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Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest

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Abstract. Mangrove forests are characterized by distinctive tree-height gradients that reflect complex spatial, within-stand differences in environmental factors, including nutrient dynamics, salinity, and tidal inundation, across narrow gradients. To determine patterns of nutrient limitation and the effects of nutrient availability on plant growth and within-stand nutrient dynamics, we used a factorial experiment with three nutrient treatment levels (control, N, P) and three zones along a tree-height gradient (fringe, transition, dwarf) on offshore islands in Belize. Transects were laid out perpendicular to the shoreline across a mangrove forest from a fringe stand along the seaward edge, through a stand of intermediate height, into a dwarf stand in the interior of the island. At three sites, three trees were fertilized per zone for 2 yr. Although there was spatial variability in response, growth by *R. mangle* was generally nitrogen (N) -limited in the fringe zone; phosphorus (P) -limited in the dwarf zone; and, N- and/or P-limited in the transition zone. Phosphorus-resorption efficiency decreased in all three zones, and N-resorption efficiency increased in the dwarf zone in response to P enrichment. The addition of N had no effect on either P or N resorption efficiencies. Belowground decomposition was increased by P enrichment in all zones, whereas N enrichment had no effect. This study demonstrated that essential nutrients are not uniformly distributed within mangrove ecosystems; that soil fertility can switch from conditions of N to P limitation across narrow ecotonal gradients; and, that not all ecological processes respond similarly to, or are limited by, the same nutrient.

Introduction

The spatial extent of tropical and subtropical mangrove ecosystems is small compared with other tropical forests (Lugo et al. 1990). However, the ecological role of these forested wetlands is magnified relative to their area by their position at the ecotone between terrestrial and marine systems. Mangrove forests support adjacent marine ecosystems, stabilize shorelines, and protect inshore areas (e.g., Odum and Heald (1975)), yet little is known about the intra-wetland processes that regulate those interactions.

Tree stature and productivity vary dramatically among and even within mangrove forests. Mature trees in old growth mangrove forests in the Caribbean range in height from 45 m or more in riverine systems and bird rookeries to $\leqslant 1.5$ m in vast dwarf stands behind the coastal fringe (Golley et al. 1962; Lugo and Snedaker 1974; Lugo 1997). Dramatic gradients in tree height and productivity also form abruptly within mangrove forests (Cintrón et al. 1985; Woodroffe 1995). Primary production, tree stature, and growth rates in these forests have been correlated with many environmental variables, including latitude, salinity, nutrient availability, flooding frequency, oxidation-reduction status of soil, sulfide concentrations, surface hydrology, and tidal force (MacNae 1968; Lugo and Snedaker 1974; Onuf et al. 1977; Pool et al. 1977; Boto and Wellington 1983; Cintrón et al. 1985; Lugo 1990; Jiménez and Sauter 1991; Clough et al. 1982; McKee (1993, 1995)).

In contrast with the temperate zone where coastal ecosystems have been shown experimentally to be nitrogen (N) limited (e.g., Valiela and Teal (1979)), the few tropical and subtropical mangrove wetlands that have been studied appear to be primarily phosphorus (P) limited (Boto and Wellington 1983; Feller 1995; Feller et al. 1999). Phosphorus deficiency has been shown to be a major factor limiting plant growth in dwarf mangrove forests (Feller 1995). On offshore mangrove islands in Belize, fertilization with P produced vigorous growth responses by dwarf trees and caused substantial and complex changes to within-stand and within-plant nutrient dynamics, including a distinct decrease in P-use efficiency and increase in N-use efficiency (Feller et al. 1999). However, McKee (1993) found that porewater nutrients on these Belizean islands were not uniformly distributed across narrow ecotonal gradients from dwarf to taller, fringe mangrove zones. She found that high N:P ratios in the dwarf zone were indeed indicative of P limitation, but that relatively low N:P ratios in the fringe pointed more to N limitation. A comparable pattern of N versus P limitation across an Australian mangrove forest was reported by Boto and Wellington (1983). This pattern suggests complex spatial, within-stand differences in nutrient dynamics across narrow ecotonal gradients in these coastal wetlands. In this study, our goals were to determine the pattern of nutrient limitation across a mangrove forest and to discover how enrichment with N and P affects a suite of ecological processes along a tree-height gradient extending from the mangrove-sea ecotone into the hinterland. We test three hypotheses:

1. Nutrient availability is not uniform within mangrove forests and can switch from N to P limitation across narrow environmental gradients (Boto and Wellington 1983; McKee 1993). From a previous fertilization experiment (Feller 1995) and analysis of porewater (McKee 1993), we predict that plant growth is P limited in the interior of the forest and N limited along the seaward fringe.
2. As the availability of a limiting nutrient increases, the mechanisms used by plants to recycle and conserve that nutrient become less efficient (Loveless 1961; Small 1972; Stachurski and Zimka 1975; Tilton 1977; Chabot and Hicks 1982; Shaver and Melillo 1984; Vitousek 1984; Schlesinger et al. 1989; Escudero et al. 1992). This hypothesis predicts that under N-limiting conditions, N will be tightly conserved via efficient internal nutrient cycling mechanisms. Similarly,

under P-limiting conditions, P will be more efficiently and tightly conserved.

3. Belowground decomposition increases with increased availability of a limiting nutrient in the substrate, and leaf litter decomposition is controlled by tissue quality (Aber and Melillo 1982; Fell and Master 1984; Melillo et al. 1982; Shaver and Melillo 1984; Twilley 1988). Based on this hypothesis, decomposition will depend on the pattern of nutrient limitation, and we predict the response to enrichment will vary among the zones along the tree-height gradient.

Materials and methods

Study site

This study was conducted at Twin Cays, a peat-based, 92-ha archipelago of intertidal mangrove islands in a carbonate setting, just inside the crest of the barrier reef of central Belize, 12 km off shore (16°50′ N, 88°06′ W). These islands receive no terrigenous inputs of freshwater or sediments. Twin Cays developed approximately 7000 yr B.P. on a limestone base formed by a Pleistocene patch reef (I.A. Macintyre, personal communication). Based on corings, mangrove islands in this part of the Belizean barrier reef have an underlying peat deposit $\sim$7–10 m thick and have been mangrove communities throughout the Holocene (Macintyre et al. 1995). Since 1980, this group of islands has been the primary study site for the Smithsonian Institution's National Museum of Natural History Field Station on nearby Carrie Bow Cay (Rützler and Feller (1988, 1996, 1999)).

Several studies provide detailed descriptions of the vegetation, forest structure, geomorphology, geochemistry, and hydrology of Twin Cays and vicinity (e.g., Wright et al. (1991) and McKee (1993), Feller (1995), Feller and Mathis (1997), Feller et al. (1999), Koltes et al. (1998), Woodroffe (1995)). The vascular vegetation at Twin Cays is dominated by *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* L. (black mangrove), and *Laguncularia racemosa* (L.) Graetn.f. (white mangrove). The forest structure is characterized by a tree-height gradient that includes a narrow seaward fringe of pure stands of uniformly tall (5–6 m) *R. mangle* trees, varying in width from 5–20 m wide, which occurs in the low intertidal around the periphery of the islands. Tree density and basal area in the fringe are variable, with values ranging from 4,500 to 6,400 stems/ha and 19.9 m^2/ha to 78.6 m^2/ha, respectively (Woodroffe 1995; Feller and Mathis 1997). Tree height decreases rapidly to landward through a more heterogeneous transition zone (2–4 m tall) that varies in width from 5–30 m wide. This zone represents the highest elevation along the intertidal gradient. Although *R. mangle* is also common in the transition zone, *A. germinans* and *L. racemosa* are intermixed. Estimates for tree density and basal area in the transition zone range from 4,800 to 6,800 stems/ha and 13.0 to 20.9 m^2/ha, respectively (Woodroffe 1995). Further inland, the interior portions of Twin Cays are dominated by pure stands of low stature ($\leqslant$1.5 m) *R. mangle* trees, hereafter referred to as the dwarf zone. Tree density in this zone is

extremely variable, with values ranging from 17,000 to 40,000 stems/ha (Woodroffe 1995; Feller and Mathis 1997). However, basal area, which ranges from 7.5 to 12.9 m^2/ha, is much lower in the dwarf zone than in the fringe or transition zone.

Experimental design

In January 1995, trees for experimental manipulation were chosen at three sites on two of the largest islands of the Twin Cays archipelago. These sites were selected along the main channels in areas with uninterrupted shoreline, similar forest structure and hydrology, and enough space to accommodate a replicate of the experimental array. Three transects, 25- to 50-m long and 10-m apart, were oriented perpendicular to the shoreline at each site. The 10-m intervals were left between transects as buffer zones against possible lateral migration of fertilizer treatments. Transects were subdivided into fringe, transition, and dwarf zones based on tree height. The fringe zone was composed of tall *R. mangle* trees (5–6 m), and was flooded and drained >700 times per yr. The transition zone, which was dominated mainly by a *R. mangle* thicket (2–4 m), was flooded only during high spring tides and storms (<50 times per yr). The dwarf zone was composed exclusively of *R. mangle* ($\leqslant$ 1.5 m) and was perennially flooded in shallow ponds except at unusually low tides.

