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Spatial and temporal variability in growth of *Rhizophora mangle* saplings on coral cays: links with variation in insolation, herbivory, and local sedimentation rate

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Summary

1 We used demographic growth analysis to quantify seasonal and annual patterns of shoot and root module production by *Rhizophora mangle* saplings growing on three coral cays in Belize, Central America. We investigated scaling relationships among root and shoot modules, leaf life-span, effects of herbivores on module and whole plant growth, and differences in growth under different sedimentation regimes.

2 Production of new shoots and aerial roots occurred seasonally. Annual peaks in solar insolation occurred in May; relative rates of change in numbers of shoot meristems and leaves, and stem length peaked one month following. Relative rate of change in numbers of aerial roots peaked one month following this shoot flush, and roots elongated primarily during the dry season.

3 Increased water depth was positively correlated with the ratio of root length to shoot length in saplings. Mean shoot growth rate was significantly lower at cays exhibiting relatively low sedimentation rates, as well as at similar locales within cays.

4 Average leaf life-span was 9 months. During an outbreak of the mangrove skipper *Phocides pigmalion*, insect herbivores shortened leaf life-span by increasing leaf abscission rate. Insect folivores reduced above-ground net primary production available for export to adjacent marine ecosystems by 5–20%. Up to seven-fold increases in percentage of roots bored by isopods occurred concomitantly with annual peaks in new root production. Relative elongation rate of roots decreased five-fold following isopod attack. However, whilst both insects and isopods tracked production of and consumed new modules, neither consumer contributed significantly to variance in whole-plant growth.

5 Demographic growth analysis is a powerful tool with which to predict dynamic responses of module production and whole-plant growth in response to local environmental conditions. Our analyses illustrate that growth of mangroves are sensitive to seasonal patterns of insolation, to decreasing sedimentation and to increasing water depth. Given that growth of mangrove saplings on coral cays declines significantly with sedimentation rate, persistence of these forests is unlikely if sea level in the Caribbean increases as predicted.

Keywords: demographic growth analysis, herbivory, mangroves, net primary productivity, relative growth rate

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Introduction

Mangrove forests, composed of a set of taxonomically diverse tree species that share convergent adaptations to saline, anoxic habitats (e.g. Stewart & Popp 1987; Ball 1988), are among the world's most productive ecosystems (Lugo & Snedaker 1974). The majority of recent research documenting patterns of primary production, carbon and nutrient cycling, and detrital export to adjacent ecosystems has focused on riverine, and to a lesser extent, fringe and scrub mangrove forests (e.g. Twilley *et al.* 1992; Alongi *et al.* 1992; Lee

1995). Components of net primary production vary spatially with latitude, geomorphological setting, and mangrove physiognomy (Clough 1992; Saenger & Snedaker 1993), but studies examining temporal variability of mangrove growth, demography, and productivity are uncommon.

Mangroves interact dynamically with their changeable geomorphological environments (Thom 1967, 1982; Woodroffe 1992) by colonizing shallow water shelves, and by modifying local sedimentation patterns (Davis 1940; Wolanski *et al.* 1980). Thom (1982) classified the environmental settings in which mangroves occur, but did not include carbonate platforms, as these are uncommon in the riverine and estuarine Indo-Pacific mangroves that he studied. These were added as a distinct type of environmental setting by Twilley (1995) in his comparative review of relationships between mangrove ecosystems and the geomorphology of their local environments. The interactive effects of local sedimentation regimes and mangrove demography and production of such systems have not been previously quantified.

Autochthonous sediments on carbonate platforms are the predominant setting for mangrove forests on islands in the Caribbean, the low Pacific islands, and the Bahamas, as well as on the Great Barrier Reef and other reef-dominated lagoons (Woodroffe 1992; Twilley 1995). These forests represent the seaward interface between upland communities and seagrass beds and coral reefs, and will be among the first ecosystems to experience the rise in sea level predicted under global climate change (Davis *et al.* 1994). Prognoses for mangrove performance under transgressions are uncertain and are derived almost exclusively from analyses of sediment cores (Ellison 1993; Parkinson *et al.* 1994; Snedaker 1995). Direct studies of mangrove growth *in situ* are needed to formulate realistic hypotheses.

Ecophysiological responses to local, dynamic environments are translated into system-wide patterns of primary production via individual plant growth and population dynamics (Chapin 1993; Clark 1993). Demographic analysis, informed by a comprehensive understanding of both biotic *and* abiotic factors that affect mangroves, is essential for accurate predictions of mangrove growth and production in natural and managed forests (Gong & Ong 1995). Yet to date, a long-term profile of growth, survivorship and reproductive output is available only for one species of mangrove, *Avicennia marina* var. *australasica* Walp. Moldenke (Avicenniaceae) in Australia (Clarke 1995).

In this paper, we employ demographic growth analysis (*sensu* McGraw & Garbutt 1990) to describe patterns of growth and production of three populations of *Rhizophora mangle* L. (Rhizophoraceae) saplings growing on accreting edges of coral cays in Belize, Central America. Our objectives in this three-year study were: (1) to document within- and among-cay variation in temporal patterns of leaf, stem, and aerial root production of *R. mangle* saplings on carbonate platforms; (2) to determine if observed growth differences among cays result from plastic allometric shifts in module allocation (size or number); (3) to examine influences of primary consumers on module production, turnover, and whole-organism growth; (4) to elucidate correlations between sapling growth and edaphic and climatic variables including seasonal and interannual insolation, rainfall, and local sedimentation patterns.

This detailed, baseline study is the first to examine potential relationships between mangrove growth, net assimilation rates, seasonal climate, and sediment accretion rates; to offer long-term allometric data on mangrove saplings (an intermediate life stage for which data in tropical systems in general are rare: Kohyama 1987; Clark & Clark 1992; King 1994; Turner *et al.* 1995); and to investigate impacts of direct consumers, including folivores and root-boring crustaceans, on module growth and survivorship and whole-organism production. We compare our data with measurements from mangroves and other tropical species elsewhere in the world, and offer hypotheses regarding significant determinants of mangrove growth in current and future environments.

Methods

STUDY SITES

We studied growth of *R. mangle* saplings on three small islands within the Belizean barrier reef lagoon: Wee Wee Cay (16°45′N, 88°08′W); Spruce Cay (16°43′N, 88°09′W), and Norvall Cay (16°43′N, 88°10′W) (Fig. 1). These cays occur within 6 km of each other, are each 2–4 ha in size, are ringed by coral reef, and are accreting slowly towards the north-east (Fig. 1, and data presented below). Like other coral cays within the reef complex (Macintyre *et al.* 1987), these are presumed to have appeared above sea level 3000–5000 years bp. The present-day mangrove swamps, classified as mangroves fringing oligotrophic waters of carbonate platforms (*sensu* Twilley 1995), overlie coral/limestone bedrock at a depth-to-bedrock of 1–3 m.

