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Simulated sea level change alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.)

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Abstract Tropical coastal forests – mangroves – will be one of the first ecosystems to be affected by altered sea levels accompanying global climate change. Responses of mangrove forests to changing sea levels depend on reactions of individual plants, yet such responses have not been addressed experimentally. We report data from a long-term greenhouse study that assessed physiological and individual growth responses of the dominant neotropical mangrove, *Rhizophora mangle*, to levels of inundation expected to occur in the Caribbean within 50–100 years. In this study, we grew potted plants in tanks with simulated semidiurnal (twice daily) high tides that approximated current conditions (MW plants), a 16-cm increase in sea level (LW plants), and a 16-cm decrease in sea level (HW plants). The experiment lasted 2½ years, beginning with mangrove seedlings and terminating after plants began to reproduce. Environmental (air temperature, relative humidity, photosynthetically active radiation) and edaphic conditions (pH, redox, soil sulfide) approximated field conditions in Belize, the source locale for the seedlings. HW plants were shorter and narrower, and produced fewer branches and leaves, responses correlated with the development of acid-sulfide soils in their pots. LW plants initially grew more rapidly than MW plants. However, the growth of LW plants slowed dramatically once they reached the sapling stage, and by the end of the experiment, MW plants were 10–20% larger in all measured growth parameters. Plants did not exhibit differences in allometric growth as a function of inundation. Anatomical characteristics of leaves did not differ among treatments. Both foliar C:N and root porosity decreased from LW through MW to HW. Relative to LW and HW plants, MW plants had 1–7% fewer stomata/mm^2, 6–21% greater maximum photosynthetic rates, 3–23% greater absolute relative growth rates (RGRs), and a 30% higher RGR for a given increase in net assimilation rate. Reduced growth of *R. mangle* under realistic conditions approximating future inundation depths likely will temper projected increased growth of this species under concomitant increases in the atmospheric concentration of CO_2.

Key words Growth · Mangroves · Photosynthesis · *Rhizophora mangle* · Sea level rise

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Introduction

The response of tropical coastal forests – mangroves – to rapid climate change accompanied by altered sea level and rising carbon dioxide, is of worldwide concern from both scientific and policy perspectives (Pernetta 1993; UNEP 1993; Davis et al. 1994; Ellison 1994; Semeniuk 1994; Field 1995; Ong 1995; Snedaker 1995). Mangroves supply essential ecosystem services (sensu Silver et al. 1996; Twilley et al. 1996) to tropical economies by contributing substantially to timber and charcoal supplies, productivity of near-shore fisheries, and physical protection of coastlines (reviewed in Food and Agriculture Organisation 1994). However, it is largely unknown how mangrove structure and function will change in response to eustatic increases in sea level, tidal amplitude, and tidal bore velocity that are predicted widely (e.g., Granger 1991; Wigley and Raper 1992; Jelgersma et al. 1993; Wolanski and Chappell 1996). Literature reviews (Pernetta 1993; UNEP 1993; Ellison and Farnsworth 1996a), comparative studies of mangroves growing in different geomorphological and tidal

settings (Semeniuk 1994; Ellison and Farnsworth 1996b; Wolanski and Chappell 1996), and fossil reconstruction of mangrove dynamics during Holocene transgressions (Ellison and Stoddart 1991; J.C. Ellison 1993, 1994) have yielded a range of hypotheses regarding mangrove responses to sea level changes. Prognoses range from total mangrove ecosystem collapse (e.g., Ellison and Stoddart 1991), modest landward migration limited by coastal development (Parkinson 1989) or topography (Bacon 1994), or poleward migration along the coasts (Snedaker 1995), to relatively little change in either local distribution or abundance (Snedaker et al. 1994). All of these responses depend to a large extent on the reactions of individual plants to rapid environmental change.

Here, we report evidence from a long-term, experimental study that assessed ecophysiological and individual growth responses of the neotropical mangrove dominant, *Rhizophora mangle*, to predicted levels of inundation. We grew potted plants in tanks where semidiurnal (twice daily) high tides approximated three water depths relative to the soil-air interface: 'normal' depths mimicking intertidal (mean water) conditions currently existing at the source locale of the seedlings (Belize, Central America; Kjerfve et al. 1982); 'high tidal' conditions with water 16 cm deeper – the average depth increase expected on Caribbean coasts in 50–100 years (Granger 1991), and depths that were shallower by 16 cm relative to the normal high water level, simulating sites in the Caribbean, such as areas of the Dominican Republic, where relative sea level is expected to decrease due to tectonic uplift (Granger 1991). The mean water treatment is analogous to the relative tidal elevation of plants growing at their 'optimal' field location in the intertidal in Belize (Ellison and Farnsworth 1993). In addition to clarifying how mangroves will respond to changes in relative sea level, this study can also help to elucidate the ways in which individual mangrove species perform optimally in certain tidal zones, a question of long-standing importance in community studies of mangrove forests (Chapman 1976).

To date, responses by mangroves to inundation have been rarely examined *experimentally* under controlled conditions that explicitly enable comparisons among field and glasshouse studies (Curran et al. 1986; McKee 1993), and no studies to our knowledge have been designed specifically with future tidal scenarios in mind. McKee (1993) demonstrated that edaphic properties, of known importance to mangrove performance in the field, can be simulated closely in greenhouse experiments in order to improve extrapolations of results from controlled environments to field populations. Because the design used here is modeled on that used to study the effects of elevated CO_2 on plant performance – plants are grown under 'current' conditions and under conditions expected to occur in the mid- to late-21st century – the experiment reported here also complements a recent greenhouse study investigating effects of elevated CO_2 on mangrove growth and production (Farnsworth et al. 1996). In that study, we documented significant increases in photosynthetic rates, leaf, stem, and root production, and a decrease in the time to first reproduction of *R. mangle* seedlings and saplings grown in 700 ppm CO_2 relative to plants growing in 350 ppm CO_2.

We postulated that physiological and growth responses by *R. mangle* to changing water depths would temper growth enhancements associated with elevated CO_2 observed in this species (Farnsworth et al. 1996) and other mangrove species (Ball and Munns 1992). This hypothesis derived from previous descriptive field studies of *R. mangle* in Belize, in which we showed that individual trees exhibited increased root:shoot ratios and decreased growth rates in deeper water where the sedimentation rate was lowered (Ellison and Farnsworth 1996b). In addition, transplant experiments in the field demonstrated reduced growth of *R. mangle* seedlings in both high- and low-tidal zones relative to those growing in the mid-intertidal (Ellison and Farnsworth 1993).

Other studies have also reported generally negative effects of prolonged waterlogging on the growth and metabolism of seedlings of several mangrove species (Naidoo 1985; Hovenden et al. 1995; McKee 1996). However, comparative field studies caution against extrapolating from responses observed at a single ontogenetic phase. For example, responsiveness of mangrove anatomy, morphology, growth, and photosynthetic rates to changing light conditions at various tidal heights varies with plant developmental stage (Farnsworth and Ellison 1996). Moreover, because viviparous seedlings of *R. mangle* are quite large when dispersed, more than a year can ensue before maternal effects on early seedling growth are offset by local environmental conditions (Lin and Sternberg 1995; Farnsworth et al. 1996). We also expected that mangroves, which already possess a suite of adaptations facilitating growth in chronically flooded habitats (Scholander et al. 1962; Kozlowski 1984; Tomlinson 1986; Armstrong et al. 1994; Ball 1996), would respond to different tidal levels with 'quantitative' and gradual physiological and structural adjustments (Ball 1988; Pezeshki et al. 1990; Ball and Pidsley 1995; Youssef and Saenger 1996). Therefore, we report a study on mangroves that explores consequences of environmental change under realistic conditions and that extends from seedling growth stages through first reproduction.