Our experimental design was a 3 × 3 factorial (nutrient × zone) analysis of variance (ANOVA) that involved three levels of the nutrient treatment and three levels of zone, blocked at the three sites (1, 2, 3). In each zone, three replicate trees were selected. These trees were approximately 4 m apart and were independent of each other. The factors were nutrients (control, N, and P) and zone (fringe, transition, dwarf). Eighty-one trees, nine per transect and 27 per site, were selected to accommodate the experimental treatment (i.e., 3 nutrients × 3 zones × 3 replicate trees per zone × 3 sites = 81). To minimize the disturbance to the system, we fertilized individual trees rather than plots, which would require heavier and more extensive applications of fertilizers. This method of direct fertilizer application to the root zone of our target trees was used because our study site is flooded; consequently, fertilizer broadcasted on the surface would be washed away.

The three nutrient treatment levels in 300-g doses were N fertilizer as urea (NH_4, 45:0:0), P fertilizer as triple superphosphate (P_2O_5, 0:45:0), and control (no nutrient enrichment), as described in Feller (1995). Within each site, the nutrient treatment level for each transect was determined randomly. Granular urea and triple superphosphate were enclosed in dialysis tubing (Spectrapor Membrane Tubing, 50-mm diameter, 6000–8000 molecular weight cutoff) in 150-g doses. To deliver the fertilizer, we cored two holes (7 cm diameter × 30 cm deep), into the peat substrate on opposing sides of each tree. A dose (150 g) of fertilizer in dialysis tubing was placed in each of two holes, cored into the peat substrate on opposing sides of a tree beneath the outermost margin of the canopy and approximately 30 cm from a grounded prop root from the target tree. Because of the nature of mangrove forests where the tangle of prop roots in a given area may come from a number of trees in the surrounding area, we carefully identified the root system supporting

each of these trees. Each hole was sealed with a peat plug. For control trees, holes were cored and sealed but no fertilizer was added. Trees were fertilized twice a year at 6-mo intervals from January 1995 through January 1997. These methods were based on previous studies, in which they resulted in dramatic growth increases in response to addition of the limiting nutrient and created small patches of fertilized trees immediately around the target tree (Feller 1995; Feller et al. 1999).

Growth responses and nutrient dynamics

Based on previous experimental studies in mangrove forests, fine-grained measurements of plant growth at the shoot and leaf level are more sensitive bioassays of nutrient limitation than changes in height and dbh (Feller (1995, 1995); Feller et al. 1999). Consequently, to determine plant responses to experimental treatments, we monitored the growth of five, initially unbranched shoots (first order) in sunlit positions in the outer part of the canopy of each tree in this experiment. Individual shoots were labeled with small pieces of aluminum tags. Leaves in the apical position on each shoot were labeled with waterproof ink on their abaxial surfaces to mark the starting point for growth measures. To demarcate growth over a 2 yr period, the apical leaves on each shoot and its subsequently produced lateral shoots were marked at 6-mo intervals at the same time when the trees were refertilized. At the end of the second year, growth was determined for the last 6-mo interval (i.e., July 1996–January 1997). We measured shoot elongation (cm) and the number of new leaves and new shoots per shoot. Branches that became infested by wood-boring insects during the course of the study were omitted from the analysis.

We measured nutrient concentrations in green and senescent leaves and calculated nutrient resorption efficiency and biomass production per unit of nutrient (N and P) invested for each experimental tree. Resorption efficiency was calculated as the percentage of N and P recovered from senescing leaves before leaf fall (Chapin and Van Cleve 1989):

$$100\times\frac{N,\quad\text{or}\quad P(mg{\cdot}cm^{-2})_{\text{green leaves}}-N,\quad\text{or}\quad P(mg{\cdot}cm^{-2})_{\text{senescent leaves}}}{N,\quad\text{or}\quad P(mg{\cdot}cm^{-2})_{\text{green leaves}}}=RE.$$

Biomass production per unit of nutrient was calculated as the inverse of the nutrient concentration in senescent leaves (g biomass/g N or P). Leaf samples for analyses were harvested in January 1997. By that time, all the leaves on the targeted trees had been produced under the influence of the experimental treatment. From a sunlit position in the top of the canopy, we collected fresh, fully mature green leaves (hereafter referred to as green leaves) from a penapical stem position and fully senescent yellow leaves with a well-developed abscission layer (hereafter referred to as senescent leaves) from a basal position on first-order branches. Senescent leaves were taken directly from the trees to eliminate nutrient loss via leaching and leaf loss by tidal flushing, which happen when litter drops to the forest floor in this mangrove wetland. We thus assumed that yellow leaves that could be removed from

a stem with only slight pressure represented the senescent leaf litter. Leaf area was determined for each leaf with a Li-Cor 3000 Portable Area Meter (Li-Cor, Lincoln, NE). Leaf samples were dried at 70 °C in a convection oven and ground in a Wiley Mill to pass through a 40- (0.38 mm-) mesh screen. Concentrations of carbon (C) and N were determined with a Perkin-Elmer 2400 CHN Analyzer at the Smithsonian Environmental Research Center, Edgewater, MD, USA. Concentrations of mineral nutrients were determined using an inductively coupled plasma spectrophotometer (ICP) by Analytical Services, Pennsylvania State University, State College, PA, USA.

Decomposition

To determine the effects of experimental treatments on belowground decomposition, we measured the loss of tensile strength of cotton burial strips embedded into the peat, 0.5 m from a fertilizer insertion point, beneath each of the fertilized *R. mangle* trees in January 1997. This standard technique provides an index of belowground decomposition. It measures the relative activity of decomposers or a "decomposition potential" using a standardized substrate and thereby integrates the effects of external variables (Maltby et al. 1988). As a control, a cotton strip (t0) was inserted into the soil and immediately removed. A second, identical strip was inserted and left in place for 3 wk (t1). We measured the cotton tensile strength (CTS) of 2-cm wide sections from each of the cotton strips at 2–4 cm, 6–8 cm, and 15–17 cm depths. Percent cotton tensile strength loss (%CTSL) was calculated for the t_1 strips relative to the t_0 strips:

$$100 \times \frac{CTS_{t0} - CTS_{t1}}{CTS_{t0}} = \%CTSL$$

During the first 6-mo interval of this experiment (January–August 1995), rates of leaf mass loss were measured at each of the 81 trees to determine the effect of zone and site on litter decomposition. For a leaf-litter source, we collected senescent leaf directly from fringe trees along a 100-m section of a tidal channel at Twin Cays. These leaves were air-dried in the shade for 1 wk. They were then put into a container and shaken to assure homogeneous mix. We placed 7–10 g of this air-dried leaf litter in 1-mm^2 mesh Fiberglas® litter bags, which were then laid flat on the ground and tethered to PVC stakes near the base of each target tree, 90° (approximately 1–2 m) from where either fertilization stake was inserted into the ground. Litterbags were incubated in situ for 180 d. Subsets of senesced leaves were oven-dried for wet-dry biomass conversion and nutrient analyses. All biomass values were expressed on an oven-dry basis. Decomposition rates were calculated for each litterbag as percent dry mass remaining in the bags in July 1995.

Hydro-edaphic measurements

To characterize tidal fluctuations across the tree-height gradient, nine wells (7 cm diameter × 30 cm deep) were cored adjacent to the control transects and parallel with each experimental tree. Water level relative to the soil surface was measured at high and low tides to determine relative depths of inundation and soil flushing.

Measurements of soil and porewater were conducted at each experimental tree approximately 1 m from the bole and a fertilizer insertion point. Soil samples were collected with a piston-type corer for determination of texture, bulk density, and percent organic matter according to standard techniques.

Soil redox potentials at 1 cm and 15 cm depths were measured with bright platinum electrodes equilibrated in situ for 30 min (McKee et al. 1988). Each electrode was checked before use with quinhydrone in pH 4 and 7 buffers (mV reading for quinhydrone is 218 and 40.8, respectively, at 25 °C). The potential of a calomel reference electrode (+244 mV) was added to each value to calculate Eh. Interstitial water was collected from a depth of 15 cm at each tree approximately 1 m from the fertilizer insertion point with a probe attached to a suction device as described in McKee et al. (1988). An aliquot of each water sample was added to an equal volume of an antioxidant buffer and was analyzed for sulfide with a sulfide microelectrode (McKee et al. 1988). Additional aliquots were used to measure pH and salinity. Filtered (0.45 μm filter), frozen samples of interstitial water were returned to the laboratory and analyzed for soluble NH_4-N and PO_4-P (EPA, Environmental Monitoring and Support Laboratory, Office of Research and Development 1983).

Bioavailable N and P were assessed with ion-exchange resin bags (Lajtha 1988). The bags were constructed of nylon mesh material (undyed panty-hose), filled with 4 g of a mixed-bed (H^+/OH^-) exchange resin (16–50 mesh), and conditioned with 1 M NaCl. After rinsing with deionized water, the bags were inserted into the bottom of holes (2 cm diameter × 15 cm depth) in the field and covered with a soil plug. After incubation in situ for 30 d, the bags were retrieved and desorbed with 0.5 M HCl (PO_4^{-3} and NO_3^-) or 1 M KCl (NH_4^+). The extract was analyzed with a Lachat system (QuikChem Automated Ion Analyzer, 8000 Series FIA+; Zellweger Analytical, Lachat Instruments Division, Milwaukee, WI, USA) for NH_4-N, NO_3-N and PO_4-P (EPA, Environmental Monitoring and Support Laboratory, Office of Research and Development 1983). Unincubated resin bags were used as blanks.