The prevailing climate is tropical-subtropical transitional (Hartshorn *et al.* 1984), and does not vary between the cays. During the study period (January 1992–May 1994), the mean daily air temperature recorded at the Carrie Bow Cay weather station, 4 km north-east of Wee Wee Cay, was 25 °C; mean daily water temperature was 27 °C, and daily relative humidity was 75–80%. The cays received ≈ 1500 mm of rainfall annually, with the majority falling between August and January. Mean daily tidal amplitude throughout the reef complex, including these three cays, is 30 cm (Kjerfve *et al.* 1982), and wave action

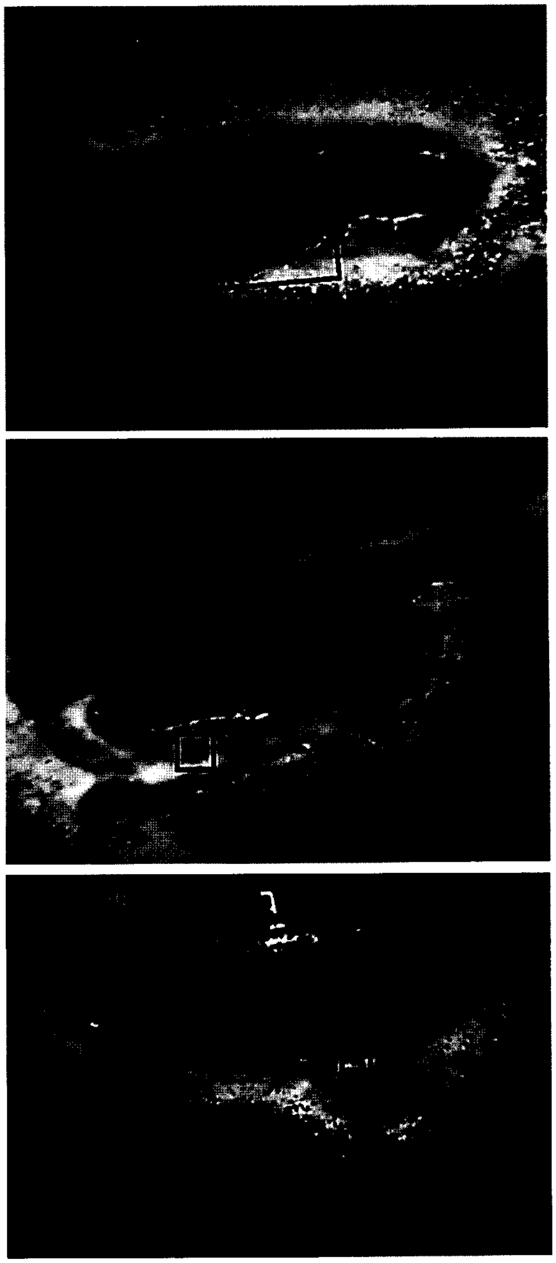

Fig. 1 Aerial photographs (altitude ≈ 300 m) of the three cays. Study areas are indicated by rectangles. At Wee Wee Cay, the study area is 50m × 100 m; at Spruce Cay, the study area is 50 m × 50 m; and at Norvall Cay, the study area is 50 m × 130 m. Arrows in each photograph indicate magnetic North.

is abated to generally < 1 m amplitude by the Belizean barrier reef.

STUDY SPECIES

Rhizophora mangle is the only plant species growing on Spruce Cay and Norvall Cay, and the predominant species on the fringe and seaward carbonate platform of Wee Wee Cay. On Belizean coral islands, mature *R. mangle* rarely exceeds 10 m in height. Growth of *R. mangle* proceeds by sylleptic, opposite branching (Gill & Tomlinson 1971b) and conforms architecturally to Attim's model (*sensu* Hallé *et al.* 1978), with continuous or seasonal patterns of shoot production (Gill & Tomlinson 1969). Like other mangrove members of the Rhizophoraceae, *R. mangle* produces prominent aerial stilt roots that originate from the bole and lateral branches (Gill & Tomlinson 1977). Aerial roots grow up to 1 mm per day before they reach the ground, into which they anchor by proliferating rootlets (Gill & Tomlinson 1971a, 1977). These prop roots function principally for structural support and gas exchange (Scholander *et al.* 1955; Gill & Tomlinson 1971a), and are distinct from nutrient-absorbing roots normally identified in plant growth analysis.

At the three study areas, *R. mangle* saplings grow in full sun, and the low densities (< 1 saplings per 10 m^2) preclude competition for light among individuals. Sapling morphology resembled that of fertilized saplings described by Feller (1995) at Twin Cays, 10 km north-west of Wee Wee Cay. This apparent lack of nutrient limitation and light competition indicated that these saplings should conform to their architectural model of growth (Hallé *et al.* 1978), and that our estimates of above-ground growth and production would approach the maximum expected of saplings growing in oligotrophic environments.

GROWTH ANALYSIS AND ESTIMATES OF PRIMARY PRODUCTIVITY

At the end of December 1991, we marked all naturally occurring *R. mangle* saplings on the accreting edges of Wee Wee Cay (38 saplings in $\approx 5000\,m^2$), Spruce Cay (48 saplings in $\approx 2500\,m^2$), and Norvall Cay (49 saplings in $\approx 6500\,m^2$). We operationally defined a *R. mangle* 'sapling' as a plant having 1 or 2 aerial roots and 1–3 growing shoot tips, and showing no evidence of prior reproduction. Plants were marked individually with numbered, expandable plastic bands (National Band and Tag Co., Newport, Kentucky, USA). In January, March, June, July and August 1992, January, March, June and July 1993, and January, March and May 1994, we measured the height of the main stem (± 1 cm) and the lengths of all lateral branches (± 1 cm). We simultaneously counted numbers of growing shoot meristems, total number of leaves, and total number of aerial roots on each plant.

We also followed dynamics of leaf growth on four cohorts of leaves on each plant. In January 1992, June 1992, March 1993 and June 1993, we marked 3–5 leaves on each sapling, and noted number of acropetal and basipetal leaf pairs. We chose newly emerged, undamaged, terminal leaves, and marked one randomly chosen leaf of the terminal pair with a numbered, plastic band looped around the petiole. At marking and subsequent census dates, we measured leaf length ± 1 mm, new leaf production (acropetal pairs added per time interval), and loss of older leaves (basipetal leaf pairs lost). These data allowed us to estimate leaf area and growth, chart phenology of leaf production, estimate leaf life-span, and examine the relationship of leaf production to turnover on a branch.

All existing and emerging aerial roots were similarly banded; root length was measured (± 1 mm) at each census date. We distinguished unrooted aerial roots ('hanging roots') from those initiated above-ground but rooted in the substrate ('ground roots'). Because destructive below-ground harvesting could not be done at these sites, we did not measure below-ground fine root production.

To determine correlations between module size and biomass, samples of leaves, stems, and stilt roots were collected in March 1994 from an additional set of planted saplings at Wee Wee Cay, measured as described above, dried at 70 °C to constant mass, and weighed. For productivity estimates, due to seasonal variation in modular relative growth rates (see below), it made little sense to compute *daily* gains in biomass of either individual modules or entire plants. Thus, we used the net change in plant module size between January 1992 and May 1994 to estimate average *annual* relative change in above-ground biomass by these saplings, an estimate that integrates across seasonal variation. Annual relative growth rate (RGR: g g^{-1} $year^{-1}$) of total above-ground biomass (leaves + stems + aerial roots) divided by leaf area ratio (LAR: m^2 g^{-1}) provided an estimate of annual net assimilation rate (NAR: g m^{-2} $year^{-1}$).