Materials and methods

One hundred mature propagules (viviparous seedlings) of *R. mangle* were collected from Wee Wee Caye, Belize, Central America (16°45′ N, 88°08′ W) in August 1993 (see Farnsworth et al. 1996 and Ellison and Farnsworth 1996b for complete site and species descriptions). These seedlings were planted individually in 7″ (18 cm diameter) plastic 'azalea' pots filled with compost. We used compost because it is very similar in texture and chemistry (see Results) to the peat in which this species grows on Belizean mangrove cayes (MacIntyre et al. 1987). Initially, these plants were kept on benches flooded to a depth of 5 cm with full-strength (35‰) artificial seawater (Instant Ocean, Aquarium Systems, Mentot, Ohio) in a heated greenhouse at Mount Holyoke College. Height

(±1 mm) and diameter (±0.1 mm) just above the cotyledonary scar of all propagules were measured immediately upon planting. Propagules were left on these benches for 11 months, by which time they had all rooted and produced a single pair of leaves.

Tank design and experimental treatments

Four identical 3 m long × 1.3 m wide × 40 cm deep × 2 cm thick opaque polyethylene tanks were custom-built for this experiment by Fln-Mar Plastics, Holyoke, Mass. Each tank held about 1.3 m^3 (ca. 1,200 l) full-strength (35‰) artificial seawater. Tanks were framed with lumber to prevent their expansion and distortion during and after filling. The tanks were plumbed in a recirculating series so that at any given time, two tanks were at 'high tide' and the other two were at 'low tide'. Every 6 h (0300, 0900, 1500, and 2100 hours), water flowed through automated pumps (Gorman-Rupp Industries no.14518-202, Bellville, Ohio) from a high-tide tank into a low-tide tank; full tidal exchange took about 1 h. Although smaller, our tank system is basically identical to that developed by Curran et al. (1985). We rotated plants between tanks every 2 weeks to minimize 'block' effects and to simulate tidal precession in the Caribbean of about 30–45 min per day. Concurrent with rotating the plants, we also replaced all the seawater in the system and removed algal buildup from the bottom of the tanks. Plants were fertilized every 2 weeks with Peters 20-20-20 N-P-K (Scotts, Allentown, Pa.). Supplemental mercury vapor lights (Energy Technics Horticultural Lighting, York, Pa.) were placed over all tanks from 21 September and 21 March each year to maintain a 12-h photoperiod characteristic of tropical latitudes.

On 1 July 1994, all seedlings were transplanted into 8″ (20 cm diameter) plastic azalea pots, remeasured, and placed into the tanks. The tanks were not filled until 3 weeks later, during which time we harvested a set of pretreatment seedlings (see measurements below). Seedlings were randomly assigned to one of three treatments: low water (LW), mean water (MW), and high water (HW) relative to depth at high tide (eight seedlings per treatment per tank). At high tide, LW plants were flooded to 16 cm above the rim of the pot (16 cm was also the median height from soil to cotyledonary scar of the seedlings), MW plants were flooded to the rim of the pot, and only the bottom 2 cm of the pots of the HW plants were under water. All plants were top-watered daily with fresh water to prevent desiccation. Pots were nested within cylindrical, perforated, plastic sleeves (cut from 20-cm-inner-diameter PVC sewer pipe) that raised the plants to the appropriate depth and permitted water exchange with the pots.

Environmental measurements

Air temperature (°C) and relative humidity (%) above each tank, available photosynthetically active radiation (PAR μmol m^{-2} s^{-1}) above three tanks, and water temperature (°C) in two tanks were continuously monitored with Campbell temperature and humidity probes (Campbell Scientific, Logan, Utah) and Li-Cor quantum sensors (Li-Cor, Lincoln, Neb.) connected to a Delta-T datalogger (Delta-T Devices, Cambridge, UK). Because of early difficulties with configuring the datalogger, we only began collecting these data in March 1995. Just prior to the final harvest, we measured soil pH of 5-g soil samples extracted in distilled water (1:1 w/v) with an Orion pH electrode (Orion Instruments, Boston, Mass.), soil redox potential at 2 cm and 10 cm depths in each pot at both low tide (all three treatments) and high tide (HW and MW treatments only) using an Orion combination redox electrode, and soil sulfide with an Orion silver/sulfide electrode and double-junction reference electrode. Because the soils were not totally saturated [gravimetric soil moisture = 48%; no differences among treatments (P = 0.59)], we were unable to extract pore water for sulfide analysis using the methods of McKee et al. (1988). Instead, we took 20-g samples of soil from each pot and transferred them immediately into 20 ml of a 1:1 solution of distilled water and antioxidant buffer (20 g sodium hydroxide, 80 g sodium salicylate, and 18 g ascorbic acid per liter; prepackaged by Orion Instruments). These samples were extracted for 24 h (following methods of Kryger and Lee 1995, 1996), and then filtered to yield soil-free liquid for sulfide measurements.

Measures of growth and physiology

All plants were measured on the following seven dates: 19 July and 15 September 1994, 15 May and 1 October 1995, 23 February, 13 June, and 19 October 1996. The first measurement occurred after 1 year of growth and 1 day prior to the beginning of the tidal treatments. At each date, we measured stem diameter, plant height to the top of the primary axis, and lengths of all lateral branches, and we counted the total number of leaves on each plant. Once plants began to flower, we kept data on number of plants in flower and number of inflorescences per plant. As the plants reached reproductive maturity, we quantified apparent differences in canopy shape among plants in the three treatments by measuring the height of the canopy (from the lowest branch to the main shoot apex), and the spread of the lowest two sets of branches. No plants died during the experiment. To prevent pot-binding, we transplanted all unharvested plants into 10″ (25 cm diameter) azalea pots after the May 1995 harvest.

On 19 July 1994, 12 plants (4 per treatment) were chosen at random for continual physiological monitoring. On each of the seven measurement dates, leaf-level photosynthesis and conductance were measured (using a Li-Cor LI-6200 portable photosynthesis system) under light-saturating conditions (>900 μmol m^{-2} s^{-1}, using supplemental lighting when necessary) on a single, young but fully expanded leaf on each of these 12 plants. On each date, 12 additional, randomly chosen plants were measured similarly, then harvested and separated into leaves, stems, aerial roots, underground roots, and buds or flowers. From these harvested plants, we took small (<1 cm wide) slices of terminal, fully expanded leaves and fixed them in formalin-acetic acid-alcohol. Freehand thin sections of these fixed leaf samples were photographed (×50) and digitized (SigmaScan 4.0, Jandel Scientific, San Rafael, Calif.) to determine total leaf thickness, and percent thickness of cuticle, epidermis, hypodermis, palisade, and mesophyll (leaf anatomy follows Tomlinson 1986). A 40-mm^2 leaf disk (average fresh mass 0.015 g) was removed with a steel hole-punch and extracted in 80% acetone for determination of total chlorophyll using a Spectronic 20 (Bausch and Lomb, Rochester, N.Y., methods of Arnon 1949 with correction factors of Porra et al. 1989). Total leaf area was measured using a Li-Cor 3000 bench-top leaf area meter. All separated tissue was weighed fresh, dried at 70°C to constant mass, and weighed dry (±0.01 g). One-gram samples of dried leaf tissue were ground under liquid nitrogen and analyzed for percent C, H, and N using a Control Equipment 240 elemental analyzer (Exeter Analytical, Lowell, Mass; analytical methods of Ma and Rittner 1979). Foliar Na content (% dry mass) of the same leaf samples was determined, following digestion of dried leaf material in strong acid with heating, with atomic absorption spectrophotometry (Perkin-Elmer 403, Norwalk, Conn, methods in Perkin-Elmer 1982). Fifty-gram samples of soil from each treatment group were dried to constant mass, powdered, digested in strong acid, and analyzed for C, H, N, Na, P, K, and Mg as above.