Statistical analysis

Statistical analyses were carried out using Systat 8.0 (Wilkinson 1996). We used a 3 × 3 factorial (nutrient × zone) analysis of variance (ANOVA), blocked at three sites, to look for differences in variables based on harvested materials and measurements in this experiment. When an ANOVA found a significant main effect or interaction, we used post hoc hypothesis tests in General Linear Model Pairwise Comparison to test relationships between means. Fisher's Least Significant Difference Test was used to perform multiple pairwise comparisons. To analyze for het-

eroscedasticity, probability plots of all variables and ANOVA residuals were examined. Appropriate transformations were used to stabilize variances.

Results

Plant growth responses

Both nutrient enrichment (control, N, P) and zone along the tree-height gradient (fringe, transition, dwarf) had significant effects on the plant growth variables measured in this study, but the magnitude of responses also varied significantly by the site (Site 1, 2, 3) where the experiment was set up (Table 1). In the fringe, the addition of N had a slight but significant effect on shoot elongation at one site and caused a significant increase in new leaf and shoot production in the fringe at two sites (Figure 1A–1I). In the transition zone at Site 1, both N and P fertilizers caused an increase in leaf and shoot production (Figure 1D–1G). In contrast, in the transition zone at Site 2, only the P fertilizer caused increases in the three growth variables (Figure 1B, 1E, 1H). And, in the transition zone at Site 3, the N fertilizer caused the largest increases in growth (Figure 1C, 1F, 1I). In the dwarf zone at all three sites, the P fertilizer caused significant and consistent growth increases in shoot elongation and leaf and shoot production. At Site 1, the growth responses for the N-fertilized fringe trees and the N- or P-fertilized transition trees were similar. At Sites 2 and 3, growth responses for N- or P-fertilized transition trees were consistently greater than the N-fertilized fringe trees. The effects of nutrient enrichment were also evident at a system level. In the dwarf zone, the shoot-level growth responses to P fertilizer provided obvious markers for measuring the spatial extent of fertilizer influence. In this zone, the areas covered by the canopies of control and N-fertilized trees were 1.2 ± 0.3 m^2 and 1.1 ± 0.3 m^2, respectively, compared to 19.8 ± 4.1 m^2 for P fertilized trees.

Chemical composition of plant tissue

Nutrient enrichment and zone had striking and complex effects on the within-plant dynamics of N and P that varied, in some cases, by site (Table 2). The N concentration of green leaves [N_G] from N-fertilized trees was significantly higher than from control ($F = 16.650$, df = 1, 72, $P < 0.001$) or P-fertilized trees ($F = 9.650$, df = 1, 72, $P < 0.01$; Table 3). Along the control transects, dwarf trees had significantly higher [N_G] than did fringe trees ($F = 6.218$, df = 1, 72, $P = 0.013$), but values for the transition zone were intermediate and did not differ from dwarf or fringe trees (ANOVA, $P > 0.05$). However, there were no significant interactions among nutrient treatment, zone, or site on [N_G].

Both nutrient enrichment and zone had significant effects on the N concentration in senescent leaves [N_S], with significant nutrient (zone and zone (site interactions (Table 2). The [N_S] was significantly higher in N-fertilized trees than in

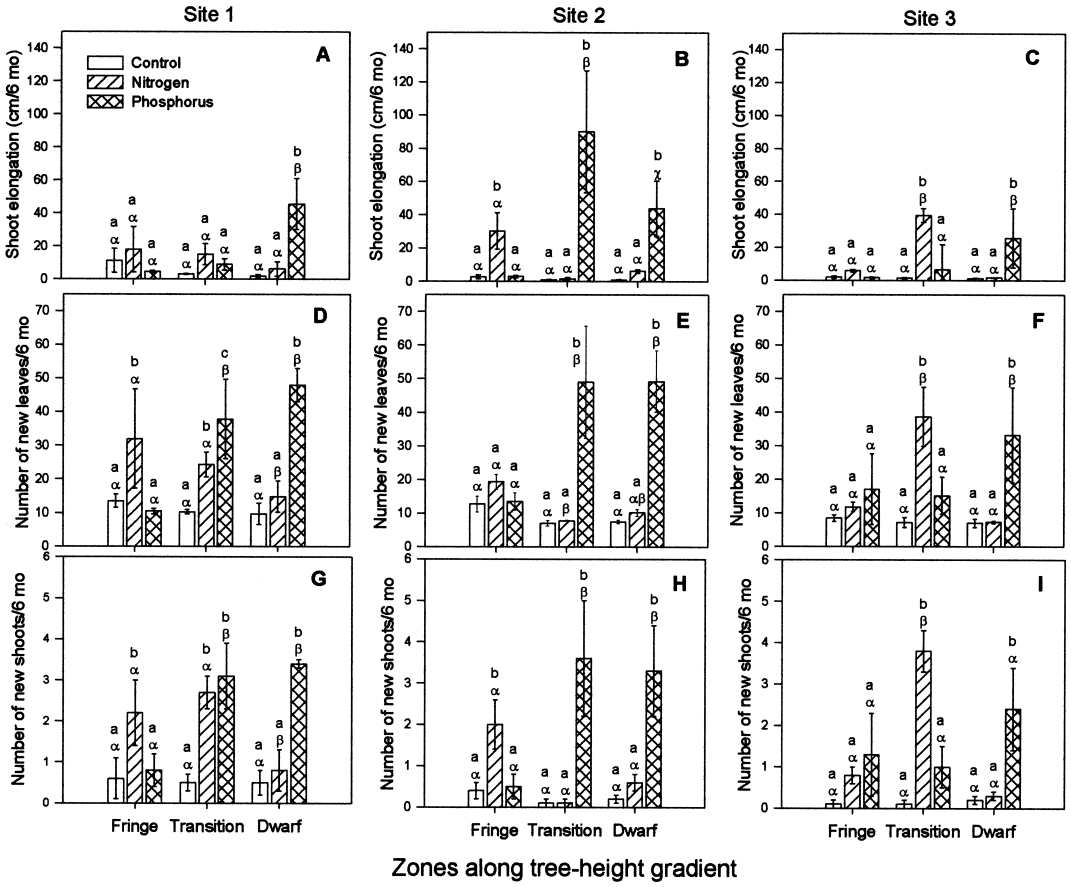

Figure 1. (A–C) New shoot growth, (D–F) number of new leaf pairs, and (G–H) number of new shoots over a 6-mo interval in fertilized *Rhizophora mangle* tree by nutrient enrichment (control, N, P) and by zone along tree-height gradient (fringe, transition, dwarf). Values are means ± 1 SE. Within a zone the same lowercase Latin letter indicates treatment means are not significantly different; among zones the same Greek letter indicates treatment means are not significantly different ($P < 0.05$). $N = 81$ trees (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees).

Table 1. Summary of three-way ANOVAs performed on plant growth responses from fertilized *Rhizophora mangle* trees at Twin Cays, Belize, by Nutrients (control, N, P) and Zone (fringe, transition, dwarf) blocked at 3 Sites over a 6-mo period (August 1996-January 1997). Values are F-ratios and P values. N = 81 (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees). Data were square-root transformed prior to analysis.

		Shoot length (cm/6 mo)		Number of new leaf pairs/6 mo		Number of new shoots/6 mo	
Source	df	*F*-ratio	*P*	*F*-ratio	*P*	*F*-ratio	*P*
Nutrients (Nt)	2	26.257	0.000	35.620	0.000	37.196	0.000
Zone	2	4.924	0.011	6.417	0.003	3.660	0.033
Site	2	1.233	0.300	3.021	0.058	5.463	0.007
Nt × Zone	4	11.104	0.000	11.503	0.000	14.858	0.000
Nt × Site	4	6.082	0.000	4.829	0.002	6.470	0.000
Zone × Site	4	1.041	0.396	0.344	0.847	0.531	0.713
Nt × Zone × Site	8	5.750	0.000	5.589	0.000	4.050	0.001

Table 2. Summary of three-way ANOVAs performed on percent nitrogen (N) and phosphorus (P) concentration in green and senescent leaves from fertilized *Rhizophora mangle* trees by Nutrients % (control, N, P) and Zone (fringe, transition, dwarf) blocked at 3 sites at Twin Cays, Belize. Values are *F*-ratios and P values. N = 81 trees (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees). Data were arcsine square-root transformed prior to analysis.