EFFECTS OF HERBIVORY ON MANGROVE GROWTH

As burrowing isopods [primarily *Phycolimnoria clarkae* Kensley and Schotte (Limnoriidae)] are known to reduce root growth in *R. mangle* (Perry 1988; Ellison & Farnsworth 1990), we noted all attacks on roots by such crustaceans. Amount of leaf area removed by insect and crab folivores (± 10%) also was visually estimated at each census date on the cohorts of marked leaves described above. Our visual estimations of leaf area removed are within 5% of the amount measured with a Li-Cor leaf area meter (Farnsworth & Ellison 1993).

SEDIMENTATION AND GROWTH

Substrate elevation was measured on each sampling date at a fixed point within the root cluster of each sapling. When plants were initially tagged, we placed a 1-m-long × 1.25-cm-diameter steel reference rod into the substrate < 10 cm from the main stem, and set among the aerial roots. At each census date, substrate elevation (depth below highest high water: *HHW*) at this reference rod was measured (± 1 mm) using fibreglass level rods and a Topcon AT-G2 autolevel equipped with a micrometer for precision measurements (Forestry Suppliers, Inc., Jacksonville, Mississippi, USA). Substrate elevation measurements were made relative to permanent *HHW* benchmarks that we established at each cay in December 1991. Note that these benchmarks were not true tidal datum benchmarks, which are unavailable for these cays. Depth contours at each study site were mapped (using measurements on a 5-m grid) in June 1993 to determine if saplings constituted local high or low points (zones of relative sediment accretion or erosion) relative to their surroundings.

STATISTICAL ANALYSES

Data were analysed using SYSTAT release 5.0 (Systat, Inc., Evanston, Illinois, USA). Values reported throughout are means ± 1 standard error of the mean. We used nonlinear regression to fit growth curves, and generalized linear models (GLM) for between-cay comparisons (since sample sizes were unequal among the three cays). Data were transformed when necessary to meet assumptions of nonlinear regression and GLM. We examined scaling relationships between plant modules computing Model II (major axis) regressions (Niklas 1994; Sokal & Rohlf 1995) for all possible pair-wise combinations of module lengths and numbers. Differences in module scaling relationships among cays were tested by statistically comparing equality of slopes of these allometric regressions (Sokal & Rohlf 1995). There were no initial among-cay differences in any of the measured sapling size parameters. Only three saplings died during the study period: one at Wee Wee Cay, and two at Norvall Cay.

Results

GROWTH ANALYSIS AND ESTIMATES OF PRIMARY PRODUCTIVITY

Stem and root length (Fig. 2a), and numbers of new shoots (Fig. 2b) and leaves (Fig. 2c) increased exponentially over time (univariate tests in Table 1). Production rates of new stem and root length, and new shoot meristems and leaves, differed significantly among the three cays (Fig. 2, multivariate tests in Table 1). Wee Wee Cay saplings grew significantly faster in all parameters measured than Norvall Cay saplings, which in turn grew significantly more rapidly than Spruce Cay saplings (Fig. 2). As with shoots and leaves, the rate of production of new roots was highest at Wee Wee Cay, intermediate at Norvall Cay, and slowest at Spruce Cay (Fig. 2d, Table 1).

Leaf production rates were similar among the three cays, although the winter 1992 branch cohort marked at Wee Wee Cay produced twice as many leaves per shoot after $2\frac{1}{2}$ years than branches at the other two cays. With one exception (winter 1992 leaf cohort at Spruce Cay; see below) leaf survivorship was identical both among cays and among leaf cohorts (Fig. 3; $P > 0.5$, log-rank test for comparison among sur-

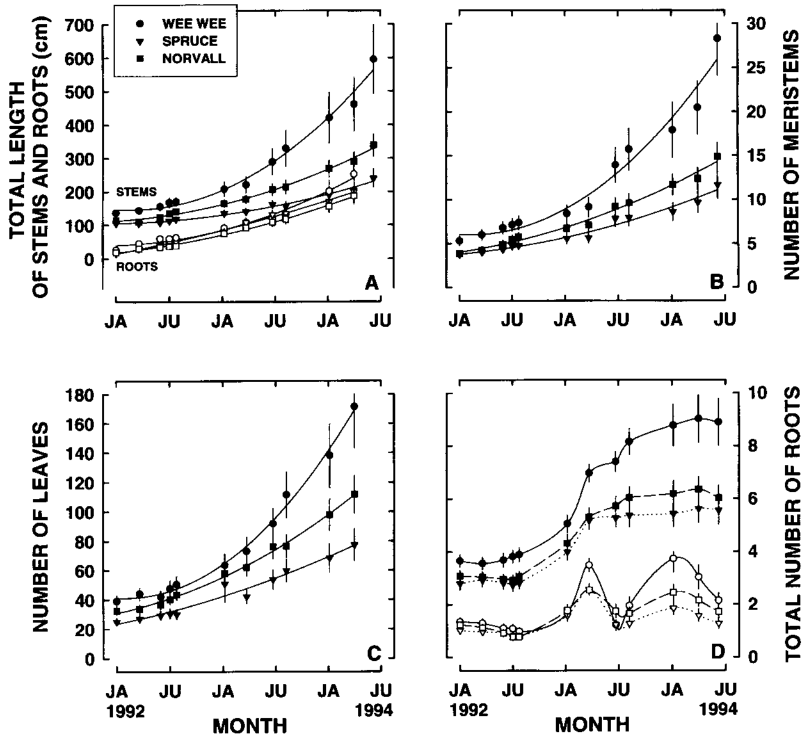

Fig. 2 Growth of stems (solid symbols) and roots (open symbols) (A); increases in number of shoot meristems (B); and leaves (C); and changes in numbers of new (open symbols) and cumulative number of aerial roots (solid symbols) (D) of saplings at the three cays. Lateral roots emerging and grounding between censuses were never counted in the hanging root pool. Values shown are means ± 1 standard error of the mean. Lines in A, B, and C are fitted by nonlinear regression, whilst lines in D are fitted spline curves. See text and Table 1 for statistics.

vivorship curves [Fox 1993]). Average life-span of an individual leaf, computed as mean time to 50% survivorship of a cohort, was 270 days (Fig. 3).

Analysis of scaling relationships (*sensu* Niklas 1994) between standing number or length of modules (shoot meristems, leaves, hanging roots, shoot length, and root length) allowed us to determine if differences in growth of particular modules observed among cays (Fig. 2) resulted from different relative allocation to module numbers or lengths, or simply from differences in overall plant size. Comparisons among slopes indicated no differences among cays in three shoot architectural relationships: stem length – meristem number; leaf number – meristem number; and leaf number – stem length (Table 2). Individual shoots had similar maximal lengths; that is, they showed apparent deterministic growth. Therefore, we concluded that differences among cays in shoot length, and meristem and leaf production illustrated in Fig. 2, resulted simply from differences in overall plant size (total numbers of shoots produced), not allometric differences in shoot module production.

Nor were there any among-cay differences in scaling relationships between number of leaves, shoot meristems, or stem length relative to *number* of new roots (Table 2). However, there were significant among-cay differences ($P < 0.05$) in scaling relationships between aerial root *length* relative to number of roots, number of leaves, number of shoots, and stem length (Table 2). Saplings at Spruce Cay produced significantly longer aerial roots per root, leaf, shoot and cm of shoot than did saplings at the other cays (Table 2), and had a significantly greater mean aerial root-length : shoot-length ratio (0.56 ± 0.02) than did saplings at Wee Wee Cay (0.43 ± 0.01), which in turn significantly exceeded root-length : shoot-length ratios at Norvall Cay (0.40 ± 0.01; MS = 8.788, $F_{2,134} = 12.34$, $P < 0.001$, ANOVA).