The 12 plants for which we had taken physiological measurements at each harvest date were themselves harvested in October 1996. For this set of plants, we also measured stomatal density using acetate peels, and aerenchyma volume of belowground lateral roots [as root porosity (%)] with a 25-ml pycnometer (following methods in Youssef and Saenger 1996 as modified from Jensen et al. 1969). Thus, overall we have one set of 12 plants for which we have a time series of growth and physiological data for over 2 years, while for each harvest, we also have an additional set of independent measurements of growth, physiology, and harvest data.

Statistical analyses

Data were analyzed using Systat version 5.03 (Systat, Evanston, IL.) and S-Plus version 3.3 (MathSoft, Seattle, WA). We used distribution-free (nonparametric) statistics for harvest data because of small sample sizes (four per treatment per harvest) and repeated-measures MANOVA (von Ende 1993) and general linear models for growth analysis. For the latter, data were transformed when necessary to eliminate heteroscedasticity. We examined normal probability plots and residual plots to ensure that the data met the assumptions of MANOVA and regression. As in our paper on effects of elevated CO_2 on *R. mangle* (Farnsworth et al. 1996), we used ln(total plant mass) as a covariate when testing for treatment effects on the composite variables, area per leaf, leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA). This ANCOVA allowed us to determine whether apparent differences in growth were due to direct treatment effects (i.e., allometric differences among treatments) or to treatment-mediated differences in overall plant size (see also Evans 1972; Hunt 1990; Coleman et al. 1994).

Results

Environmental and soil conditions

During all except the winter months, maximal light levels (Fig. 1) over tanks were well above the saturation levels described for *R. mangle* by Farnsworth and Ellison (1996) and artificial lighting maintained tropical-length photoperiods throughout the winter. Daily irradiance in Belize shows similar variability (Ellison and Farnsworth 1996b) due to 'northers' (frontal systems of cool air common from November through March), and artificial lighting was similarly needed for field measurements of maximal photosynthetic rates (Farnsworth and Ellison 1996). Average air temperature and relative humidity (Fig. 1) in the greenhouse were nearly equal to those measured in Belize (Ellison and Farnsworth 1996b), although the range of air temperatures in the greenhouse was 10–20°C greater than those observed in the field. Water temperatures in the tanks (Fig. 1) were significantly cooler than those found in the field. Despite these differences in ambient conditions, plant growth and photosynthetic rates described below did not differ from those observed for seedlings and saplings in Belize (Farnsworth and Ellison 1996; Ellison and Farnsworth 1996b).

Soil characteristics were also analogous to those encountered in field studies. Soils were strongly anoxic, as indicated by redox potential measurements at both 2-cm and 10-cm depths (Fig. 2). There were no differences in redox potential among treatments at either 2 cm (taken at low tide: $P = 0.23$; high tide: $P = 0.34$, Wilcoxon signed-rank test) or 10 cm (low tide: $P = 0.38$; high tide: $P = 0.20$). However, at low tide, the soil redox

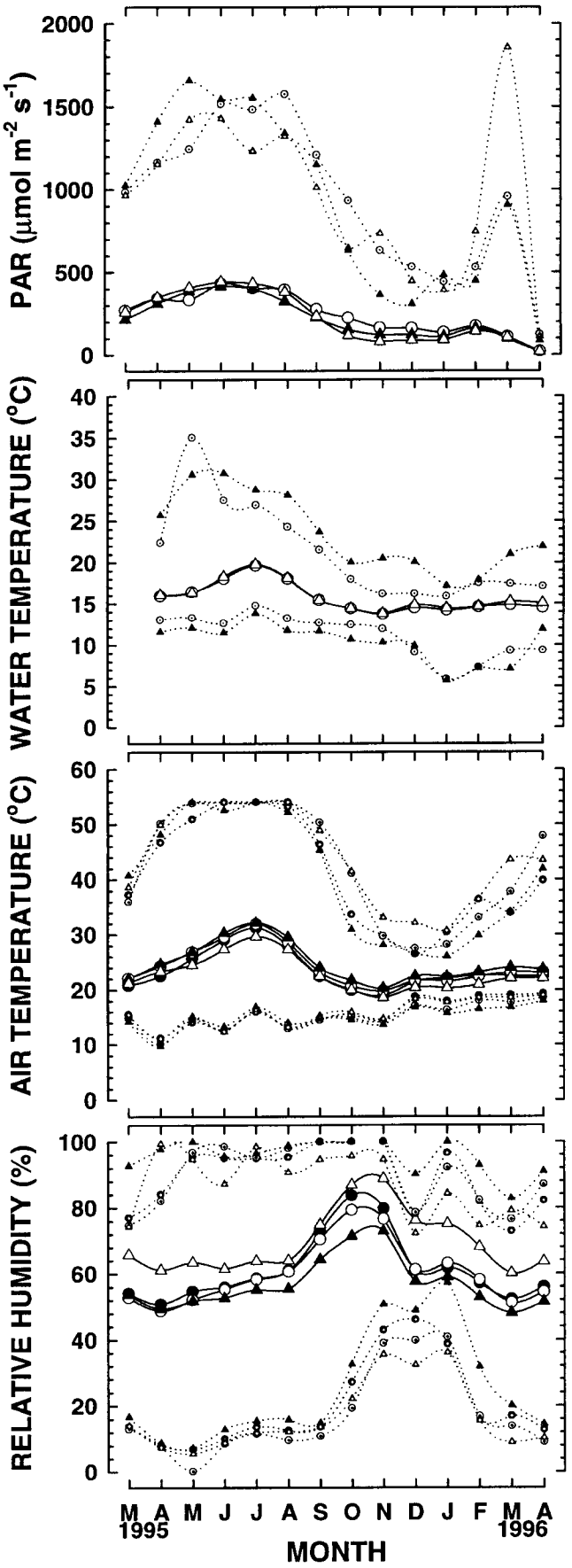

Fig. 1 Monthly environmental conditions around the tanks. *Large symbols* and *solid lines* are averages, while *small symbols* and *dotted lines* are monthly maxima and minima. Minimum monthly photosynthetically active radiation (*PAR*) values = 0, and are not drawn on the figures (● tank 1; ○ tank 2; ▲ tank 3; △ tank 4)

