Growth and Nutrient Conservation in *Rhizophora mangle* in Response to Fertilization along Latitudinal and Tidal Gradients

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ABSTRACT. Mangroves form heterogeneous marine ecosystems with spatial differences in structural complexity, biodiversity, biogeochemistry, and hydrology that vary at local and regional scales. Although mangroves provide critical ecosystem goods and services, they are threatened globally by human activities, including nutrient over-enrichment. Our goal was to determine if enrichment with nitrogen (N) or phosphorus (P) interacts with forest structure and latitude to alter growth and nutrient dynamics. We established a series fertilization experiments across more than 2,000 km and 18° of latitude from the Indian River Lagoon (IRL), Florida, to Twin Cays, Belize, to Bocas del Toro, Panamá. At each site, we fertilized individual trees with one of three treatment levels (control, +N, +P) in two intertidal zones (fringe, scrub) and measured their responses for four years. We tested the effects of nutrient over-enrichment on growth, resorption efficiency, and resorption proficiency of the red mangrove *Rhizophora mangle*. All sites were nutrient limited, but patterns of nutrient limitation varied by zone and latitude. At IRL, growth was N limited; at Twin Cays, the fringe was N limited, but the scrub forest was P limited; at Bocas del Toro, the fringe was N limited, but the scrub forest was both N- and P limited. Nutrient enrichment had dramatic and complex effects on nutrient conservation. Adding nutrients to mangrove ecosystems affected growth and the nutrient recycling, but the pattern depended on location, site characteristics, and the nature of nutrient limitation. Predicting how forests will respond to nutrient over-enrichment requires an assessment of spatial heterogeneity at multiple scales of response.

INTRODUCTION

Mangrove ecosystems are coastal wetlands dominated by woody plants that span gradients in latitude (30°N to 37°S), tidal height (<1 m to >4 m), geomorphology (oceanic islands to riverine systems), sedimentary environment (peat to alluvial), climate (warm temperate to both arid and wet tropics), and nutrient loading (oligotrophic to eutrophic). Throughout their distribution, mangroves are critical not only for sustaining biodiversity in these intertidal forests but also for their direct and indirect benefit to human activities. As a detritus-based ecosystem, the leaf litter from these trees provides the basis for adjacent aquatic and terrestrial food webs (Odum and Heald, 1975). Mangroves function as nurseries for many of the sport and commercial fishes found in deeper waters and provide feeding grounds

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for large reef fishes (Nagelkerken et al., 2000; Mumby et al., 2004). As a result, mangrove-assimilated energy and nutrients are exported to surrounding coral reefs (Dittmar and Lara, 2001). Besides supporting and renewing coastal fishing stock, mangroves also benefit human economic development by stabilizing shorelines. This stabilization is a critical function in tropical coastal areas that may be battered periodically by tropical storms, hurricanes, and tsunamis (Danielson et al., 2005; Barbier, 2006).

Despite repeated demonstration of their ecological and economic importance, mangroves are one of the world's most threatened ecosystems (Valiela et al., 2001; Alongi, 2002; Barbier and Cox, 2003; Rivera-Monroy et al., 2004; Duke et al., 2007). In addition to direct destruction, increasing input of human-caused nutrient pollution is widely recognized as one of the major threats to mangroves and other marine environments worldwide (NRC, 1995, 2000, 2001; Duce et al., 2008). However, system-specific attributes may lead to large differences among coastal and estuarine systems in their sensitivity and susceptibility to these increasing nutrient levels (Cloern, 2001). The complex suite of direct and indirect responses in coastal systems to nutrient over-enrichment include changes in water chemistry, distribution and biomass of plants, sediment biogeochemistry, decomposition processes, nutrient cycling, nutrient ratios, phytoplankton communities, habitat quality for metazoans, and ecosystem functions.