We observed clear seasonal changes in relative rates of shoot and root production. Relative changes in rates of stem and aerial root elongation (cm cm^{-1} day^{-1}), number of shoot meristems (shoots shoot^{-1} day^{-1}), leaf numbers (leaves leaf^{-1} day^{-1}), and total number of aerial roots (roots root^{-1} day^{-1}) between each sampling date were calculated as $[\ln(S_{t+1}) - \ln(S_t)]/\Delta t$, where S_t is module length or number at time t (Kaufmann 1981). Production rates of shoots, and shoot growth rates showed pronounced peaks in June and July, following peak annual insolation in May of 1992, 1993 and 1994 (Fig. 4). Shoot phenological patterns were identical at all three cays, but the amplitude of peaks in shoot production was highest at Wee Wee cay (Fig. 4). Relative increases in the three shoot growth parameters were correlated significantly with the following month's relative increase in root number (root number : shoot number: $r = 0.72$, $P = 0.019$; root number : number of leaves $r = 0.64$, $P = 0.047$; root number : total stem elongation: $r = 0.65$, $P = 0.043$). Seasonal increases occurred in production both of new hanging roots (open symbols

Table 1 Results of repeated-measures MANOVA [following analytical methods described by von Ende (1993)] on stem and root extension, and production of new shoots, leaves, and roots by saplings at the three cays. For the univariate tests, only the time × cay (within-subjects) results are shown, as the significance of this value indicating that the shapes of the curves differ also implies that their levels differ and they are not flat. For the multivariate tests, only Wilks' λ is presented, as there are no differences in P-values for the other multivariate statistics (Pillai's trace and Hotelling Lawley trace)

Univariate tests Dependent variable	Effect	MS	d.f.	F	P
Shoot length	time × cay	117296.535	22,1397	7.750	<0.001
Root length	time × cay	4116.836	20,1000	0.926	0.554
Shoot meristems	time × cay	239.714	22,1397	8.766	<0.001
Leaves	time × cay	7747.478	20,1270	5.339	<0.001
All roots	time × cay	13.437	22,1397	5.239	<0.001
Hanging roots only	time × cay	4.280	22,1397	3.030	<0.001

Multivariate tests Dependent variable	Effect	Wilks' λ	d.f.	F	P
Shoot length	time × cay	0.351	22,234	2.432	0.001
Root length	time × cay	0.654	20,182	2.150	0.004
Shoot meristems	time × cay	0.460	22,234	2.420	0.001
Leaves	time × cay	0.698	20,236	2.324	0.001
All roots	time × cay	0.698	22,234	2.092	0.004
Hanging roots only	time × cay	0.751	22,232	1.625	0.042

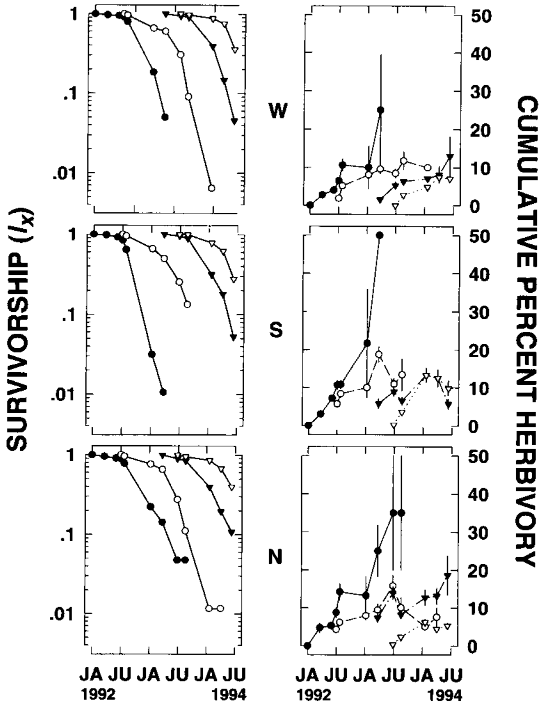

Fig. 3 Percentage survivorship (left; on a $\log_{10}$ scale) and percentage herbivory, measured as cumulative loss of leaf tissue (right; means ± 1 standard error), of the four cohorts of banded leaves at the three cays (W, Wee Wee; S, Spruce; N, Norvall).

in Fig. 2d) and total number of roots (hanging + ground roots: solid symbols in Fig. 2d) approximately one month following shoot flush. Seasonal changes in relative root elongation rate were normally in the opposite direction to seasonal changes in relative shoot elongation rate, due to the ≈1 month lag between shoot flush and root flush (Fig. 4). The ground root pool increased as new aerial roots grew during the rainy season, and as above-ground lateral roots branched adventitiously from existing grounded roots. Whilst relative root elongation rate at Wee Wee Cay and Norvall Cay reached peak levels in 1994 similar to those in 1993, it declined throughout the study period at Spruce Cay (Fig. 4).

Non-destructive leaf, stem, and root length measures were strongly correlated with destructive measures of leaf area and mass, stem mass, and root mass, respectively, (Table 3), and hence were used to calculate leaf weight ratio (*LWR*), specific leaf area (*SLA*), leaf area ratio (*LAR*), relative growth rate in biomass (*RGR*), and net assimilation rate (*NAR*) (Table 4). At Wee Wee Cay, the estimated mean annual increase in above-ground biomass was 35.8 ± 19.1 kg sapling^{-1} (range 0–618.4 kg sapling^{-1}), with an estimated total of 2647 kg ha^{-1} year^{-1} in the 0.5 ha study area. This annual increase in biomass was an order of magnitude greater than that estimated at Spruce Cay, where the mean annual increase in above-ground biomass was 4.7 ± 1.06 kg sapling^{-1} (range 0–25.1 kg sapling^{-1}), with a total of 848 kg ha^{-1} year^{-1} in the 0.25 ha study area. The estimated annual increase in above-ground biomass at Norvall Cay was 7.9 ± 3.07 kg sapling^{-1} (range 0–132.7 kg sapling^{-1}), with a total of 562 kg ha^{-1} year^{-1} in the 0.65 ha study area. Although the increase per sapling at Norvall Cay was nearly twice that of Spruce Cay, the lower sapling density at Norvall Cay resulted in that cay having had the lowest annual increase in above-ground biomass per hectare. At all three cays, the annual increase in above-ground biomass was ≈15% lower in 1993 than it was in 1992 because of the lower total insolation in 1993 (Fig. 4).