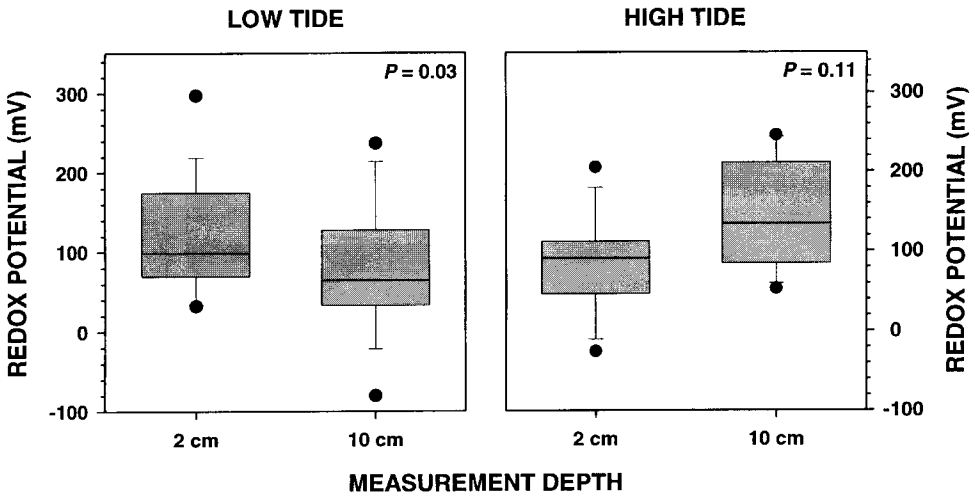

Fig. 2 Soil redox potentials measured at 2-cm and 10-cm soil depths, at low tide and high tide. Within each panel, *boxes* illustrate median redox potential (*central horizontal line*), upper and lower quartiles (*edges of each box*), upper and lower deciles (*to end of vertical 'whiskers'*) and extreme observations (*solid symbols*). Probability values for within-panel contrasts are from Wilcoxon signed-rank tests on matched pairs

potential at 2 cm was significantly higher than that at 10 cm. This pattern was reversed at high tide (Fig. 2). In other words, at low tide, pots were relatively less anoxic near their surface, while at high tide, pots were relatively less anoxic near their base (Fig. 2). Soil pH varied significantly among treatments ($P = 0.009$, Kruskal-Wallis rank-sum test), and in all cases was more acidic than the surrounding seawater (pH = 8.5). The median soil pH at LW, 7.6, was significantly greater than the median soil pH of 7.3 at MW ($P < 0.05$), which in turn was nearly three orders of magnitude greater than the median soil pH of 4.5 at HW. Soil sulfide levels increased ($P = 0.08$, Kruskal-Wallis rank-sum test) with increasing soil acidity [HW: mean = 1.29 ± 0.190 (SD), median = 1.35 mM; MW: 1.07 ± 0.293; 1.08 mM; LW: 0.89 ± 0.149; 0.90 mM].

There were no temporal trends within treatments in the values (% of dry mass) of all soil nutrients or C:N ratio, nor any among-treatment differences (pooled over time) in the content of any soil nutrient ($P > 0.30$, all cases, Kruskal-Wallis rank-sum test; Table 1). Soil C:N ratios of both HW and LW pots tended to be lower than in MW pots ($P = 0.078$, Kruskal-Wallis rank-sum test).

Table 1 Soil chemical characteristics (mean ± SD), pooled over all samples and treatments ($n = 84$)

Element	Percent of dry mass
C	12.73 ± 4.832
H	1.53 ± 0.527
N	0.82 ± 0.283
Na	1.23 ± 0.729
Mg	0.58 ± 0.192
P	0.21 ± 0.058
K	0.38 ± 0.124
C:N	15.44 ± 1.063

Patterns of growth and biomass allocation

Prior to flooding, there were no significant differences in stem height among the plants assigned to the three treatments (overall mean = 17.6 ± 3.89 cm, $n = 96$, $P = 0.134$, ANOVA). HW plants were significantly thinner (5.2 ± 0.65 mm) than either MW (5.6 ± 0.44 mm) or LW plants (5.6 ± 0.58 mm) ($P = 0.013$, overall ANOVA), although stem diameters of the latter two groups did not differ. Therefore, we included initial stem diameter as a covariate in subsequent tests for differences in growth among the three treatment groups.

MW and LW plants increased total stem length and diameter, and produced new branches and leaves much more rapidly than HW plants (Fig. 3). Although LW plants grew fastest during the first year of the experiment, their growth rate slowed thereafter while the growth rate of MW plants increased. By the end of 2½ years in the tanks, MW plants were growing faster and had about 20% more branches and about 10% more stem length and leaves than LW plants (Fig. 3). Stems remained thickest in LW plants, however. Despite the initial larger stem diameter of LW and MW plants relative to HW, there were no significant effects of initial stem diameter in repeated-measures models relating plant growth to treatment ($P > 0.25$, all cases). Additional univariate repeated-measures tests indicated that stem length and leaf number increased as a power function through time, while stem diameter and branch production increased linearly through time (Fig. 3).

Despite clear differences in overall plant size (Fig. 3), we observed few significant differences among harvested plants in the allocation of biomass to different plant parts (Fig. 4). Over time, plants in all treatments showed an increase in relative biomass allocation to underground roots relative to stems and leaves. Principal-components analysis (using Systat version 5.03) of the correlation matrix of relative biomass allocation to leaves, stems, hypocotyl, underground roots, aerial roots, and inflorescences at the final harvest (Table 2) enabled us to distinguish HW plants from the other two