Relatively little is known about how the structure and function of mangrove ecosystems are altered by nutrient enrichment. In temperate salt marshes and mangroves, ecological processes have been shown to be nitrogen- (N) limited (Valiela and Teal, 1979; Feller et al., 2003b). The few tropical and subtropical mangrove wetlands that have been studied were shown to be both phosphorus- (P) and N limited (Boto and Wellington, 1984; Feller, 1995; Feller et al., 1999, 2003a, 2003b; Lovelock and Feller, 2003; Lovelock et al., 2004). Because mangroves are responsive to processes operating at multiple spatial scales, comparisons along a broad latitudinal gradient in climate and across narrow tidal gradients will improve our understanding of the relative impacts of global versus local factors on the structure and function of these ecosystems. In this study, we focused on the mangrove *Rhizophora mangle* (red mangrove), an evergreen tree that has a large geographic range throughout the Atlantic-East Pacific region (Duke, 1992). Along the Atlantic coasts of North and South America, its distribution is continuous and spans almost 60° of latitude from its northern limit along the coast of Florida at 29°42.94′N (Zomlefer et al., 2006) to its southern limit along the coast of Brazil at 27°53′S (Shaeffer-Novelli et al., 1990). In this study, our goals were to determine how nutrient availability varies among *R. mangle* forests spanning a temperate to tropical gradient and how nutrient over-enrichment affects plant growth and nutrient conservation. We manipulated nutrient availability and measured responses of trees fertilized with nitrogen (+N) or phosphorus (+P) growing along intertidal gradients in similar habitats at three locations along this latitudinal gradient to test the following hypotheses.

1. Nutrient availability varies along a latitudinal gradient with a decreasing supply of P relative to N toward the tropics (Vitousek, 1984; Vitousek and Sanford, 1986; Crews et al., 1995). This hypothesis predicts increasing P limitation in mangrove forests at lower latitudes and N limitation at higher latitudes (Güsewell, 2004; McGroddy et al., 2004; Reich and Oleksyn, 2004; Kerkhoff et al., 2005).
2. Delivery, uptake, or assimilation of P is more strongly affected by tidal flushing and concomitant factors that vary spatially than is that of N (Smith, 1984; McKee et al., 2002). This hypothesis predicts differences in N versus P limitation within mangrove forests at different intertidal elevations (Ross et al., 2006). Specifically, N limitation is predicted for the low intertidal where tidal flushing is greater (residence time is shorter) than in the high intertidal where P limitation is predicted.
3. Because of difference in growth rates along climatic gradients, the mechanisms used by plants to recycle and conserve nutrients will be more efficient at higher latitudes (Oleksyn et al., 2003). This hypothesis predicts increased nutrient conservation by mangroves growing near their temperate limit (Lovelock et al., 2007).
4. As nutrient availability increases, nutrient conservation mechanisms become less efficient (Shaver and Melillo, 1984; Vitousek, 1984; Schlesinger et al., 1989; Escudero et al., 1992). This hypothesis predicts that the effects of nutrient loading on mangrove forests will differ depending on whether a system is N- or P limited, with the expectation that the limiting nutrient will be more efficiently and tightly conserved (Feller et al., 1999).

MATERIALS AND METHODS

Site Descriptions

We compared the effects of nutrient over-enrichment on plant growth and nutrient dynamics in *Rhizophora mangle* L. at three locations along the Atlantic and Caribbean coasts from Florida to Panamá spanning a climatic gradient of more than 2,000 km and 18° of latitude (Figure 1):

FIGURE 1. The three study sites used in this study span more than 18° of latitude and extend from the Indian River Lagoon (IRL), Florida, in the north, to Twin Cays, Belize, and to Bocas del Toro, Panama, in the south.

(1) Indian River Lagoon (referred to hereafter as IRL), Florida; (2) Twin Cays, Belize (referred to hereafter as Twin Cays); and (3) Bocas del Toro, Republic of Panamá (referred to hereafter as Bocas) (Table 1). Table 2 provides a summary of the characteristics for the three locations (Koltes et al., 1998; McKee et al., 2002; Feller et al., 2003a; Feller and Chamberlain, 2007; Lovelock et al., 2005). Forest structure at the three locations was heterogeneous and characterized by complex gradients in tree height that included a narrow seaward fringe of uniformly tall (~4 m) trees dominated by *R. mangle*, varying in width from 5 to 20 m (Figure 2). Tree height decreased rapidly to landward with interior areas dominated by old-growth stands of low stature, or "scrub," trees (~1.5 m) (Table 3). The black mangrove (*Avicennia germinans* L.) and the white mangrove (*Laguncularia racemosa* (L.) Gaertn. f.) were also present in each of these locations, typically near the landward ecotone. The hydrogeomorphic settings were variable among the three locations. IRL and Bocas were continental in contrast with Twin Cays, which is a low oceanic island. However, Twin Cays and Bocas were more similar in mineralogy (Phillips et al., 1997; Macintyre et al., 2004; Coates et al., 2005), with mangrove forests atop a carbonate platform and deep peat deposits. All sites were microtidal with mixed semidiurnal tides (Kjerfve et al., 1982; Kaufmann and Thompson, 2005). The fringe zones at the three locations were similarly well flushed, but the hydrological conditions of the scrub zones varied. At Twin Cays, these interior portions of the forest were completely inundated and waterlogged (McKee et al., 2007). In contrast, the Bocas scrub zone drained completely at low tide (Lovelock et al., 2005). At IRL, the scrub zone drained completely at low tide during the summer but remained inundated for days during the winter (Feller et al., 2003b).