Table 2 Pair-wise scaling relationships (based on Model II regressions) between numbers and lengths of aerial root and shoot modules. For each pair, the values given are the slope for the equation (ordinate character) = β_1 (abscissa character), and the percentage of variance (r^2) explained by the regression model. All values for β_1 are significantly different from 0 ($P < 0.001$). When there were no between-cay differences in β_1 (indicated by NS), a common model was fit to data from all sites

Character		Wee Wee			Spruce			Norvall		All Sites	
abscissa	ordinate	β_1	r^2		β_1	r^2		β_1	r^2	β_1	r^2
Number of shoots	total stem length (cm)	21.8	97	NS	16.4	98	NS	20.3	98	20.7	97
Number of leaves	total stem length (cm)	2.8	97	NS	1.4	93	NS	2.2	98	2.4	96
Number of leaves	number of shoots	8.1	98	NS	10.8	93	NS	9.2	98	8.8	97
Number of roots	total stem length (cm)	148.5	76	NS	158.4	74	NS	166.3	76	157	75
Number of roots	number of shoots	6.5	77	NS	8.7	72	NS	7.4	75	7.3	75
Number of roots	number of leaves	52	82	NS	59.8	71	NS	76.6	79	60.8	79
Root length (cm)	total stem length (cm)	1.8	93	*	0.7	88	*	1.1	93	—	-
Root length (cm)	number of shoots	0.08	93	*	0.04	86	*	0.05	90	—	—
Root length (cm)	number of leaves	0.61	94	*	0.37	83	*	0.48	93	—	
Root length (cm)	number of roots	0.01	83	*	0.007	76	*	0.008	79	—	—

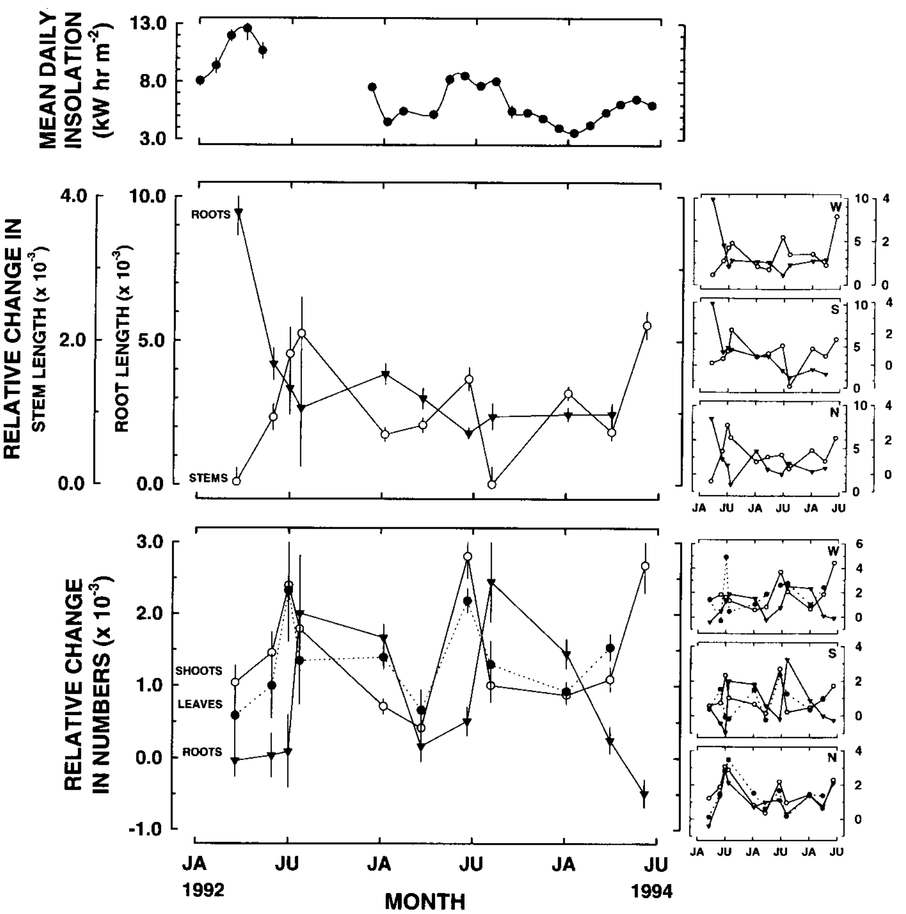

Fig. 4 Seasonal patterns in relative changes in number of shoots, leaves, and roots (lower panel); length of roots and stems (middle panel); and mean daily insolation (upper panel). Data on relative changes (means ± 1 standard error of the mean) are shown for all sites pooled (large panels) and for each cay separately (small panels to right). Mean daily insolation data (± 1 standard error of the mean) are from the Carrie Bow Cay weather station, 4 km north-east of Wee Wee Cay.

EFFECTS OF HERBIVORY ON MANGROVE GROWTH

All marked leaves were attacked by folivores (Lepidoptera and grapsid crabs). Folivore attack rates increased rapidly during the first six months of a leaf's life-span, and levelled out thereafter (Fig. 3). Total percentage leaf area lost rarely exceeded 20%, except for leaves in the first marked cohort at Spruce Cay (Fig. 3). There, first-cohort leaves lost a mean of 25% of leaf area within the first year and a mean of 50% three months later, due to an outbreak of the lepidopteran *Phocides pigmalion* Cramer (Hesperiidae),

Table 3 Functions used to relate measurements of module size to parameters needed for standard growth analysis. All regression parameters are significantly different from 0 ($P < 0.0001$)

Measured parameter	Estimated parameter	Function	r^2	N
Leaf length in mm (L_L)	Leaf area in mm^2 (A)	$A = 0.276L_L^2 + 67.26$	0.738	95
Leaf length in mm (L_L)	Leaf dry mass in g (W_L)	$W_L = (3 \times 10^{-7})L_L^3 + 0.177$	0.829	100
Stem length in mm (L_S)	Stem dry mass in g (W_S)	$W_S = (0.003L_S + 0.338)^3$	0.836	66
Aerial root length in mm (L_R)	Root dry mass in g (W_R)	$W_R = (0.007L_R + 0.616)^3$	0.886	18

Table 4 Estimates of leaf weight ratio (*LWR*), specific leaf area (*SLA*), leaf area ratio (*LAR*), annual relative biomass production rate (*RGR*), and annual net assimilation rate (*NAR*) for the saplings at the three cays

Site	*LWR* (g g^{-1})	*SLA* (m^2 g^{-1})	*LAR* (m^2 g^{-1})	*RGR* (g g^{-1} year^{-1})	*NAR* (g m^{-2} year^{-1})
Wee Wee Cay	0.409 ± 0.040	0.008 ± 0.001	0.003 ± 0.001	1.77 ± 0.116	547
Spruce Cay	0.512 ± 0.059	0.008 ± 0.001	0.004 ± 0.001	1.95 ± 0.172	490
Norvall Cay	0.550 ± 0.048	0.007 ± 0.001	0.004 ± 0.001	1.84 ± 0.129	522
All Cays Pooled	0.497 ± 0.030	0.008 ± 0.001	0.004 ± 0.001	1.85 ± 0.080	561

which reached densities of > 7 larvae per sapling in May–June 1993. Survivorship of the first leaf cohort at Spruce Cay declined rapidly during this outbreak, and differed significantly in shape from all the other leaf cohort survivorship curves (Fig. 3; $P = 0.001$, log-rank test). For this first leaf cohort at Spruce Cay, herbivory at sampling date (t) negatively affected leaf survivorship at the next ($t + 1$) sampling date ($r^2 = 0.72$, $P = 0.032$, linear regression). However, herbivory was not correlated with subsequent leaf survivorship of other cohorts at Spruce Cay, or any cohorts at the two other cays ($P > 0.2$, all cases). Amount of leaf tissue lost to insect herbivores did not contribute significantly to between-plant variance in subsequent production of new growing shoot meristems, new leaves, or future stem extension ($P > 0.5$, all cases).

Isopods attacked 190 of 764 (25%) of aerial roots produced, and frequency of isopod attack closely tracked production of new hanging roots (Fig. 5).