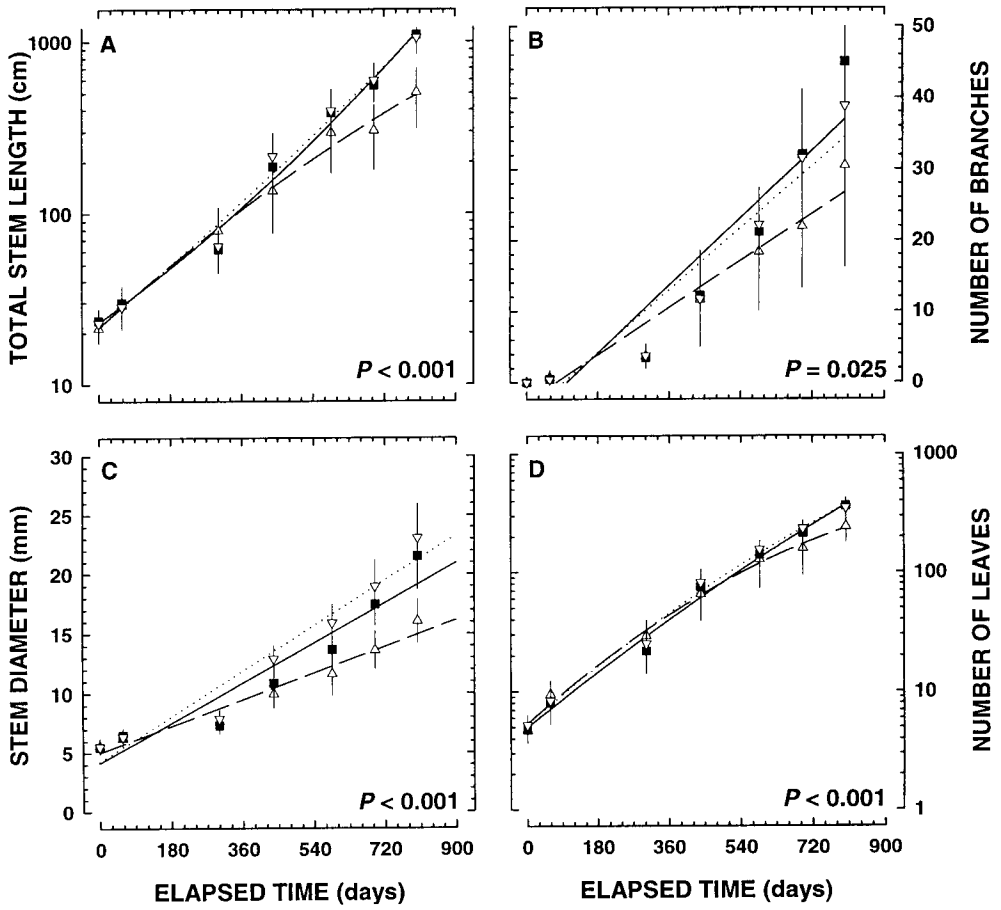

Fig. 3 Increase in total stem length (**A**), number of branches (**B**), stem diameter (**C**) and number of leaves (**D**) for plants in the three treatments. Values shown are means ± 1 SD; *lines* are best-fit linear (**B** and **C**) or quadratic (**A** and **D**) regressions. Note the logarithmic scales in **A** and **D**. *P*-values indicate significance of univariate tests of the Time × Treatment interaction in a repeated-measures MANOVA (following analytical methods of von Ende 1993). A significant *P*-value indicates that the shapes and levels of the curves differ significantly (△ - - - - HW plants, ■ —— MW plants, ▽ ····· LW plants)

Table 2 Results of principal-components analysis on the correlation matrix of relative biomass allocation at the final harvest (September 1996). The table illustrates the loadings of each compartment on the first three principal components

Variable	Component		
	1	2	3
Leaves	0.131	−0.852	0
Stems	0.564	0.337	−0.591
Hypocotyl	0	−0.104	0
Underground roots	−0.799	0.164	−0.308
Aerial roots	0	0.326	0.729
Inflorescences	0	0.129	0.157
Variance explained (%)	57.9	33.5	6.5

groups based on their relatively high allocation to leaves (component 2; $P = 0.05$, Kruskal-Wallis rank-sum test of component 2 among treatments; cf. Fig. 4). There were no significant differences among treatments in either component 1, loading allocation to stems and underground roots (Table 2; $P = 0.66$) or component 3, loading allocation to stems and aerial roots (Table 2; $P = 0.55$).

Four composite measures of total plant growth – area per leaf, LAR (m^2/g), LWR (g/g), and SLA (m^2/g) – did not vary among treatments after correction for among-treatment differences in plant size [$P > 0.15$, all cases; area per leaf: mean = 16.8 ± 4.38 (SD) cm^2; LAR: 0.002 ± 0.001 m^2/g; LWR: 0.29 ± 0.096 g/g; SLA: 0.006 ± 0.002 m^2/g]. Similarly, average branch length did not differ among treatments ($P = 0.34$), and averaged 18.5 cm. However, canopy shape did differ among treatments. At the end of the experiment, HW plants had much more 'compact' canopies than either MW or LW plants. Both canopy depth (distance from lowest branch to main shoot apex) and maximal canopy width (average of two perpendicular measurements) varied among treatments (HW: depth = 42.3 ± 8.58 cm, width = 61.3 ± 11.07; MW: depth = 97.9 ± 21.90, width = 80.5 ± 10.10; LW: depth = 101.0 ± 11.42, width = 95.2 ± 12.56). These data also illustrate that canopy shape differed among the treatments, as HW plants had significantly 'shallower' canopies (width: depth = 1.4 ± 0.23) than either MW (width: depth = 0.9 ± 0.21) or LW plants (width: depth = 0.9 ± 0.13) ($P = 0.001$, Kruskal-Wallis rank-sum test among treatments).

Reproduction

LW and MW plants began to flower in January 1996, while HW plants did not begin to flower until September

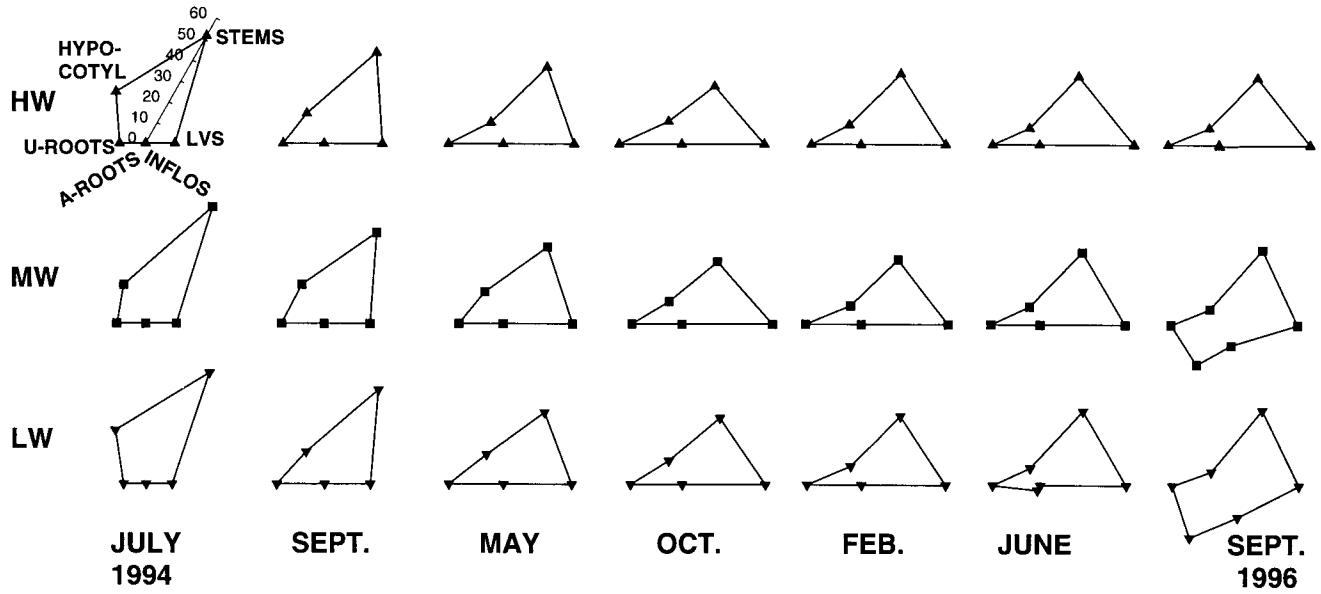

Fig. 4 Polar plots illustrating multidimensional patterns of biomass allocation among plants at all harvest dates. Polar plots are polar projections of bar charts where the distance of each vertex from the center of the plot (equivalent to the 'bar') represents the percent of biomass in that compartment [leaves, stems, hypocotyl, underground roots, aerial roots (A-ROOTS), or inflorescences (INFLOS)]. In lieu of bars, only the values indicating percent of biomass are noted, and they are connected into a polygon (see A.M. Ellison 1993 for further discussion of polar plots). Visually, a change in 'shape' of the icon from left to right indicates a change in relative biomass allocation patterns over time, while top-to-bottom differences indicate differences among treatments. All plots are equivalently scaled. In all 1994 and 1995 icons, both percent aerial roots and percent inflorescences = 0, while for 1996 icons (MW and LW; HW only for Sept. 1996), percent allocation to aerial roots and inflorescences is multiplied by 10 for clarity

1996. Of those plants that did flower, LW always produced more inflorescences (2–4 flowers each) than MW or HW plants (Fig. 4; Feb. 1996: $P = 0.08$; June 1996: $P = 0.01$; Sept. 1996: $P = 0.001$). Reproductive plants did not begin to set fruit until the second flowering episode, 2.5 years after planting.