Source of variation	df	N_{green}	$N_{senescent}$	P_{green}	$P_{senescent}$
Nutrients (Nt)	2	9.439^{***}	11.755^{***}	105.772^{***}	95.476^{***}
Zone	2	3.361^{*}	12.738^{***}	20.260^{***}	0.416^{ns}
Site	2	1.255^{ns}	0.238^{ns}	9.167^{***}	2.121^{ns}
Nt × Zone	4	0.245^{ns}	4.073^{**}	21.676^{***}	3.945^{**}
Nt × Site	4	0.464^{ns}	1.197^{ns}	5.015^{**}	0.838^{ns}
Zone × Site	4	1.724^{ns}	3.289^{*}	2.006^{ns}	1.018^{ns}
Nt × Zone × Site	8	1.369^{ns}	0.559^{ns}	1.835^{ns}	0.631^{ns}

Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant

control ($F = 6.890$, df = 1, $P = 0.011$) or P-fertilized trees ($F = 23.366$, df = 1, $P = 0.000$; Table 4). The $[N_S]$ increased significantly across the tree-height gradient, i.e., dwarf > transition ($F = 4.738$, df = 1, 72, $P = 0.033$); transition > fringe ($F = 5.142$, df = 1, 72, $P = 0.027$). Within the fringe zone, there was little variation in the $[N_S]$ among the three nutrient-treatment levels (Table 3). In the transition zone, the N fertilizer resulted in a significant increase in $[N_S]$. However, within the dwarf zone, the P fertilizer caused a significant decrease in the $[N_S]$ compared to either control or N-fertilized trees. The significant zone (site interaction for $[N_S]$ occurred

Table 3. Percent nitrogen (N) and phosphorus (P) measured in green and senescent leaves in *Rhizophora mangle* from fringe, transition, and dwarf zones in response to nutrient enrichment (control, N, P). Contrasts for significant Nutrient × Zone interactions were calculated using Fisher's LSD post hoc tests. Because there were no three-way interactions, means ± (1 SE) were pooled from the three sites. Within a zone on each row, values with the same superscript letter are not significantly different at $P \leq 0.05$. Nutrient ratios were calculated. N = 81 trees (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees).

Zone:	Fringe			Transition			Dwarf		
Nutrient:	Control	N	P	Control	N	P	Control	N	P
†$\%N_{green}$	0.89	1.05	0.93	0.91	1.09	0.95	0.96	1.25	1.03
	(0.06)	(0.05)	(0.09)	(0.03)	(0.08)	(0.05)	(0.05)	(0.07)	(0.05)
$\%N_{senescent}$	0.28^{a}	0.33^{a}	0.29^{a}	0.32^{a}	0.46^{b}	0.28^{a}	0.49^{a}	0.52^{a}	0.30^{b}
	(0.02)	(0.02)	(0.02)	(0.02)	(0.03)	(0.06)	(0.05)	(0.03)	(0.04)
$\%P_{green}$	0.060^{ab}	0.058^{a}	0.064^{b}	0.052^{a}	0.050^{a}	0.070^{b}	0.038^{a}	0.040^{a}	0.077^{b}
	(0.004)	(0.002)	(0.002)	(0.003)	(0.003)	(0.004)	(0.001)	(0.001)	(0.002)
$\%P_{senescent}$	0.011^{a}	0.010^{a}	0.023^{b}	0.010^{a}	0.009^{a}	0.032^{b}	0.007^{a}	0.007^{a}	0.035^{b}
	(0.003)	(0.003)	(0.003)	(0.003)	(<0.000)	(0.003)	(<0.000)	(<0.000)	(0.010)
$N:P_{green}$	15.3	18.0	14.4	17.8	22.8	14.0	24.0	32.9	13.4
	(1.6)	(0.9)	(1.4)	(0.6)	(2.3)	(1.2)	(1.5)	(2.1)	(0.5)
$C:N_{senescent}$	163.3	130.6	148.7	136.6	99.5	158.4	94.4	86.5	172.6
	(15.9)	(8.2)	(8.0)	(8.8)	(8.5)	(23.7)	(8.9)	(4.8)	(19.2)
$C:P_{senescent}$	4018.5	4394.4	2150.4	4697.4	4939.3	1539.6	6037.0	5887.5	1501.8
	(482.1)	(449.0)	(279.3)	(638.5)	(248.5)	(234.32)	(208.5)	(325.4)	(212.4)

Note: †There was no significant nutrient × zone interaction for percent N in green leaves.

Table 4. Results of two-way ANOVAs performed on nutrient resorption efficiencies for nitrogen (N) and phosphorus (P) from fertilized *Rhizophora mangle* trees (Twin Cays, Belize) by nutrient enrichment (control, N, P), zone (fringe, transition, dwarf), blocked at 3 sites at Twin Cays, Belize. N = 81 trees (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees). Data were arcsine square-root transformed prior to analysis.

		N Resorption Efficiency		P Resorption Efficiency	
Source of variation	df	*F*-ratio	*P*	*F*-ratio	*P*
Nutrients (Nt)	2	3.433	0.040	41.902	0.000
Zone	2	4.233	0.020	3.080	0.055
Site	2	1.799	0.176	0.890	0.417
Nt × Zone	4	2.760	0.038	2.121	0.092
Nt × Site	4	0.794	0.535	0.231	0.920
Zone × Site	4	2.099	0.095	0.580	0.679
Nt × Zone × Site	8	0.441	0.890	0.377	0.928

as a result of slight but significantly lower $[N_S]$ for dwarf trees at Site 1 than at Site 2 ($P = 0.004$).

When $[N_S]$ is expressed as leaf biomass per unit of N (g biomass/g N), it shows that patterns of nutrient-use efficiency for N (NUE_N) were similarly affected by

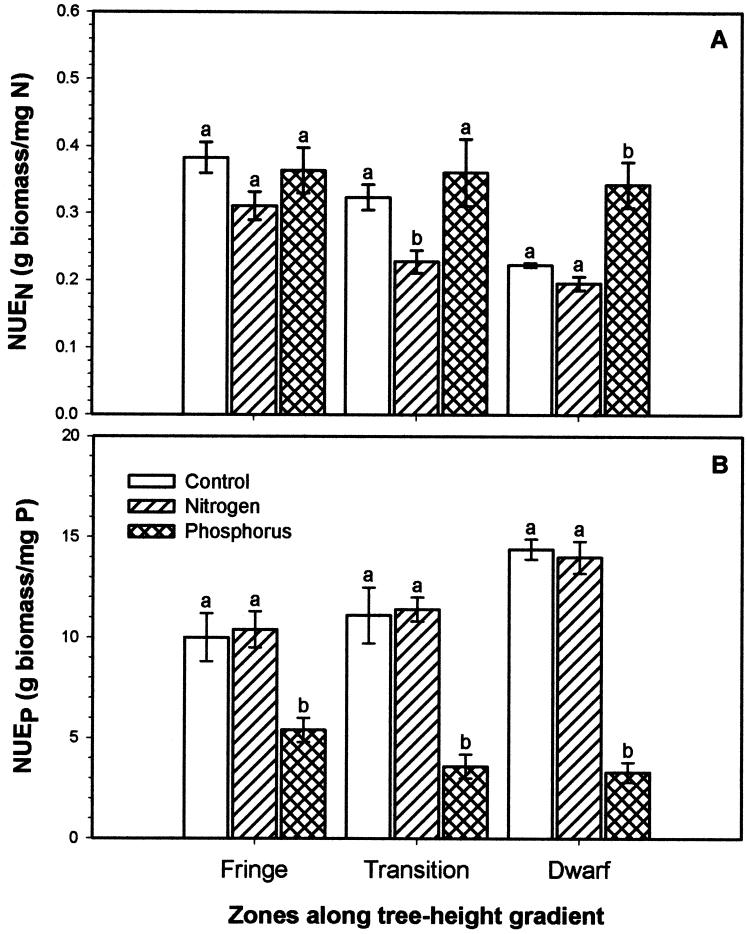

Figure 2. (A) Nitrogen-use efficiency (NUE_N) and (B) phosphorus-use efficiency (NUE_P) in fertilized *Rhizophora mangle*, by nutrient enrichment (control, N, P) and by zone along a tree-height gradient (fringe, transition, dwarf). Values are means ± 1 SE. Bars within a zone with the same lowercase letter above are not significantly different at $P < 0.05$. $N = 81$ trees (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees).

nutrient treatment and zone (Figure 2A). The N fertilizer caused a large decrease in NUE_N in the transition zone, but not in the fringe or dwarf zones. In contrast, the P fertilizer had no effect on NUE_N in either the fringe or transition zones, but caused a very large increase in NUE_N in the dwarf zone.

Nutrient enrichment and zone, but not by site, had significant effects on N-resorption efficiency (calculated as the percent difference between $[N_G]$ and $[N_S]$ on a leaf area basis, i.e., g N/cm^2), with significant nutrient × zone interactions (Figure 3A). Values did not vary among the nutrient-treatment levels within the fringe and transition zones. However, the N-resorption efficiency of control trees was significantly lower in the dwarf zone than in the fringe ($F = 11.834$, df = 1,72, $P =$

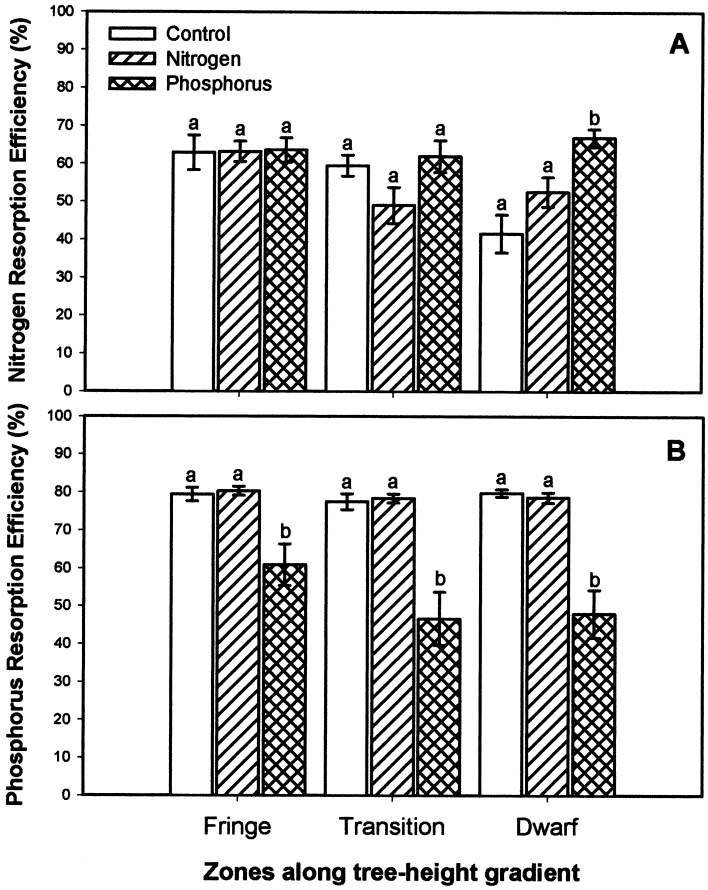

Figure 3. (A) Nitrogen-resorption efficiency and (B) phosphorus-resorption efficiency in fertilized *Rhizophora mangle*, by nutrient enrichment (control, N, P) and by zone along a tree-height gradient (fringe, transition, dwarf). Values are means ± 1 SE. Bars within a zone with the same lowercase letter above are not significantly different at $P < 0.05$. $N = 81$ trees (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees).