Following attack, root relative elongation rate declined by a factor of 5, from 0.0027 ± 0.006 to 0.0005 ± 0.002 cm cm^{-1} day^{-1} ($P = 0.001$, paired t-test), with no significant among-cay differences in this effect. However, isopods did not contribute significantly to measured between-plant variance in subsequent root and shoot production.

SEDIMENTATION AND GROWTH

Depth contour mapping in June 1993 showed that overall substrate elevation in the study areas averaged 43.8 cm below *HHW* at Wee Wee Cay, 55.5 cm below *HHW* at Spruce Cay, and 44.7 cm below *HHW* at Norvall Cay (Fig. 6). Moreover, substrate elevation beneath each sapling was significantly higher than the mean elevation of the four closest sampled reference points (Fig. 6; under saplings at Wee Wee: 41.5 cm; $P = 0.032$; saplings at Spruce: 48.2 cm; $P < 0.001$; Norvall: 39.9 cm; $P = 0.001$; paired t-tests). Thus,

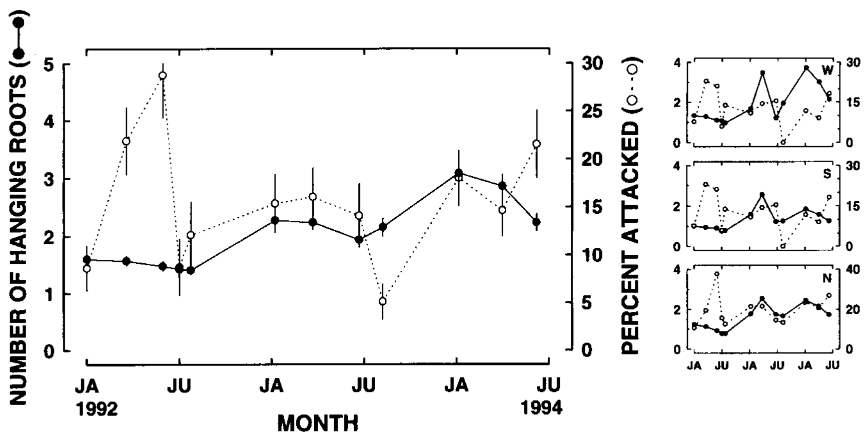

Fig. 5 Seasonal patterns in number of new hanging roots produced and percentage of those roots attacked by isopods (*Phycolimnoria clarkae*). Values shown are means ± 1 standard error of the mean. Data are shown for all sites pooled (large panel) and for each cay separately (small panels to right).

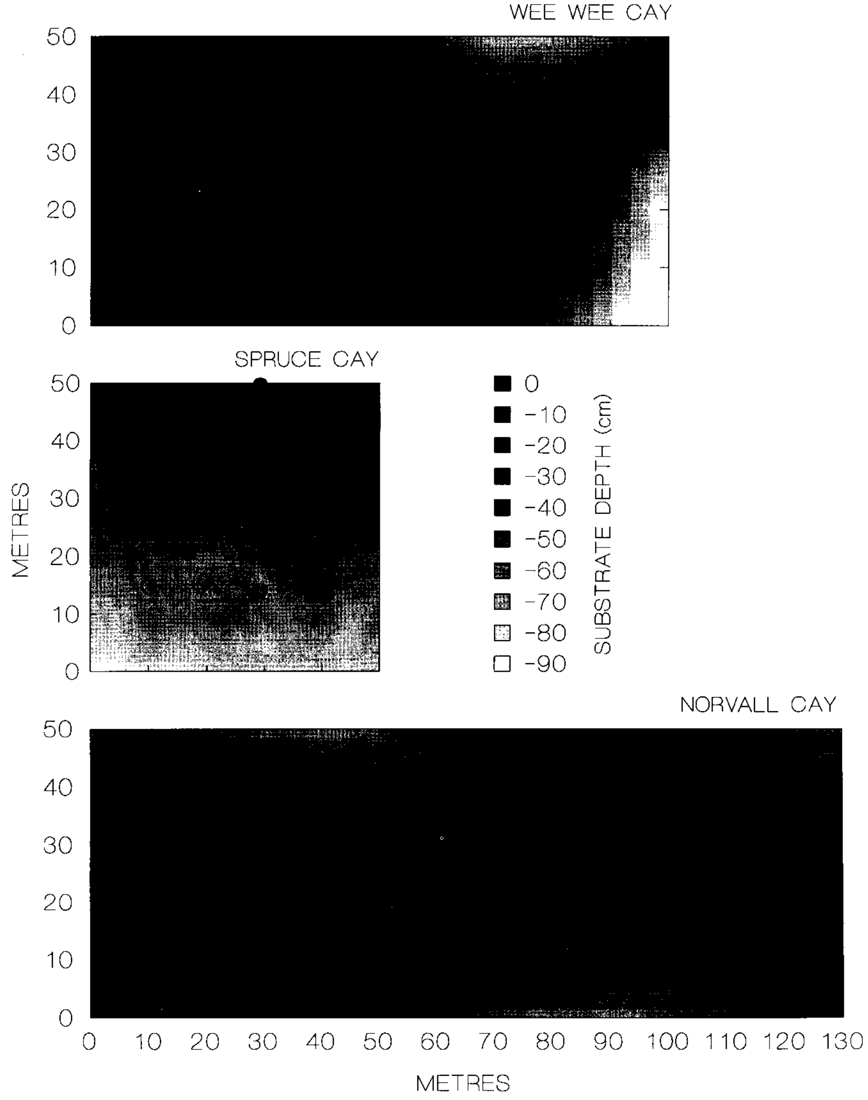

Fig. 6 Contour plots of water depth below *HHW* (depth to substrate) in July 1993 of the three study areas, orientated as in Fig. 1. Depths are shaded in 10-cm intervals, ranging from 90 cm below *HHW* (white) to *HHW* (black). Sapling locations are indicated by circles (size not to scale) and substrate depth directly beneath each sapling are indicated by shading on the same grey-scale as the site maps. Circles shaded darker than adjacent cells indicate saplings that are in relatively shallow sediment, whilst circles shaded lighter indicate saplings that are in relatively deep water.

saplings represented local high points relative to the surrounding substrate. Plants growing in deeper water had longer aerial roots for a given stem length than plants growing in shallower water; root-length : shoot-length ratio correlated positively with substrate elevation beneath a sapling ($r^2 = 0.61$, $P < 0.001$, Model II regression of ln[root : shoot] on elevation).

Between January 1992 and May 1994, sediment beneath saplings accreted at rates of 6.2 ± 0.8 mm year^{-1} at Wee Wee Cay, 3.4 ± 0.5 mm year^{-1} at Spruce Cay, and 5.7 ± 0.9 mm year^{-1} at Norvall Cay. Accretion rates varied significantly among cays and with distance from shore (cay: MS = 0.011, $F_{2,125} = 4.227$, $P = 0.017$; distance: MS = 0.016, $F_{1,125} = 6.247$, $P = 0.014$; ANCOVA). Accretion rate was significantly lower at Spruce Cay ($P < 0.05$, Tukey's post-hoc test for multiple comparisons among means), than at Wee Wee Cay and Norvall Cay, which did not differ ($P = 0.9$). Accretion rate increased significantly with increasing distance from shore at Spruce Cay ($P = 0.041$) and Norvall Cay ($P < 0.001$), reflecting deposition of coral sediments from wave action on the reef crest, but there was no relationship between sediment accretion rate and distance from shore at Wee Wee Cay ($P = 0.182$).