In the IRL, our experimental sites were situated on the lagoonal side of two barrier islands. The fringe site was in Avalon State Park on North Hutchinson Island, St. Lucie County; the scrub site was in the Hobe Sound National Wildlife Refuge on Jupiter Island, Martin County. In this area, soil was composed primarily of marine sand with mangrove forests adjacent to coastal strand vegetation and maritime hammocks. Descriptions of forest

TABLE 1. Hydrogeomorphic characteristics of the study sites along a latitudinal gradient from the Indian River Lagoon (IRL), Florida, to Twin Cays, Belize, to Bocas del Toro (Bocas), Panama.

Characteristic	IRL	Twin Cays	Bocas
Latitude	27°33′N, 80°13′W	16°50′N, 88°06′W	9°09′N, 82°15′W
Freshwater inflow	Medium	Low	High
Type of landscape	Continental	Oceanic	Continental
Topographic relief	Medium	Low	High
Nutrient flux	High	Low	Medium
Mineralogy	Siliclastic/carbonate	Peat/limestone	Peat/limestone
Annual rainfall	1.3 m	2.8 m	3.5 m
Mean temperature range[a]	12.4°–23.6°C (w) 22.6°–31.9°C (s)	18.3°–29.9°C (w) 22.2°–31.3°C (s)	20.1°–31.1°C (w) 21.9°–31.8°C (s)
Mean tidal range	37 cm	34 cm	19 cm
Major disturbances	Anthropogenic, hurricanes	Anthropogenic, hurricanes	Anthropogenic, flooding

[a] w = winter; s = summer.

TABLE 2. Characteristics of the mangrove forest structure in the fringe and scrub zones at the Indian River Lagoon (IRL), Florida, to Twin Cays, Belize, to Bocas del Toro (Bocas), Republic of Panama. Data are from Koltes et al. (1998), McKee et al. (2002), Feller et al. (2003a), Lovelock et al. (2005), and Feller and Chamberlain (2007).

Location	Zone	Salinity (‰) (mean ± SE)	Species	Tree height (m) (mean ± 1 SE)	DBH (cm) (mean ± 1 SE)	Stem density (stems·0.1 ha^{-1})	Basal area (m^{2}·0.1 ha^{-1})
IRL	Fringe	32.7 ± 0.7	*Rhizophora mangle*	3.9 ± 0.1	4.5	3,9536.4	
			Laguncularia racemosa	3.2 ± 0.3	6.1	1,3433.9	
			Avicennia germinans	3.8 ± 0.3	4.8	6711.2	
	Scrub	32.4 ± 0.5	*Rhizophora mangle*	1.7 ± 0.1	2.5 ± 0.2	2,3861.5	
			Laguncularia racemosa	4.5 ± 0.4	4.6 ± 0.7	4771.0	
			Avicennia germinans	1.6 ± 0.0	1.2 ± 0.0	730.01	
Twin Cays	Fringe	36.9 ± 1.2	*Rhizophora mangle*	3.2 ± 0.2	7.3 ± 0.4	4012.1	
			Laguncularia racemosa	2.2^{a}	2.9^{a}	3^{a}0.2^{a}	
			Avicennia germinans	2.2^{a}	4.0^{a}	3^{a}0.01^{a}	
	Scrub	39.4 ± 1.2	*Rhizophora mangle*	0.8 ± 0.1	2.4 ± 0.2	8970.4	
Bocas	Fringe	34.4 ± 0.6	*Rhizophora mangle*	3.9 ± 0.1	5.3 ± 0.6	8501.6	
	Scrub	33.3 ± 1.9	*Rhizophora mangle*	0.7 ± 0.1	1.5 ± 0.1	3,3570.7	

[a] Based on occurrence of a single tree in each zone.

structure, hydro-edaphic conditions, growth, nutrient dynamics, and photosynthesis at the Avalon State Park site were previously reported (Feller et al., 2003a; Lovelock and Feller, 2003).