0.001) or transition zones ($F = 7.797$, df = 1, 72, $P = 0.007$). Compared to control trees, the P fertilizer caused a 40% increase in N-resorption efficiency in the dwarf zone.

Similarly, nutrient enrichment and zone had significant effects on the P concentration in green leaves [P_G], with significant nutrient ×zone and zone × site interactions (Table 2). Along the control transects, [P_G] varied significantly by zone, i.e., fringe > transition > dwarf (Table 3). Within the fringe zone, P-fertilized trees were not different from controls. However, the P fertilizer caused a 40% to 100% increase in [P_G] in the transition and dwarf zones, respectively.

Nutrient enrichment, but not zone or site, had a significant main effect on the P concentration in senescent leaves [P_G] (Table 2). In all zones, the P-fertilized trees

had two to four times as much [P_G] as control and N-fertilized trees. There was also a significant interaction between nutrient and zone. The [P_G] in the P-fertilized trees was lower in the fringe trees than in the transition or dwarf zones (Table 3). Along the control transects, [P_G] was very low (<0.01%) in all zones.

Patterns for nutrient-use efficiency for P (NUE_P) were similarly affected. In control trees, NUE_P increased across the tree-height gradient, with highest values in the dwarf zone (Figure 2B). The N fertilizer had no effect on NUE_P, but the P fertilizer caused a dramatic decrease in each zone.

Nutrient enrichment and zone had significant effects on P-resorption efficiency that were similar at all sites. Values were uniformly high ($\sim$80%) for control and N-fertilized trees in all zones (Figure 3B). Phosphorus-resorption efficiency decreased significantly in the P-fertilized trees in each zone across the tree-height gradient. The magnitude of the decrease was approximately 20% in the fringe zone compared to almost 40% in the transition and dwarf zones.

Because the N:P ratio of green leaves is considered an important indication of nutrient availiability (Van den Driessche 1974; Ingestad 1979), we calculated the effects that our nutrient treatments and zone had on this index (Table 3). Along the control transects, N:P ratios were lowest in the fringe and increased across the tree-height gradient with the highest values in the dwarf zone. The P fertilizer had no significant effects on these N:P ratios in the fringe and transition zones. However, in the dwarf zone, the P fertilizer caused a dramatic decrease in N:P ratios relative to control or N-fertilized trees. The N fertilizer caused a significant increase in N:P ratios in the transition and dwarf zones, but had no effect in the fringe zone.

Because C:N and C:P ratios of leaf litter are generally considered important indices of the decomposability of leaf litter (e.g., Bryant et al. (1983) and Fell and Master (1984)), we calculated the effects of N and P fertilizers on these variables. Nutrient enrichment, but not zone or site, had significant effects on the C:N ratios of senescent leaves (Table 3). The N fertilizer caused values to decrease significantly relative to control trees in both the fringe and transition zones, but had no effect in the dwarf zone. The P fertilizer had no effect on C:N ratios in the fringe and transition zones. However, the C:N ratios for P-fertilized trees in the dwarf zone were almost double the values calculated for the control and N-fertilized trees.

Decomposition

For belowground decomposition, nutrient enrichment, but not zone or site, had a significant effect (F = 64.840, df = 2, 72, P = 0.000) on the percentage cotton tensile strength loss (%CTSL; Figure 4). CTSL values were not different among the three zones for control and N-fertilized trees. However, the P fertilizer caused a dramatic increase in %CTSL in each zone, which indicated that belowground decomposition is P-limited across the tree-height gradient.

Zone had a significant impact on decomposition of leaf litter from a common source (F = 7.750, df = 2, 72, P = 0.001). Significantly higher rates of decomposition were observed in the fringe than in the dwarf and transition zones. After 180

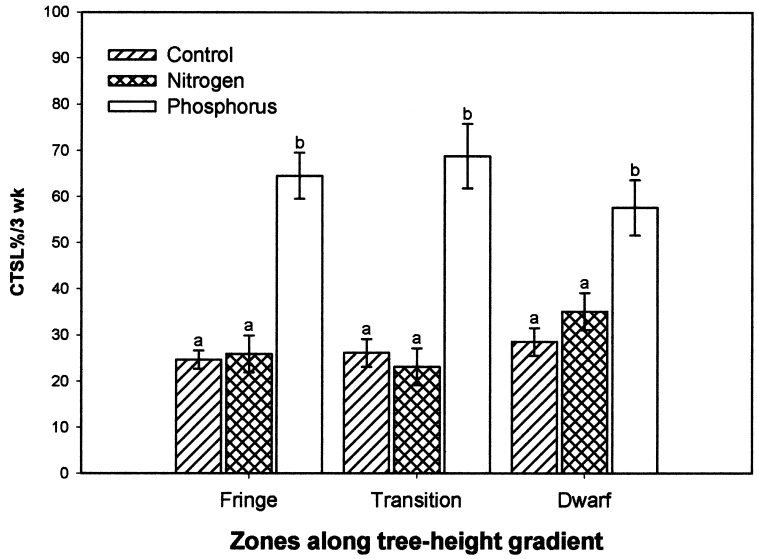

Figure 4. Tensile-strength loss of cotton strips (%CTSL) embedded in the substrate adjacent to fertilized *Rhizophora mangle* trees by nutrients (control, N, P) and by zones along a tree-height gradient (fringe, transition, dwarf). Values are means ± 1 SE. Bars within a zone with the same lowercase letter above are not significantly different at $P < 0.05$. $N = 81$ trees (3 nutrient treatments × 3 zones × 3 sites × 3 replicate trees).

d, senescent leaves in the fringe zone lost 54.6% of their initial dry mass compared to 35.4% and 36.2% in the dwarf and transition zones, respectively.

Hydro-edaphic characteristics

Water-level fluctuations relative to the soil surface showed that the dwarf zone was flooded to a greater depth (12 cm), and the soil was less flushed at low tide compared to the fringe and transition zones (Figure 5). The tidal range was maximal in the fringe zone (~ 23 cm) and decreased in the transition and dwarf zones (11–12 cm). The depth of soil flushing varied from ~ 18 cm in the fringe to ~ 10 cm in the transition, but the dwarf zone soil remained waterlogged or completely inundated over a tidal cycle.

The soil was organic (65–95%), comprised mainly of fine roots and root fragments, and had a bulk density of 0.1–0.3 g/cm^2. These characteristics did not vary significantly across zones or with nutrient treatment.

Redox potentials (Eh) at 15 cm soil depth indicated that the soil was slightly to moderately reduced across the tree-height gradient (Figure 6A). Eh in the dwarf zone was consistently lower than that in the fringe or transition zones. Porewater sulfide concentrations were also higher in the dwarf zone, consistent with the constant waterlogging and decreased soil flushing. Sulfide concentrations were also higher along the N-fertilized transect, but were unaffected by P-addition (Figure

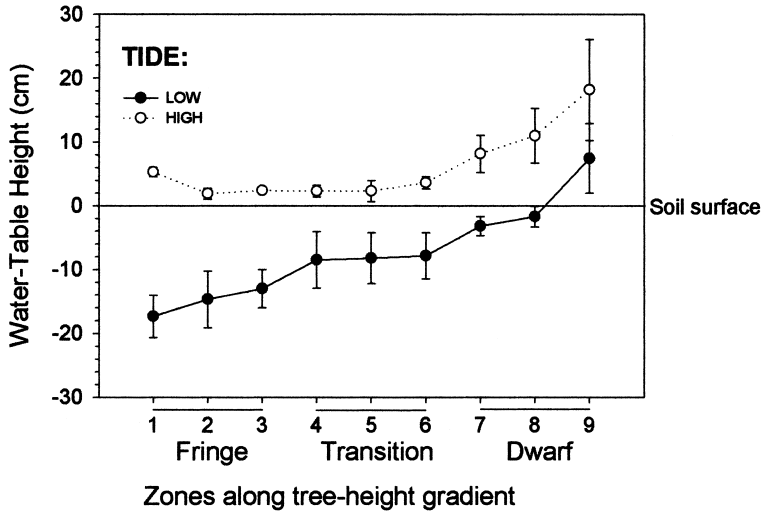

Figure 5. Variation in water level at high (open symbol) and low (closed) tides relative to the soil surface across a tree-height gradient from fringe (5–6 m tall) to transition (2–4 m tall) to dwarf ($\leq$ 1.5 m tall) zones. Values are the mean ± 1 SE (N = 3).