Shoot length produced in a given interval was positively correlated with sedimentation rate in the same interval only at Spruce Cay ($P = 0.040$). Root lengths were significantly shorter in areas of higher sediment accretion only at Wee Wee Cay ($P = 0.041$). Though not significant, similar trends in shoot length : sedimentation rate held at the other cays. The range of variation in sediment accretion rate was small relative to variation in other growth parameters; hence, other correlations between growth and sedimentation were not detected.

Discussion

GROWTH ANALYSIS AND ESTIMATES OF PRIMARY PRODUCTIVITY

Growth analysis is widely used to describe patterns of increase and partitioning of plant biomass (e.g. Evans 1972; Hunt & Lloyd 1987) and module production (e.g. Bazzaz & Harper 1977; McGraw & Garbutt 1990), and to elucidate commonalities in plant growth strategies among plant communities and successional seres (e.g. Grime & Hunt 1975; Reich *et al.* 1992; Ackerly 1995). In combination with demographic studies, plant growth analysis can link ecophysiological processes, such as photosynthesis and transpiration, with ecosystem parameters, such as carbon gain, net primary production and litter production rate (Chapin 1993; Clark 1993; Schmid & Bazzaz 1994). However, mangroves are absent from even the most comprehensive reviews of successional processes in tropical forests (Bazzaz & Pickett 1980; Reich *et al.* 1992; Ackerly 1995). Data on demography, growth and postdisturbance dynamics of mangroves, are rare (Snedaker *et al.* 1992; Ellison & Farnsworth 1993; Smith *et al.* 1994; Clarke 1995), but these data are needed to permit accurate scaling of individual-level processes up to models of ecosystem dynamics.

Our data indicate that different populations of *R. mangle* saplings exhibit constant allometric scaling relationships (*sensu* Niklas 1994) across locations between standing numbers of modules, such as leaf pairs per cm of shoot, shoot length per shoot, leaves per shoot, leaves per number of aerial roots, and number of shoots per number of aerial roots (Fig. 2, Table 2). Root length does vary plastically among cays, with possible implications for mangrove responses to different sedimentation regimes (Table 2). Overall, the relatively tight conformity of *R. mangle* to its 'standard' growth form in this carbonate platform setting enables us to calculate biomass gain parameters reliably from simple nondestructive *in situ* measurements (Tables 3 and 4).

Seasonal variation in insolation is correlated with seasonal patterns in module production and module relative growth rates (Fig. 4). Annual late-spring peaks in insolation consistently preceded subsequent month's peaks in shoot and leaf production (Fig. 4). Similar correlations have been observed for a wide range of tropical trees in many forest types (Wright & van Schaik 1994). In contrast, mangrove leaf and shoot production in monsoonal climates typically exhibits two to three annual peaks coinciding with rains that reduce soil salinity (Christensen & Wium-Andersen 1977; Wium-Andersen & Christensen 1978; Wium-Andersen 1981; Duke *et al.* 1984; Woodroffe *et al.* 1988). However, for trees growing in carbonate settings where annual variation in soil salinity is low, the single annual peak normally occurs at dry-season onset (Gill & Tomlinson 1971b; Leach & Burgin 1985; Duke 1990; this study). Our data for saplings, together with data from *R. mangle* seedlings (Farnsworth & Ellison 1996), confirm the generality of this phenological pattern throughout ontogeny.

Estimates of biomass allocation by saplings based on static samples (e.g. Kohyama 1987; Turner *et al.* 1995) may be imprecise because of temporal lags in production and turnover of root and shoot modules (Fig. 4). New leaf production and old leaf abscission, stem production, and root production (Fig. 4) do not occur simultaneously. Comparative studies of sapling allometry must account for temporal *and* spatial variation in module growth and production (Fig. 4; see also Alvarez-Buylla & Martínez-Ramos 1992; King 1994). Hence, we have developed *annual* estimates for above-ground biomass gain, that incorporate seasonal and among-cay variation in phenology (Table 4).

These saplings, growing on accreting edges of cays in full sun, exhibit exponential growth traits typical of functional 'pioneers' (*sensu* Swaine & Whitmore 1988). Yet, annual productivity varies among cays by nearly an order of magnitude, a much greater degree of variability than the ≈15% change observed between years due to differences in insolation. We conclude, therefore, that scaling relations between growth and whole system productivity appear to be mediated by cay-specific differences in sedimentation regimes.

Our estimates of *LAR*, *RGR* and *NAR* (Table 4) are very low relative to rainforest pioneer species such as *Cecropia obtusifolia* Bertol. (Cecropiaceae) and *Ochroma lagopus* Sw. (Bombacaceae) (reviewed by Ackerly 1995), although the vast majority of other growth analyses have been performed with seedlings, not saplings. This result is unexpected, given the relatively high maximum photosynthetic rates observed for both first-pair young leaves ($13.3 \pm 1.98\,\mu$mol CO$_2$ m^{-2} s^{-1}) and third-pair old leaves ($10.9 \pm 0.78\,\mu$mol CO$_2$ m^{-2} s^{-1}; Farnsworth & Ellison 1996). Photosynthetic rates of these saplings are nearly double those reported for fringing and scrub adult *R. mangle* trees in Florida (Lin & Sternberg 1992), but comparable to photosynthetic rates of *Bruguiera* spp. in Australia (Cheeseman *et al.* 1991). Neither of these studies were conducted in carbonate platform settings, however. The estimates of annual increases in standing biomass used to derive our estimates of *RGR* and *NAR* (Table 4) are comparable to those of stands of similar stature elsewhere in the world, even though no such study has been conducted in autochthonous carbonate environments (Saenger & Snedaker 1993).

Our data suggest that *R. mangle* requires two to four times more photosynthate per unit of growth than any previously studied tropical nonmangrove species. Thus, productivity and potential litter export to adjacent systems is lower than measures of photosynthetic rate alone would suggest. The low *LAR*, *RGR* and *NAR* of mangroves relative to upland pioneer species could result from between-habitat differences in leaf life-span, water-use efficiency, and root production. Our leaf life-span estimates are longer than those for the majority of tropical trees (Reich *et al.* 1992). Whilst our estimate of leaf longevity in these *R. mangle* saplings (Fig. 4) accord well with data on *R. mangle* trees growing in southern Florida (Gill & Tomlinson 1971b), 9 months is lower than figures derived for several other mangrove species (Table 5). For their observed average life-span, *R. mangle* leaves had a higher photosynthetic rate (by a factor of 1.3), but saplings showed lower SLA, *LAR*, *RGR* and shoot growth rate (by factors of 1.3, 1.2, 1.75 and 2.15, respectively) than were predicted by Reich *et al.*'s (1992) allometric relationships derived for other tropical trees (a study that excluded mangroves).

Conservative water use in high salinity (Ball 1986, 1988; Lin & Sternberg 1992; Ball & Passioura 1994), production of defensive tannins (de Lacerda *et al.* 1986; Jayasekera 1991), and increased leaf thickness (Feller 1995) extract maintenance 'costs' that reduce *RGR* and *NAR*, and that are potentially reflected in increased leaf life-span and decreased growth rate (Reich *et al.* 1992). Salinity effects on total respiration costs in obligate halophytes are often regarded as small (McCree 1986; Ball & Munns 1992), but could not be quantified directly in this study, and warrant *in situ* measurements.