At Twin Cays, our fringe and scrub sites were located on the two largest islands of this 92-ha mangrove archipelago, 10 km offshore. Descriptions of forest structure, biogeochemistry, ecophysiology, growth, and nutrient dynamics were previously reported (Rützler and Feller, 1996; McKee et al., 2002; Feller et al., 2003b, 2007; Lovelock et al., 2006a, 2006b, 2006c, 2006d). These oceanic mangroves islands are underlain by deep deposits of mangrove peat 8 to 12 m thick (Macintyre et al., 2004; McKee et al., 2007).

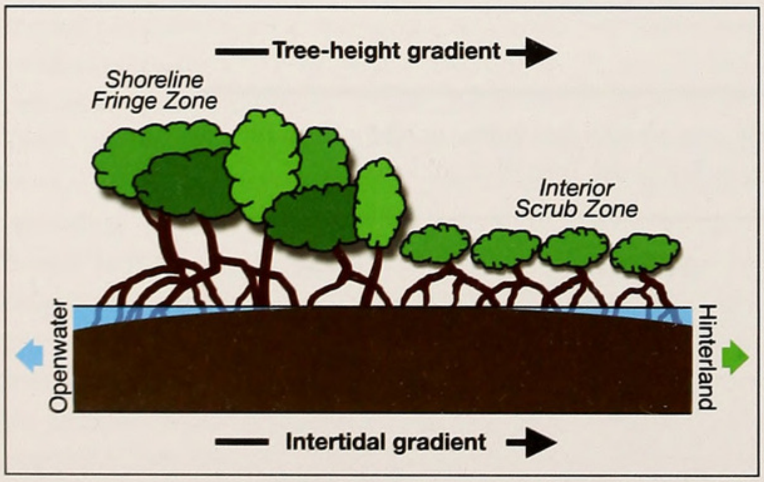

FIGURE 2. Mangrove forests at each of our study sites are characterized by a distinctive tree-height gradient with tall trees fringing the shoreline and scrub trees in the interior.

At Bocas, fringe and scrub sites were located on three islands (San Cristobal, Solarte, Isla Popa) in Almirante Bay and the Chiriqui Lagoon in a vast network of mangrove islands and mainland peninsulas covering approximately 2,885 km^{2} (De Croz, 1993; Guzman and Guevara, 1998; Guzman et al., 2005; Lovelock et al., 2004, 2005). Here, mangroves occurred adjacent to tropical rainforests and grew on peat approximately 5 m deep atop ancient coral reef limestone (Phillips and Bustin, 1996; Phillips et al., 1997). This location was outside the hurricane belt, but flooding was common. Earthquakes are episodic (Phillips et al., 1994, 1997; Phillips and Bustin, 1996) and are likely to be the major nonanthropogenic disturbance regime influencing these forests.

EXPERIMENTAL DESIGN

Fertilization experiments were set up at IRL in January 1997, at Twin Cays in January 1995, and at Bocas in January 1999. To compare responses, we used a three-way factorial analysis of variance (ANOVA) design (i.e., 3 nutrient enrichment treatment levels [Control, +N, +P] × 2 zones [fringe, scrub] × 3 locations [IRL, Twin Cays, Bocas] × 3 sites per location × 3 replicate trees per site, for a total of 162 trees). Nutrient treatment was randomly as-

TABLE 3. Three-way factorial analysis of variance (ANOVA) results on the seven response variables: shoot elongation (Growth), N-, P-, and K-resorption efficiencies (NRE, PRE, KRE), and N-, P-, and K-resorption proficiencies (NRP, PRP, KRP). The kind of transformation conducted on response variables for normalization and homogeneity of variances is given in the second line of column headings. Results are in the form of *F* statistical values for each effect and the corresponding level of significance: $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$; and ~ for $P < 0.1$.