Physiological measurements

Repeated-measures MANOVA on maximum photosynthetic rates (P_{max}: μmol CO_2 m^{-2} s^{-1} assimilated at saturating PAR) of continually monitored plants illustrated that both HW and LW plants showed modest declines in P_{max} relative to the preflood conditions, while P_{max} at MW remained constant over the course of the experiment (Fig. 5; MS = 21.52, $F_{12,42} = 2.69$, $P = 0.009$, Time × Treatment interaction; overall treatment differences: $P = 0.04$, Wilk's λ). There were no among-treatment differences in overall rates of (log-transformed) stomatal conductance (MS = 0.168, $F_{12,42} = 0.723$, $P = 0.72$, Time × Treatment interaction), which declined over time in all treatments (Fig. 5). Overall, measured P_{max} and (log-transformed) stomatal conductance were positively correlated ($r = 0.62$, $P < 0.001$; Fig. 5) and showed no seasonal variability. The rate of photosynthesis for a given rate of stomatal conductance, based on comparisons of regression coefficients for the best-fit lines shown in Fig. 5, was significantly higher among HW ($\beta_1 = 3.73$) and LW ($\beta_1 = 3.64$) plants than at MW ($\beta_1 = 2.87$; $P < 0.05$). Because of the tight correlation between transpiration rate and stomatal conductance ($r = 0.91$), responses in transpiration rates closely paralleled temporal and treatment-specific responses observed for stomatal conductance.

Relative growth rate (RGR) from one harvest to the next was computed as $[\ln(\text{mass}_{t+1}) - \ln(\text{mass}_t)]/(\text{number of days between harvests})$. We estimated the standing total biomass of those plants that were measured continually throughout the experiment from a regression of biomass on stem length derived from the harvested plants ($\ln(\text{total biomass}) = -1.22 + 1.04 \times \ln(\text{total stem length})$; $r^2 = 0.97$]. Temporal patterns of RGR differed among treatments (MS = 1×10^{-5}, $F_{10,45} = 2.74$, $P = 0.01$, Time × Treatment interaction in a repeated-measures MANOVA; overall treatment differences: $P = 0.02$, Wilk's λ; Fig. 5). The RGR at HW was constant over the course of the experiment, while RGR at MW and LW increased during the first part of the experiment and declined later. The RGR of LW plants peaked about 6 months earlier and subsequently declined more rapidly than the RGR of MW plants (Fig. 5). RGR and P_{max} were positively correlated ($r = 0.36$, $P < 0.001$; Fig. 5), while stomatal conductance and RGR were not significantly correlated with each other ($r = 0.07$; Fig. 5). Temporal patterns in rates of growth, photosynthesis, and stomatal conductance among harvested plants were qualitatively similar to and showed identical statistical differences as those observed for plants followed continually.

Net assimilation rate (NAR, g m^{-2} day^{-1}), computed for harvested plants as RGR for the measurement

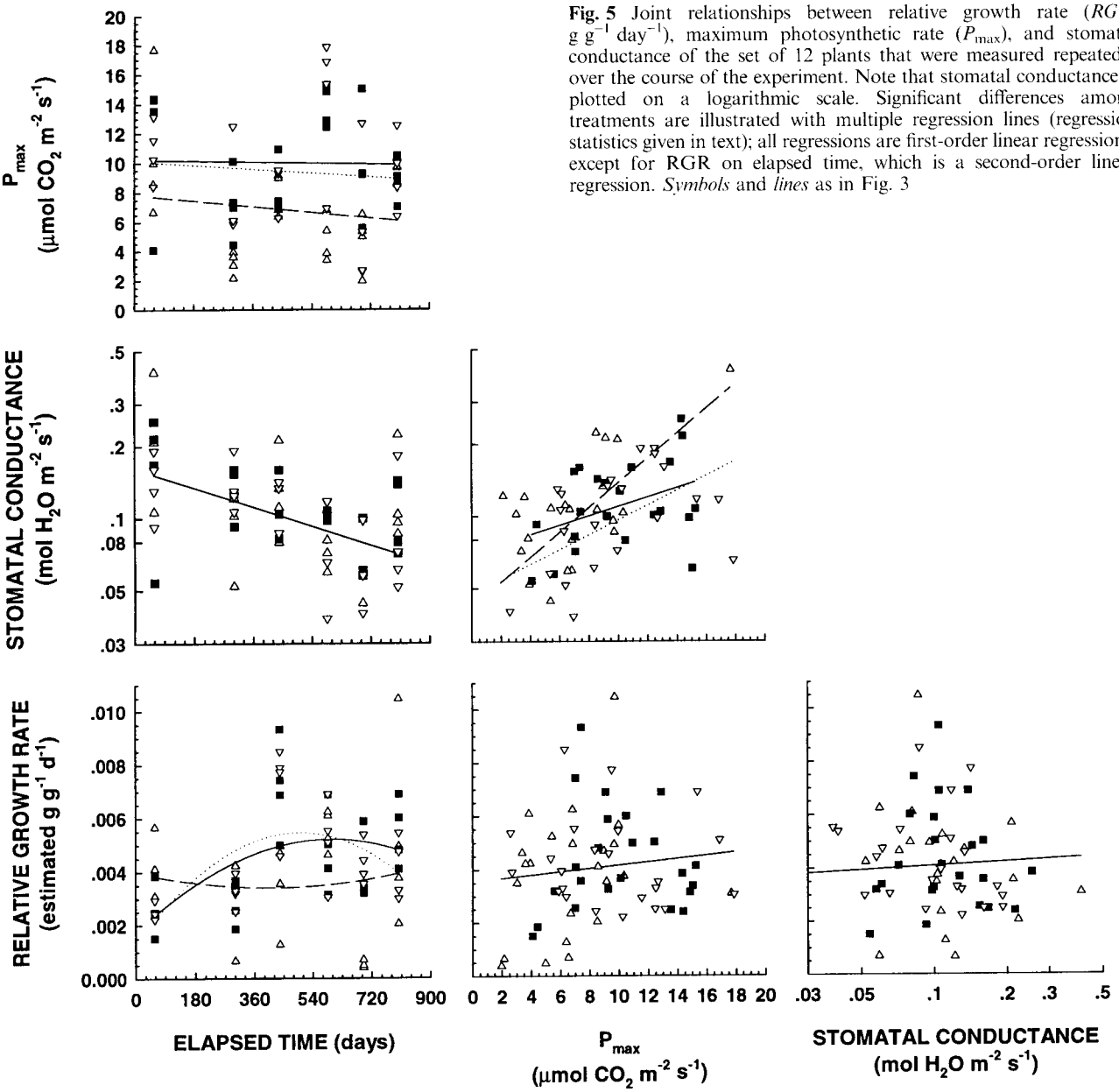

Fig. 5 Joint relationships between relative growth rate (*RGR*, $g\ g^{-1}\ day^{-1}$), maximum photosynthetic rate (P_{max}), and stomatal conductance of the set of 12 plants that were measured repeatedly over the course of the experiment. Note that stomatal conductance is plotted on a logarithmic scale. Significant differences among treatments are illustrated with multiple regression lines (regression statistics given in text); all regressions are first-order linear regressions, except for RGR on elapsed time, which is a second-order linear regression. *Symbols* and *lines* as in Fig. 3

interval preceding their harvest divided by LAR at harvest, declined over the course of the experiment for all treatment groups (Fig. 6). LW plants exhibited a 50% faster rate of decline ($P < 0.01$, comparison of regression slopes) than either MW or HW plants, while the latter two treatment groups declined at similar rates ($P > 0.10$, comparison of regression slopes). Among all treatment groups, RGR at harvest was significantly related to NAR at harvest (LW: $r = 0.84$; MW: $r = 0.71$; HW: $r = 0.73$; all cases $P < 0.001$; Fig. 6). Comparisons among regression slopes indicated that LW plants showed a 36% lower increase in RGR for a given increase in NAR than either MW or HW plants ($P < 0.01$), while the latter two treatment groups showed similar RGR responses for a given change in NAR ($P > 0.10$).