We could not address below-ground production in this study. In other geomorphological settings, below-ground biomass of *R mangle* averages 38% of total plant biomass (Golley *et al.* 1962 for fringing mature trees; Ellison & Farnsworth 1993 for basin seedlings). Snedaker (1995) reported that below-ground biomass of mature mangrove trees averages 46.5% (6 species in 5 locations). Komiyama *et al.* (1987) found that mangrove forests have 2–10 times more standing below-ground biomass than either tropical or temperate forests. Low above-ground NPP of *R. mangle* may simply reflect relatively high below-ground NPP. Additional comparative data are needed to address this hypothesis, and to improve models of carbon flux in mangrove ecosystems that, to date, do not include below-ground production (Alongi *et al.* 1992).

EFFECTS OF HERBIVORY ON MANGROVE GROWTH

Herbivores had large effects on module growth and turnover rate, but did not affect overall sapling growth. Insect herbivores affected survivorship of leaves (Fig. 3) by accelerating abscission. Similarly, root-boring isopods closely tracked root production (Fig. 5) and reduced root growth rate by over five-fold. During the outbreak of *Phocides pigmalion* at Spruce Cay, larval densities exceeded by four-fold those observed in nutrient-enriched sites in Florida (Onuf *et al.* 1977), and many saplings lost over 50% of their standing leaf tissue. Herbivore densities also

Table 5 Estimates of mangrove leaf life-span (in months) from around the world. Nomenclature follows Tomlinson (1986)

Species	Location	Life-span	Source
Avicenniaceae			
Avicennia marina (Forsk.) Vierh.	Thailand	13	Wium-Andersen & Christensen (1978)
Avicennia marina (Forsk.) Vierh.	Australia	13	Duke (1990)
Avicennia marina (Forsk.) Vierh.	Australia	15	Clarke (1994)
Combretaceae			
Lumnitzera littorea (Jacq.) Voigt.	Thailand	9	Wium-Andersen & Christensen (1978)
Myrsinaceae			
Aegiceras corniculatum (L.) Blanco	Australia	>24	Clarke (1994)
Rhizophoraceae			
Bruguiera cylindrica (L.) Bl.	Thailand	13	Wium-Andersen & Christensen (1978)
Bruguiera gymnorrhiza (L.) Lamk.	Australia	27	Duke *et al.* (1984)
Ceriops tagal (Perr.) C.B. Rob.	Thailand	24	Wium-Andersen & Christensen (1978)
Ceriops tagal (Perr.) C.B. Rob.	Australia	42	Duke *et al.* (1984)
Kandelia kandel (L.) Druce	Hong Kong	9–14	Lee (1991)
Rhizophora apiculata Bl.	Thailand	17–18	Christensen & Wium-Andersen (1977)
Rhizophora apiculata Bl.	Australia	22	Duke *et al.* (1984)
Rhizophora × lamarckii Montr.	Australia	27	Duke *et al.* (1984)
Rhizophora mangle L.	Florida	6–12	Gill & Tomlinson (1971b)
Rhizophora mangle L.	Belize	9	this study
Rhizophora mucronata Lamk.	Thailand	11	Wium-Andersen (1981)
Rhizophora stylosa Griff.	Australia	19	Duke *et al.* (1984)
Rubiaceae			
Scyphiphora hydrophyllacea Gaertn.f.	Thailand	10	Wium-Andersen (1981)

increased at the other cays during this time, and were associated with slightly truncated survivorship of leaf cohorts at these sites (Fig. 3).

Normal levels of insect herbivory resulted in loss of ≈ 10% of standing leaf area, comparable to the amount lost by both seedlings and mature trees at other sites in Belize (Farnsworth & Ellison 1991). Since leaves alone account for at least 40% of above-ground biomass (Table 4), herbivores may reduce the amount of above-ground net primary production (*ANPP*) available to detritus-based food webs in mangrove and adjacent ecosystems by ≈5% (cf. Lee 1991). However, despite their substantial impacts on specific modules, neither folivores nor isopods explained significant amounts of variation in growth or production of other modules, much less of the whole plant. This result contrasts markedly with negative effects of herbivores on *R. mangle* seedling growth (Ellison & Farnsworth 1993), and sapling growth in nutrient-limited conditions (Feller 1995), although Clarke (1995) found herbivory of little consequence to growth or mortality of *Avicennia marina* saplings in South Australia. On oligotrophic carbonate platforms, disturbance, sea level, wave action, and sedimentation rates may be more significant determinants of sapling performance.

SEDIMENTATION AND GROWTH

Our data indicate that sediment is accreting beneath mangrove saplings on these three cays at 3–6 mm year^{-1}, rates comparable to recent estimates for fringing mangroves at Terminos Lagoon, Mexico developed from measurements of ^{210}Pb and ^{137}Cs decay rates (Lynch *et al.* 1989). Thom (1967, 1982) pointed out that local geomorphology and tidal energetics control the relative amount of sediment trapping by mangroves. On Belizean mangrove cays, sediment accretion is most likely due to trapping by mangrove prop roots of carbonate silts derived from the fringing reefs surrounding each of the cays (cf. Davis 1940), rather than from mangrove peat production, which normally occurs higher in the intertidal zone (Ellison 1993; Parkinson *et al.* 1994).

Biological impacts of sediment accretion on mangroves have not been studied in any geomorphological setting. Over the course of this study, the only environmental factor we examined that varied significantly among cays was sedimentation regime. Therefore, we hypothesize that significant differences in sapling growth and allometry may be attributable to local differences in accretion dynamics. Site-specific differences in all growth parameters (Fig. 2) and the slopes of root : shoot ratios (Table 2) are highly correlated with local differences in water depth and sedimentation. Saplings growing in deeper water at Spruce Cay have longer aerial roots for a given amount of total shoot length, and exhibited significantly lower meristem production and elongation rates than saplings experiencing higher accretion rates. This result parallels increases in fine-root : shoot biomass allocation patterns and growth rates observed in field-grown seedlings transplanted into deeper water along a tidal gradient (Ellison & Farnsworth 1993), and in seedlings grown under high levels of artificial flooding (Farnsworth *et al.* 1995). Clarke & Allaway (1993) similarly found that soil disturbance promoted seedling growth, but mechanisms by which sedimentation regime influence mangrove growth are unknown.

These correlative data suggest that *in situ* measurements and experiments examining responses of mangroves to flooding and sedimentation are needed to augment correlative peat core analyses (Maul & Martin 1993; Snedaker 1995), in order to develop prognoses for mangrove performance under global climate change. These studies are particularly critical for carbonate systems that do not receive allochthonous riverine inputs and are especially sensitive to transgressions (Ellison & Stoddart 1991; Parkinson *et al.* 1994). Mangrove saplings represent local high points relative to the substrate around them (Fig. 6), and passive trapping of sediment by mangrove roots may ameliorate perceived sea level change only if sedimentation and concomitant root and shoot growth consistently keep pace. We emphasize that we could not measure local changes in sea level during our study. Sedimentation rates at Spruce Cay are significantly lower than increases in sea level observed between 1940 and 1970 (Aubrey *et al.* 1988), whilst sedimentation rates at Wee Wee and Norvall Cays are comparable to historic trends. If depressed sapling growth at that cay is indicative of growth expected under predicted rates of sea level rise (Granger 1991; Wigley & Raper 1992), persistence of mangroves on comparable carbonate cays is unlikely.

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