl. Nevertheless, leaf number, leaf area and leaf dry weight per plant for the seedlings under the monthly fluctuating salinity with the mean of 500 mol m^{-3} NaCl were significantly lower than those under the constant 500 mol m^{-3} NaCl treatment (Figs 3, 4; Table 3). These differences may become more evident with a longer experimental period.

In summary, red mangrove seedlings growing under a fluctuating salinity will suffer more stress than seedlings growing at a constant salinity similar to the mean salinity of the respective fluctuating salinity treatments. This effect is more evident in the fluctuating salinity treatments with the mean salinity of 100 or 250 mM NaCl under our greenhouse conditions. If this finding can be interpolated to field situations, lower photosynthesis and growth observed previously in several scrub red mangrove forests in southern Florida can be attributed to the salinity fluctuation of soil water in these forests (Lin and Sternberg, 1992*b*; Lin and Sternberg, unpublished data). Scrub mangrove forests in southern Florida usually occur in coastal inland areas with higher elevation, and are inundated only occasionally by high tides. Due to the significant seasonality in rainfall and evaporation in southern Florida (M. Ross, pers. comm.), such areas are always associated with higher salinity fluctuation of soil water available for mangroves (Sternberg, Ish-Shalom, Ross, and O'Brein, 1991; Lin and Sternberg, 1992*b*). Therefore, lower photosynthesis, growth rate, and thus lower tree height and smaller leaves for plants in scrub forest relative to those in fringe forest could probably be explained by the fluctuation in salinity in the scrub forest habitat (Lin and Sternberg, 1992*a*, *b*; Lin and Sternberg, unpublished data), although other factors such as hypersalinity and different levels of irradiance may also help to explain the differences in photosynthetic gas exchange and plant growth between the two growth forms (Björkman, Demmig, and Andrews, 1988; Lin and Sternberg 1992*c*).

ACKNOWLEDGEMENTS

This study was supported by National Sciences Foundation, USA (grant number: BSR 8908240). The authors thank Ms Yuan Ke for the assistance in the culture of mangrove seedlings in the greenhouse. This is publication No. 403 from the programme in Ecology, Behaviour and Evolution of the Department of Biology, University of Miami, Coral Gables, Florida, USA.

LITERATURE CITED

BALL MC. 1988*a*. Ecophysiology of mangroves. *Trees* **2,** 129–42.

BALL MC. 1988*b*. Salinity tolerance in the mangroves, *Aegiceras corniculatum* and *Avicennia marina*. I. Water use in relation to growth, carbon partitioning and salt balance. *Australian Journal of Plant Physiology* **15,** 447–64.

BALL MC, FARQUHAR GD. 1984*a*. 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.

BALL, MC, FARQUHAR GD. 1984*b*. Photosynthetic and stomatal responses of the grey mangrove, *Avicennia marina*, to transient salinity conditions. *Plant Physiology* **74,** 7–11.

BEADLE C. 1985. Plant growth analysis. In: Coombs J, Hall DO, Long SP, Scurlock, JMO, eds. *Techniques in bioproductivity and photosynthesis*, 2nd edn. New York: Pergamon, 20–5.

BJÖRKMAN O, DEMMIG B, ANDREWS TJ. 1988. Mangrove photosynthesis: response to high irradiance stress. *Australian Journal of Plant Physiology* **15,** 43–61.

BURCHETT MD, FIELD CD, PULKOWNIK A. 1984. Salinity, growth and root respiration in the grey mangrove, *Avicennia marina*. *Physiologia Plantarum* **60,** 113–18.

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

DOWNTON WJS. 1982. Growth and osmotic relations of the mangrove, *Avicennia marina* (Forsk.) Vierh. *New Phytologist* **91,** 597–606.

FARQUHAR GD, BALL MC, VON CAEMMERER S, ROKSANDIC Z. 1982. Effect 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,** 121–37.

HUTCHINGS P, SAENGER P. 1987. *Ecology of mangroves*. St Lucia: University of Queensland Press.

LIN G, STERNBERG LdaSL. 1992*a*. Differences in morphology, carbon isotope ratios, and photosynthesis between scrub and fringe mangroves in Florida, USA. *Aquatic Botany* **42,** 303–13.

LIN G, STERNBERG LdaSL. 1992*b*. Comparative study of water uptake and photosynthetic gas exchange between scrub and fringe red mangrove. *Rhizophora mangle* L. *Oecologia* **90,** 399–403.

LIN G, STERNBERG LdaSL. 1992*c*. Effects of growth form, salinity, nutrient, and sulphide on photosynthesis, carbon isotope discrimination and growth of red mangrove (*Rhizophora mangle* L.). *Australian Journal of Plant Physiology* **19,** 509–17.

LUGO AE, SNEDAKER SC. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* **5,** 39–64.

MACNAE W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Advances in Marine Biology* **6,** 73–270.

NAIDOO G. 1985. Effects of waterlogging and salinity on plant water relations and on the accumulation of solutes in three mangrove species. *Aquatic Botany* **93,** 369–76.

NAIDOO G. 1987. Effects of salinity and nitrogen on growth and plant water relations in the mangrove. *Avicennia marina* (Forsk.) Vierh. *New Phytologist* **107,** 317–26.

NAIDOO G. 1989. Seasonal plant water relations in a South Africa mangrove swamp. *Aquatic Botany* **33,** 87–100.

PEZESHKI SR, DELAUNE RD, PATRICK Jr. WH. 1990. Differential response of selected mangroves to soil flooding and salinity: gas exchange and biomass partitioning. *Canadian Journal of Forestry* **20,** 869–74.

SNEDAKER SC. 1982. Mangrove species zonation: why? In: Sen DN, Raipurohit KS, eds. *Contribution to the ecology of halophytes*. The Hague: Dr W. Junk Press, 111–25.

STERNBERG LdaSL, ISH-SHALOM N, ROSS M, O'BREIN J. 1991. Water relations of coastal plant communities near the ocean/freshwater boundary. *Oecologia* **88,** 305–10.

TEAS HJ. 1979. Silviculture with saline water. In: Hollaender A, ed. *The biosaline concept*. New York: Plenum Press, 117–61.

TOMLINSON PB. 1986. *The botany of mangroves*. London: Cambridge University Press.

WILKINSON L. 1989. SYSTAT: The system for statistics. Evanston, IL: SYSTAT, Inc.