Leaf chemistry and anatomy, stem lignification, and root porosity

The foliar C:N ratio and chlorophyll content decreased significantly from LW through MW to HW, but we observed no differences in foliar salt (%Na) concentration among treatments (Table 3). Among all plants pooled, total leaf thickness declined from a pretreatment (July 1994) 0.6 ± 0.08 mm to a post-treatment (October 1995) 0.46 ± 0.05 mm ($P < 0.001$, *t*-test). During this same period, the epidermis thickened by 56% ($P = 0.01$) while the palisade layer was reduced by 15% ($P = 0.03$). Other leaf tissue layers showed no significant changes in thickness ($P > 0.15$) during this same time period. However, after treatments commenced, no measures of leaf structure showed any significant change

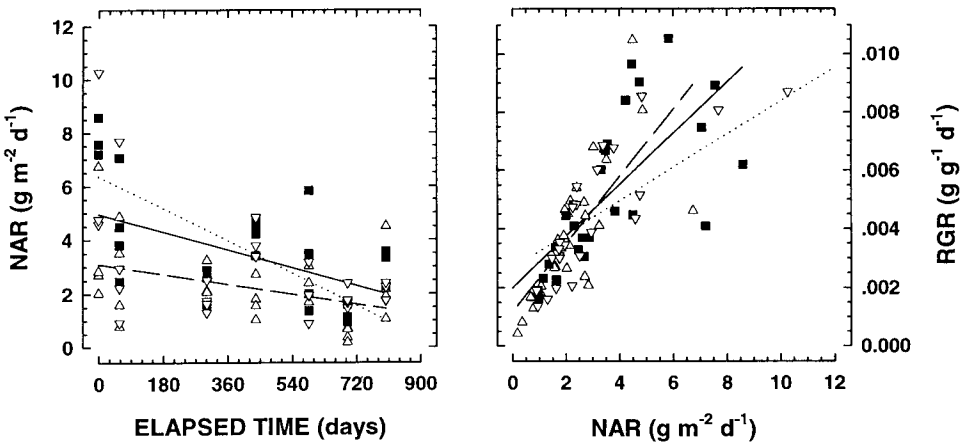

Fig. 6 Treatment-specific changes in net assimilation rate (*NAR*) over time (*left panel*), and the relationship between RGR and NAR (*right panel*). Significant differences among treatments are illustrated with multiple linear regression lines (statistics in text). *Symbols* and *lines* as in Fig. 3

Table 3 Chemical characteristics of leaves, expressed on a percentage basis (means ± SD). For a given row, different *superscripts* indicate significant ($P < 0.05$) pairwise differences among treatments. Data from all harvests are pooled ($n = 28$ per cell), as there were no significant temporal trends in foliar chemistry ($P > 0.4$, all variables in all treatments)

	Treatment		
	HW	MW	LW
% C [(g/g) × 100]	42.3 ± 1.59[a]	44.1 ± 1.97[b]	44.3 ± 2.09[b]
% N [(g/g) × 100]	2.4 ± 0.36[a]	2.0 ± 0.39[b]	1.7 ± 0.27[c]
C:N	18.1 ± 2.56[a]	23.2 ± 4.58[b]	27.1 ± 5.68[c]
% Na [(g/g) × 100]	2.6 ± 0.83[a]	2.4 ± 0.45[a]	2.7 ± 0.51[a]
Chlorophyll (mg/g)	0.12 ± 0.052[a]	0.16 ± 0.055[b]	0.17 ± 0.032[b]

among treatments across dates (cuticle: 3.5 ± 1.4%; epidermis: 7.8 ± 3.2%; hypodermis: 24.5 ± 5.1%; mesophyll: 31.4 ± 5.2%; palisade: 29.0 ± 5.0%; ANOVA results – Treatment: $P = 0.37$; Date: $P = 0.08$; Treatment × Date: $P = 0.82$). However, median stomatal density was higher in both HW and LW plants compared with MW ones (LW: 50/mm; MW: 44/mm; HW: 46/mm; $P = 0.10$, Kruskal-Wallis rank-sum test).

Stems of LW plants began to produce wood (secondary thickening) within 1 year of flooding and 3 months earlier than MW plants, while only one HW plant had a woody stem by the end of the experiment. Median root porosity increased slightly with pot height (LW: 25%; MW: 32%; HW: 48%; $P = 0.08$, Kruskal-Wallis rank-sum test).

Discussion

Our results demonstrate potential significant impacts of both increased and decreased water depth on the physiology, growth, morphology, and reproduction of *R. mangle*, the predominant species in neotropical mangrove forests. Because the experiment described here closely mimicked field tidal (cf. Curran et al. 1985) and edaphic conditions (cf. Nickerson and Thibodeau 1985; McKee et al. 1988, McKee 1993, 1995; Kryger and Lee 1995, 1996; contra Finn 1996), and because its duration spanned seedling, sapling, and reproductive stages of *R. mangle*, these data constitute reasonable predictors of the growth of this prominent mangrove species in a range of sea level conditions expected to occur throughout the Caribbean Sea within 50–100 years (Granger 1991). These results, together with complementary data from our previous study on the effects of elevated CO_2 on *R. mangle* (Farnsworth et al. 1996), substantively address two broad areas of concern regarding mangroves and global climate change. These results suggest that detrimental effects of sea level rise or fall will offset increases in growth caused by fertilization effects of anticipated elevated concentrations of atmospheric CO_2 (Farnsworth et al. 1996).

Responses of *R. mangle* to simulated sea level change

We postulate that the acid-sulfide soils that developed in the HW pots retarded the growth of HW plants throughout the course of the experiment (Fig. 3), as has been demonstrated in both other field and laboratory studies (e.g., McKee 1993). In other mangrove species, changes in root porosity and root oxidation can compensate for edaphic changes associated with acid-sulfide soils (McKee 1996; Youssef and Saenger 1996). However, root porosity of *R. mangle* was only weakly affected by the different edaphic conditions and water depths, consistent with data on this genus reported by McKee (1996) and Youssef and Saenger (1996).

Early in the experiment, LW plants grew more rapidly than MW ones, as indicated by initial higher total stem length, stem diameter, and number of leaves (Fig. 3). After 1½ years, however, the RGR of the flooded plants slowed dramatically (Fig. 5), and by the end of the experiment (2½ years after tidal treatments began), MW plants were larger in all respects except for

stem diameter (Fig. 4). At the same time that growth slowed at LW, the NAR of LW plants fell below that of the MW plants (Fig. 6), and for those relatively low rates of NAR (< 4 g m^{-2} day^{-1}), MW plants had significantly higher RGRs than LW plants (Fig. 6). While all plants in all treatments exhibited allometric growth typical of mangrove seedlings and saplings (Ellison and Farnsworth 1996b; Farnsworth and Ellison 1996), the allometry of growth did not differ among treatments. In other words, by the end of the experiment, MW plants were basically larger versions of LW and HW plants (see Coleman et al. 1994 for a further discussion of disentangling differences in size and allometry).