6B). Porewater pH was similar across zones and was unaffected by nutrient treatment (Figure 6C). Porewater salinity increased slightly across the tree-height gradient from near seawater concentration (35 g/L) in the fringe zone to just over 40 g/L in the dwarf zone, but was unaffected by fertilizer treatment (Figure 6D).

Porewater concentrations of PO_4-P were low ($\sim$2 μM) and showed little variation across the zones. Fertilization with P resulted in a significant increase in PO_4-P concentration to 57 μM, as indicated by a significant treatment H date interaction (F = 26.2, P < 0.0001). Concentrations of NH_4-N in porewater varied across the control transects and were lowest in the transition zone (1.57± 0.29 μM), highest in the dwarf zone (11.42 ±5.01 μM), and intermediate in the fringe (3.75 ±1.46 μM). Fertilization with N resulted in significant increases in porewater NH_4-N to >600 μM (Nutrient treatment H date interaction; F = 18.30, P<0.0001). Implantation of resin bags allowed assessment of bioavailability of nutrients because the method integrates porewater concentration and rate of nutrient delivery (e.g., by diffusion or mass flow). Bioavailable N (NH_4 + NO_3) and P (PO_4^{3-}) were significantly affected by N and P fertilizer treatments (Fig. 7, Table 6). Most of the N adsorbed by the resin was NH_4, although low amounts of NO_3 were detected. The values for NH_4 and NO_3 were thus added together to give a total bioavailable N. The ratio of bioavailable N:P showed a change in relative bioavailability of these nutrients across the tree-height gradient. Along the control transects, N:P was $\sim$10 in fringe and transition zones and $\sim$28 in the dwarf zone. Fertilization with N increased the ratio in all zones to 18 or higher, whereas P addition decreased the ratio to 7 or lower. Thus, the fertilizer treatments significantly altered the bioavailability of N relative to P across the tree-height gradient.

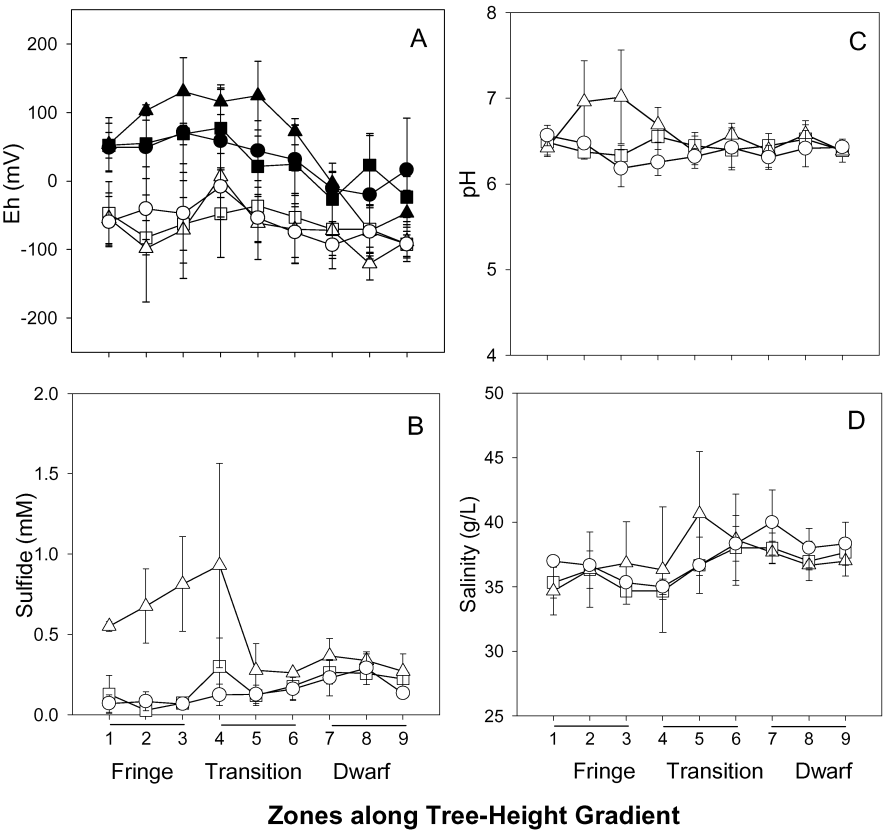

Figure 6. Variation in soil factors across tree-height gradient from fringe (5–6 m tall) to transition (2–4 m tall) to dwarf (⩽ 1.5 m tall) zones after 2 yr of nutrient enrichment. Values are for (A) soil redox potential (Eh), (B) porewater sulfide, (C) porewater pH, and (D) porewater salinity. Symbols represent nutrient treatment levels: control (square), nitrogen (triangle), and phosphorus (circle); closed and open symbols represent 1 and 15 cm soil depths, respectively. Values are the mean ± 1 SE (N = 9).

Discussion

Plant growth responses to nutrient enrichment

This study demonstrates a significant switch from N to P limitation across a narrow tree-height gradient in mangrove forests on small offshore islands in Belize (Figure 1). This switch occurred along transects perpendicular to the shoreline that extended from the water's edge 70–100 m into the hinterland. Increased growth by dwarf trees in response to fertilization with P, but not N, indicated P limitation in the interior of the island, which is consistent with earlier experimental results (Feller 1995). Although the magnitude of the response was not uniform from site to site, the taller trees in the fringe responded to the addition with N, but not P, providing

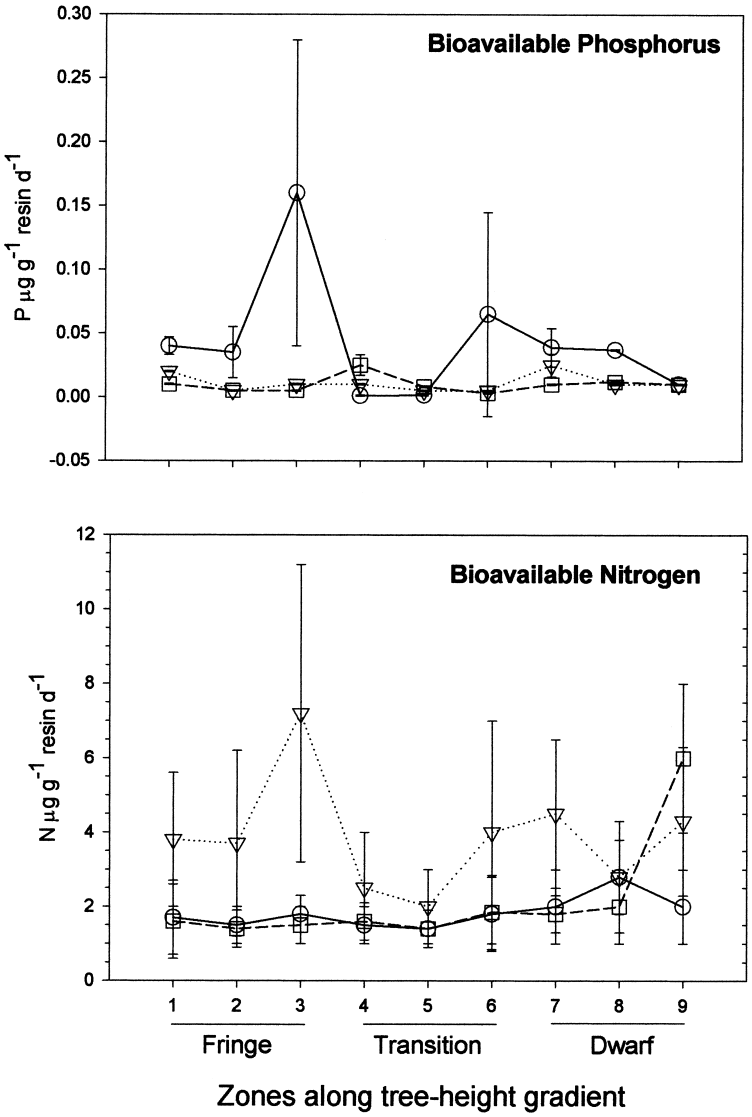

Figure 7. Variation in bioavailable phosphorus (PO_4-P) and nitrogen (NH_4-N + NO_3-N) measured with resin bags across a tree-height gradient from fringe (5–6 m tall) to transition (2–4 m tall) to dwarf (⩽ 1.5 m tall) zones after 2 yr of nutrient enrichment (control, N, P). Values are the mean ± 1 SE (N = 9).

experimental evidence of N limitation at the seaward margin of the forest. Positive growth response to both N and/or P fertilization in the transition zone suggested that the switch from N to P limitation was occurring in that zone. These data support our Hypothesis 1 (e.g., Boto and Wellington (1983) and McKee (1995)), which states that nutrient availability varies within a mangrove forest and can switch from N to P limitation across narrow environmental gradients.

Table 5. Summary of repeated-measures ANOVAs for physicochemical conditions measured across a tree-height gradient from fringe (5–6 m tall) to transition (2–4 m tall) to dwarf ($\leq$1.5 m tall) zones, before (1995) and 2 yr after (1997) fertilization began. Factors were nutrient enrichment (control, N, P), zone (dwarf, fringe, transition), and date (1995, 1997). Contrasts for nutrient × date interactions are given.