P_{max} also declined over time for both LW and HW plants, while it remained constant for MW ones (Fig. 6). P_{max} was also 25% lower for a given stomatal conductance for both HW and LW plants relative to those at MW. NAR, RGR, and P_{max} were consistently lower at HW throughout the experiment (Figs. 5, 6), and these plants also had significantly more vertical and compact (higher height-to-width ratio) canopies than either MW or LW plants. Such differences in canopy architecture can affect the leaf area exposed to light through differential self-shading, and could also alter susceptibility of plants to windthrow or wave damage.

These growth patterns are very similar to those observed for *R. mangle* growing under field conditions at different tidal heights. Among seedlings, early shoot growth among transplanted seedlings was highest for plants growing in the lowest intertidal (Ellison and Farnsworth 1993; Farnsworth and Ellison 1996). Seedlings transplanted to highest high water were chlorotic and died within 1 year (Ellison and Farnsworth 1993) and, in a second set of transplants, seedlings transplanted to lowest low water had 60% lower survivorship than seedlings growing at intermediate tidal heights (Farnsworth and Ellison 1996). For young *R. mangle* saplings, shoot growth was correlated inversely with water depth between mean water and low water (Ellison and Farnsworth 1996). P_{max} declined with tree age across tidal elevations, and branch architecture and leaf placement within canopies changed over time from relatively compact with leaves nearer to vertical in seedlings, to relatively open with leaves nearer to horizontal in saplings and mature trees (Farnsworth and Ellison 1996).

Comparison of effects of changing water depth and CO_2

Clearly, the strongest conclusions regarding responses of *R. mangle* to climate change would benefit from a full $CO_2 \times$ tidal change factorial experiment. Unfortunately, space and resource limitations precluded such a factorial design in this experiment. However, comparisons of relative responses of *R. mangle* to relative sea level rise or fall with those found following doubling of atmospheric CO_2 concentration illustrate that for some key physiological and growth parameters, CO_2 fertilization effects described by Farnsworth et al. (1996) will be tempered by negative responses to changing sea level (Table 4). For example, elevated CO_2 led to 30–40% increases in stem length, number of branches, and total plant mass. However, a simulated sea level rise decreased these plant growth characteristics by 10–25%, and a simulated sea level fall decreased them by 40–55%. Declines of 12–16% in stomatal density and increases in P_{max} in 700 ppm CO_2 contrast with 6–21% increases in stomatal density and decreases in P_{max} at both LW and HW. Enhancements of RGR (21%) and NAR (30%) in elevated CO_2 contrast with almost identical declines at LW (23% and 29%, respectively) and more modest declines at HW (3% and 16%, respectively). Similarly, declines in foliar C:N and increases in foliar Na observed at LW and HW ran counter to changes in leaf chemistry exhibited by plants grown in high CO_2.

Composite morphological parameters, such as SLA and LAR were relatively insensitive to different future environmental conditions, indicating little phenotypic plasticity for these traits (Table 4). These observations are supported by growth analyses (compare patterns of growth and biomass allocation in Results above with Table 2 of Farnsworth et al. 1996): LW and HW plants were simply smaller versions of plants growing at MW, while plants growing in elevated CO_2 were larger versions of plants growing in ambient CO_2.

Table 4 Responses of *Rhizophora mangle* growing at HW or LW relative to MW, and responses to growing in elevated (700 ppm) CO_2 relative to ambient (350 ppm) CO_2. Values given are ratios of mean responses at final harvests (i.e., HW/MW). Values > 1 indicate an enhancement in the parameter under predicted conditions relative to present-day conditions, while values < 1 indicate a negative response to anticipated climate change. CO_2 data are derived from Farnsworth et al. (1996). For the CO_2 data, an *asterisk* indicates a significant departure from 1 (Bonferroni-adjusted $P < 0.05$, $n = 9$ plants per treatment); low sample size and statistical power precluded significance testing for these ratios in the tidal experiment ($n = 4$ plants in each treatment at the final harvest)

Parameter	LW	HW	High CO_2
Total stem length	0.88	0.43	1.34*
Number of branches	0.75	0.55	1.39*
Total plant dry mass	0.99	0.47	1.45*
Total leaf area	1.03	0.53	1.33*
Specific leaf area	1.00	1.00	0.99
Leaf weight ratio	1.01	1.16	1.07
Number of aerial roots	1.18	–	3.25*
Root mass:shoot mass	1.25	1.18	1.45
Stomatal density	1.07	1.01	0.84*
Maximum photosynthetic rate	0.94	0.79	1.12*
Stomatal conductance	0.89	0.66	0.48*
Foliar chlorophyll	0.99	0.94	0.87*
Foliar C:N	0.98	0.64	1.31*
Foliar Na	1.11	1.61	0.79
Number of inflorescences	1.08	0.07	2.33*
Relative growth rate	0.77	0.97	1.21*
Net assimilation rate	0.71	0.84	1.30*

Finally, we interpret traits that changed in parallel in the two experiments as generalized responses to environmental stress. Plants growing at HW and LW, like plants growing in elevated CO_2, dramatically increased total root mass relative to total shoot mass (Table 4). Aerial roots and inflorescences were produced earlier and in greater number (Table 4), stems lignified sooner, and P_{max} declined more rapidly (Fig. 4; and Fig. 4 in Farnsworth et al. 1996) in 'stressed' plants relative to 'ambient' controls. Finally, while RGR normally declines with plant age because of increased respiration costs, RGR peaked 6 months sooner for LW than MW plants (Fig. 5). Similarly, RGR slowed more rapidly in elevated CO_2 than it did at ambient concentrations (Table 1 of Farnsworth et al. 1996). In summary, these responses in carbon allocation, photosynthetic rates, and RGR parallel changes observed across ontogeny in field populations of *R. mangle* (Farnsworth and Ellison 1996) and may reflect accelerated senescence of plants growing under conditions approximating coastal environments 50 years in the future.

Conclusions

Throughout the Holocene, mangroves in the Caribbean have been able to respond to relatively small changes in sea level (< 8–9 mm/year) through landward or seaward migration (Parkinson 1989; Parkinson et al. 1994) mediated by local topography (Bacon 1994), while larger changes in sea level may have led to mangrove ecosystem collapse (Ellison and Stoddart 1991; J.C. Ellison 1993). In the future, landward migration of fringing mangrove species, such as *R. mangle*, likely will be limited both by in situ differences in growth and by coastal development and associated anthropogenic barriers (Parkinson et al. 1994; Ellison and Farnsworth 1996a). Simultaneously, physiological changes and generalized stress responses in *R. mangle* may hasten its decline in Caribbean mangrove forests. As with other wetland species, interspecific variation in physiological responses of different mangrove species to factors associated with climate change would be expected to lead to changes in species composition and community structure following predicted changes in sea level and atmospheric CO_2 levels. Determination and accurate prediction of community-level responses in mangrove forests to global climate change will require experiments using multiple species in realistic laboratory experiments and under controlled field conditions.

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