Source of variation	$Eh_{1\ cm}$	$Eh_{15\ cm}$	Salinity	Sulfide	pH
Nutrient enrichment	ns	ns	ns	****	ns
Zone	****	****	***	****	ns
Nutrient × Zone	ns	ns	ns	**	ns
Date	ns	ns	ns	**	ns
Date × Nutrient	ns	ns	ns	**	ns
Date × Zone	ns	ns	ns	ns	ns
Date × Nutrient × Zone	ns	ns	ns	*	ns
Contrasts by Nutrient enrichment (1995 vs. 1997)					
Control	-	-	-	***	-
Nitrogen	-	-	-	ns	-
Phosphorus	-	-	-	***	-

Note: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; **** $P \leq 0.0001$; ns = not significant

Table 6. Summary of two-way ANOVAs for bioavailable nitrogen (NO_3-N + NH_4-N) and phosphorus (PO_4-P) measured across a tree-height gradient from fringe (5–6 m tall) to transition (2–4 m tall) to dwarf ($\leq$1.5 m tall) zones 2 yr after fertilization began. Grouping factors were nutrient enrichment (control, N, P) and zone (fringe, transition, dwarf). Values are *F*-ratios. Contrasts for main effect of Nutrient enrichment are given.

Source of variation	Bioavailable nitrogen	Bioavailable phosphorus
Nutrient enrichment	6.370^{**}	4.530^{*}
Zone	1.730^{ns}	0.722^{ns}
Nutrient × Zone	0.909^{ns}	1.010^{ns}
Contrasts by Nutrient enrichment		
Control vs. N	***	ns
Control vs. P	ns	***

Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant

In this experiment, we applied small doses of N or P fertilizers directly into the soil near the base of individual trees. Our results indicate that this treatment approach substantially increased soil nutrient concentrations (Figure 7, Table 6) and created an enriched patch of soil that encompassed the target tree and its neighbors. Although the spatial extent of a fertilizer treatment effect is difficult to determine in the fringe zone because of overlapping crowns of adjacent trees, the area of influence is obvious in the dwarf zone where the trees are much smaller and the canopy is more open. Consistent with previous results (e.g., Feller (1995)), the addition of small doses of P fertilizer applied locally and directly to the root zone at the base of dwarf trees over 2 yr enriched the substrate for approximately 2 m around the

fertilizer insertion point, creating small patches of vigorously growing trees. These results suggest that even low inputs of anthropogenic enrichment may have substantial impacts in some mangrove ecosystems.

Possible explanations for the N to P gradient across the tree-height gradient

The tree-height gradient closely mirrored the soil flushing pattern (Figure 5), suggesting that variation in hydrology across the island was influencing growth of *R. mangle*. Several investigators have concluded that depressed growth in some vegetation stands is the consequence of environmental stresses, which singly or interactively inhibit plant growth (Sullivan and Daiber 1974; Valiela and Teal 1974; Broome et al. 1975; Gallagher 1975; Patrick and DeLaune 1976; Mendelssohn (1979a, 1979b)). The gradient in vegetation height at Twin Cays is somewhat analogous to that reported for *Spartina alterniflora*-dominated marshes at temperate latitudes. In those systems, stunted plant growth in inland zones is caused by flooding-induced limitation of N uptake (Mendelssohn 1979b; Bradley and Morris 1990). Primary P-limitation to *S. alterniflora* growth can occur on sandy substrates (Broome et al. 1975), and P can be secondarily limiting to N in some marshes (Morris et al. 1988). In a South Carolina salt marsh, for example, *S. alterniflora* did not respond to P addition alone, but did exhibit growth stimulation to both N and P applied together, indicating that P became limiting after N levels exceeded a threshold (Morris et al. 1988).

At Twin Cays, however, the situation is clearly more complicated and involves spatial variation in N relative to P and mangrove ability to acquire these nutrients in the presence of stress factors such as flooding and salinity. Tidal flushing may increase nutrient delivery, so that even if porewater concentrations were the same in all zones, the total amount supplied to roots would be greater in the more tidally-active fringe zone. Also, tidal flushing aerates the soil (Howes et al. 1986) and may remove toxins such as sulfide and salts (King et al. 1982). Where drainage of water at low tide is restricted (e.g., in dwarf zone), soil conditions become more stressful to plant growth. The mechanisms for plant growth limitation under soil waterlogging, which have been detailed for *S. alterniflora*, are: (1) soil anoxia-induced root oxygen deficiencies that severely limit ATP production and increase carbon loss from the plant in the form of ethanol (end product of alcoholic fermentation) (Mendelssohn et al. 1981; Mendelssohn and McKee 1983); and (2) sulfide inhibition of root metabolism, energy production and nutrient uptake (Bradley and Morris 1990; Koch et al. 1990). Thus, even though intertidal species such as *R. mangle* are highly adapted to growth in waterlogged soils, variation in factors affecting nutrient acquisition and use may strongly affect growth and productivity across narrow ecotones.

An alternative mechanism is growth limitation due to elevated salinity, as hypothesized by Lin and Sternberg (1992) for *R. mangle* in south Florida. The physiological effects of salinity and interactions with N nutrition have also been documented for *S. alterniflora*. In this plant, salt tolerance involves both salt excretion through leaf salt glands (an energy-requiring process) and synthesis of N-based

compounds that act in osmoregulation (Cavalieri and Huang 1981; Naidoo et al. 1992). As salinity increases, both the N concentration required to sustain growth and the energy requirement in *S. alterniflora* increases (Bradley and Morris 1992). Sea salts also competitively inhibit uptake of NH_4^+, which diminishes the ability of *S. alterniflora* to osmoregulate (Bradley and Morris 1991). At Twin Cays, the porewater salinity in the dwarf zone averaged 37–40 g/L (Figure 6D) and ranged from 36–47 g/L in the wet season to 36–54 g/L in the dry season (Feller 1995; McKee 1995). Although hypersalinity may contribute, it cannot alone account for the low stature and stunted growth of dwarf mangroves at Twin Cays because porewater salinities are lower than in areas with much taller trees (50 to 70 g/L) (McKee 1995).

The above observations may explain the tree-height gradient, but what could cause the shift from N to P limitation? Boto and Wellington (1983) suggested that differences in tidal exchange of nutrients and sediment were responsible for N vs. P limitation across an Australian mangrove forest. At Twin Cays, bioavailable N:P ratios were two times higher in the dwarf compared to the fringe zone, consistent with Boto and Wellington's hypothesis, but this pattern does not necessarily reflect a cause and effect relationship. Because the soil substrate at Twin Cays is peat with high organic matter content, the external source of nutrients is soluble components in water rather than mineral sediment. Several factors, including N_2 fixation, nitrification-denitrification, mineralization of litter, bacterial immobilization, and plant uptake, may affect concentrations of NH_4-N in porewater. The higher N:P ratio in porewater could be due to higher rates of N input or, conversely, to lower rates of denitrification or lower N uptake by plants. Boto and Wellington (1984) further hypothesized that P should be more available where Eh was lower, because redox couples such as iron would be in the reduced, more available form. Any P that was bound to iron would thus be released under more reducing conditions. However, availability of P in carbonate systems, such as Twin Cays, would not be expected to be greatly affected by redox status, since much of the inorganic P is bound to calcium, rather than to iron or manganese (redox couples) (e.g., Reddy (1983) and Moore and Reddy (1994)). The variation in soil Eh, but not bioavailable PO_4^{-3} (Figures 6 and 7) supports this interpretation.

The switch from N to P limitation may be related to differences in characteristics of ions, in combination with spatial variation in tidal fluctuation affecting mass flow of ions to root surfaces. All nutrient ions may be moved by mass flow to root surfaces, but immobile ions may be more limited by diffusional movement than mobile ions (Nye and Tinker 1977). Strongly adsorbed anions such as PO_4-P have diffusion coefficients as low as 10^{-9} cm^2 s^{-1} whereas diffusion coefficients of NO_3^- and NH_4^+ in dilute solution are $\sim 10^{-5}$ and 10^{-7} cm^2 s^{-1}, respectively (Nye and Tinker 1977). Greater water movement would diminish nutrient depletion zones around mangrove roots, maximizing diffusion of tightly bound ions such as phosphate. More mobile ions with higher diffusion rates would be less affected by limits to diffusion. Differences in soil flushing across the tree-height gradient could thus affect nutrient ions differently and thereby root access to them.

In the fringe zone, PO_4-P is readily carried to root surfaces by tidal movement. In the dwarf zone, P is more likely to be limiting because stagnant conditions would limit diffusion of PO_4-P to root surfaces. Thus, roots would have to "forage" for P through root growth. Fine roots with a large surface area per unit mass would substantially improve acquisition of relatively immobile P from the substrate (Nye and Tinker 1977; Robinson 1996). Excessive waterlogging in the dwarf zone, however, would affect root morphology and metabolism. Maintenance of oxygen flux to growing root tips in the anoxic sediment is facilitated by air-space tissue (aerenchyma) inside roots, but internal oxygen concentrations are determined by the rates of supply and loss to sinks, such as respiration and leakage to surrounding soil (McKee et al. 1988; Armstrong et al. 1991; McKee 1996). The rate of root oxygen leakage is strongly affected by occurrence of fine lateral roots, which increase surface area (Sorrell 1994). When external oxygen demand increases, internal concentrations decline and root metabolism is affected (McKee and Mendelssohn 1989; McKee 1996). Thus, where constant flooding occurs, as in the dwarf zone, there would be a tradeoff between root morphology needed to minimize oxygen leakage and maximize diffusion to root tips (e.g., thicker, less branched roots) and that needed to maximize nutrient acquisition (e.g., thin, highly branched roots). Root energy production would also be decreased by hypoxia and/or sulfide toxicity (Mendelssohn et al. 1981; McKee and Mendelssohn 1989), which in turn would limit nutrient uptake (Koch et al. 1990). In the fringe zone where frequent tidal flushing aerates the soil and flushes away toxins such as sulfide (Figure 6B), aeration limitations to root branching and fine root production may be less. In this zone, addition of N fertilizer increased growth, possibly as a consequence of enhanced photosynthesis rates and/or a change in biomass allocation.

Foliar nutrient responses to nutrient enrichment across the N to P gradient

Nutrient enrichment had a dramatic effect on foliar nutrient economy that was variable and complex across the tree-height gradient. The response to the N fertilizer was much less than that observed for P in the N- or P-limited parts of the mangrove forest. Similar results were reported for fertilization experiments in eucalyptus plantations in Australia and in *Metrosidros polymorpha* in Hawaii growing in N- and P-limited soils (Bennett et al. 1996; Vitousek 1998). The addition of N resulted in higher $[N_G]$ in each zone, even in trees where no increase in rates of growth was observed, suggesting luxury uptake of N. However, unlike the P fertilizer, the N fertilizer had no significant effect on N or P use efficiencies and resorption across the tree-height gradient.

Even in the N-limited fringe, control trees retranslocated $\sim 80\%$ of their P back into the plant prior to leaf fall, leaving <0.1 mg/g P in senesced leaves (Figures 2 and 3). Thus, under N- or P- limiting conditions, P resorption by *R. mangle* is complete and reaches maximal physiological levels (Killingbeck 1996). We found a dramatic decreases in P resorption efficiency following P addition in all zones. In the P-limited dwarf zone, we also observed a positive feedback from increased P availability on foliar N economy. Addition of P resulted in a 30% increase in N

resorption efficiency, which is similar to values reported in Feller et al. (1999). Because control and P-fertilized trees had similar [N_G], our data imply that in *R. mangle* nutrient resorption is strongly controlled by P availability. In contrast, some other studies have found that differences in resorption efficiency were explained largely by higher initial tissue nutrient concentrations (Aerts 1996; Lodhiyal and Lodhiyal 1997; Vitousek 1998; Saur et al. 2000).

With respect to the availability of P, but not N, these data support our Hypothesis 2 that states that as the availability of a limiting nutrient increases, the mechanisms used by plants to recycle and conserve that nutrient become less efficient (Loveless 1961; Small 1972; Stachurski and Zimka 1975; Tilton 1977; Chabot and Hicks 1982; Shaver and Melillo 1984; Vitousek 1984; Schlesinger et al. 1989; Escudero et al. 1992). However, N resorption efficiency and NUE_N did not support the hypothesis clearly. This hypothesis predicts that internal P and N cycling should be tight in the dwarf and fringe zones, respectively. It also predicts that P conservation will decrease in response to P fertilization in the dwarf zone and that N conservation will decrease in response to N fertilization the fringe zone. Although increased P availability to dwarf trees resulted in a decrease in P conservation, it promoted the ability of *R. mangle* to conserve N. This result suggests that P deficiency limits growth and other plant processes, and that N resorption is incomplete under P-limiting conditions. A number of other studies have found a linkage between nutrient availability and resorption processes (e.g., Miller et al. (1976) and Turner (1977), Boerner (1984), Shaver and Melillo (1984), Vitousek (1984), Kost and Boerner (1985), Dierberg et al. (1986), Schlesinger et al. (1989), Escudero et al. (1992), DeLucia and Schlesinger (1995), Hawkins et al. (1998), Malik and Timmer (1998), Richardson et al. (1999)). However, several other studies have found that resorption efficiency was independent of nutrient availability (e.g., Ostman and Weaver (1982) and Staaf (1982), Chapin and Kedrowski (1983), Killingbeck and Costigan (1988), Lajtha and Klein (1988), Aerts and De Caluwe (1989), Chapin and Shaver (1989), Chapin and Moilanen (1991), Del Arco et al. (1991), Millard and Proe (1991), Millard (1993), Bowman (1994), Baddeley et al. (1994), Minoletti and Boerner (1994), Aerts (1996), Correia and Martins-Loucao (1997), Vitousek (1998), Aerts et al. (1999), Son et al. (2000)).

A plant's ability to use and conserve nutrients may be determined by both resorption efficiency and leaf longevity (Eckstein and Karlsson 1999). However, the relative importance of each of these traits on nutrient use efficiency varies depending on patterns of nutrient limitation in the environment (Vitousek 1998; Cordell et al. 2001). In *R. mangle*, addition of nutrients had no effect on leaf longevity (Feller 1995). Thus, our experimental studies with this species demonstrate that resorption efficiency is a phenotypic response to P deficiency in this mangrove environment, as predicted by Pugnaire and Chapin (1993). Yet, there are large differences in nutrient use efficiencies among mangroves, and our data suggest that *Rhizophora* species have particularly efficient nutrient conservation mechanisms (Feller et al. 1999). In addition, the nutrient economy of some mangrove species may be altered because of their reliance on N-based osmoregulatory compounds, which help them maintain internal turgor pressure in saline environments (Cheeseman 1988; Popp et

al. 1988). In addition, interspecific variation in leaf longevity may also help explain some of the observed differences among mangroves in their apparent abilities to use and conserve nutrients.

Decomposition across the N to P gradient

Based on %CTSL as an index of decay and an assay for nutrient limitation, increased P availability also leads to dramatic increases in rates of belowground decomposition in all three zones, whereas N fertilization had no effect on decomposition in any of the zones (Figure 4). These data support our Hypothesis 3 for availability of P, but not N, that rates of decomposition would increase with increased availability of a limiting nutrient (Flanagan and Van Cleve 1983). Contrary to the growth responses by fertilized trees, these data imply that belowground decomposition is P-, rather than N-, limited in all zones across the tree-height gradient. This result suggests that within mangrove ecosystems not all ecological processes respond similarly to, or are limited by, the same nutrient.

Leaf-litter decomposition varied significantly across the tree-height gradient, with litter in the fringe decomposing almost twice as fast as in the dwarf zone. To separate the possible effects of zone versus nutrients, we used a common source of leaf litter in this experiment. Hence, differences in litter quality parameters, such as C:N and C:P ratios, could not explain the pattern of decomposition that we found, as they have in other systems (e.g., Cromack and Monk (1975) and Aber and Melillo (1982), Chabot and Hicks (1982), Day (1982), Melillo et al. (1982), Flanagan and Van Cleve (1983), Pastor et al. (1984), Taylor et al. (1989), Gallardo and Merino (1993), Berendse (1994), Aerts and De Caluwe (1989)). Based on the C:N ($\sim$163) and C:P ($\sim$4019) ratios, the decomposability of red mangrove leaf litter was lower in comparison with leaf litter from temperate, Mediterranean, and tropical regions (Aerts 1997). In this experiment, increased nutrient availability caused a dramatic change in C:N and C:P ratios over 2 yr (Table 3). However, our results suggest that, in mangrove ecosystems, steep environmental gradients may modify the ability of nutritive, structural, and chemical content of leaves to control decay rates of leaf litter. These results are consistent with previous results from Twin Cays (Feller et al. 1999). In other studies, mangrove leaf litter has been found to decompose faster in the subtidal than in the intertidal (e.g., Heald (1971) and Robertson (1988), Robertson et al. (1992)). However, this explanation does not account fully for the pattern we found at Twin Cays. The lowest decomposition rates occurred in the continuously flooded dwarf zone where our litterbags were incubated in a subtidal environment. The highest rates occurred in the fringe zone, which is characterized by diurnal flooding and draining. We suggest that it is more likely that regular tidal flushing, which occurs in the fringe zone and not in the other zones, creates optimal physico-chemical conditions that favor decomposition relative to other parts of the forest (Middleton and McKee 2001). It may also be that higher temperatures, which occur regularly in the dwarf and transition zones, inhibit microbial growth and decay (Robertson et al. 1992; Feller et al. 1999).

In conclusion, the growth responses by *R. mangle* to the nutrient treatments in this experiment demonstrated convincingly that essential nutrients are not uniformly distributed within mangrove ecosystems and that soil fertility can switch from conditions of N to P limitation across a narrow tree-height gradient in mangrove forests. These results exemplify the biocomplexity of mangrove ecosystems and partly explain their heterogeneous nature. Our results also provide experimental evidence that not all ecological processes within an ecosystem (e.g., plant growth, internal nutrient cycling, decomposition) are limited by the same nutrient. The impact of increased nutrients in the coastal zone will vary depending on the nutrient, the ecotonal position, and the ecological processes being measured. Our results contribute to the understanding of what nutrients limit mangrove growth and how mangrove functions may be altered by external loading of N and P. These data have significant implications for understanding the potential effects of eutrophication in coastal systems and for modeling of nutrient dynamics in mangrove ecosystems.

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