		Growth *Log(x)*		NRE *Exp(x)*		PRE *Exp(4x)*		KRE *Exp(x)*		NRP *Log(x)*		PRP *Log(1000x)*		KRP *Log(x)*	
Factor	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Location (L)	2	24.2	***	28.6	***	126	***	16.5	***	86.1	***	373	***	18.9	***
Zone (Z)	1	0.11		65.2	***	4.57	*	0.96		75.4	***	0.29		5.18	*
Treatment (T)	2	23.4	***	10.4	***	75.4	***	14.6	***	40.3	***	108	***	36.8	***
L × Z	2	12.0	***	3.21	*	1.21		0.78		2.88	~	7.15	**	1.98	
L × T	4	12.9	***	4.37	**	12.5	***	5.60	***	2.16	~	23.6	***	8.13	***
Z × T	2	17.8	***	3.27	*	4.36	*	8.97	***	4.77	**	13.4	***	25.0	***
L × T × Z	4	4.9	**	4.35	**	1.30		4.27	**	7.95	***	4.21	**	8.61	***
Residuals	140														

signed within each zone and site. Trees were amended with 150 g N as NH_4 (45:0:0), or P fertilizer as P_2O_5 (0:45:0), per centimeter diameter breast height, as described in Feller (1995). Doses (150 g) of fertilizer were sealed in dialysis tubing and placed in each of two holes 30 cm deep, cored into the substrate on opposing sides of a tree beneath the outermost margin of its canopy, and sealed. Experiments at IRL and Twin Cays were fertilized twice per year. Because of limited access, the Bocas experiment was fertilized once per year. Thus, growth responses were normalized to the annual rate of fertilizer application. For controls, holes were cored and sealed but no fertilizer was added. Direct fertilizer application to the root zone of our target trees was used because all sites were flooded at high tides and fertilizer broadcasted on the surface would have washed away.

Tree Growth

To quantify growth, we measured the length of five initially unbranched shoots in sunlit positions in the outer part of the canopy of each tree at the three locations. To compare growth responses among the three locations, we calculated the annual shoot elongation based on the amount fertilizer added per location (cm · year^{-1} kg^{-1}).

Leaf Nutrient Dynamics

To determine the relative effects of nutrient over-enrichment on the ability of *R. mangle* to conserve nutrients invested in foliage, we measured N, P, and potassium (K) concentrations in green and senescent leaves. For green leaves, we sampled the youngest, fully mature green leaves from penapical stem positions in sunlit portions of the canopy. Fully senescent yellow leaves with well-developed abscission layers were taken directly from the trees. Leaf area was determined with a Li-Cor 3000 Leaf Area Meter (Lincoln, Neb., USA). Leaf samples were dried at 70°C in a convection oven and ground in a Wiley Mill to pass through a 40 mesh (0.38 mm) screen. Concentrations of carbon (C) and N were determined with a Model 440 CHN Elemental Analyzer (Exeter Analytical, North Chelmsford, Mass., USA) at the Smithsonian Environmental Research Center, Edgewater, Md. Concentrations of P and K were determined using an inductively coupled plasma spectrophotometer by Analytical Services, Pennsylvania State University, Pa. Nutrient concentrations expressed on a leaf area basis (mg · cm^{-2}) were used to calculate N, P, and K resorption efficiencies (NRE, PRE, KRE), as below (Chapin and Van Cleve, 1989):

$$\text{resorption efficiency} = \frac{\text{N, P, or K }(\text{mg}\cdot\text{cm}^{-2})_{\text{green leaf}} - \text{N, P, or K }(\text{mg}\cdot\text{cm}^{-2})_{\text{senescent leaf}}}{\text{N, P, or K }(\text{mg}\cdot\text{cm}^{-2})_{\text{green leaf}}} \times 100$$

The absolute levels to which N, P, and K were reduced (% dry mass) in senesced leaves (indicated as $\%N_{\text{senesced leaf}}$, $\%P_{\text{senesced leaf}}$, and $\%K_{\text{senesced leaf}}$, respectively) were used directly as indices of N, P, and K resorption proficiencies (NRP, PRP, KRP), as below (Killingbeck, 1996):

> resorption proficiency = the level to which N, P, or K has been reduced in senescent leaves (% dry mass).

Note that low levels for $\%N_{\text{senesced leaf}}$, $\%P_{\text{senesced leaf}}$, and $\%K_{\text{senesced leaf}}$ are indicative of high resorption proficiency whereas high levels indicate low resorption proficiency. Concentrations less than 0.7% are considered complete resorption for N and concentrations less than 0.04% are considered complete resorption for P (Killingbeck, 1996). Higher values indicate incomplete resorption. In this study, we considered values less than 0.3% N and less than 0.01% P as the ultimate resorption potential for *R. mangle*, as proposed by Killingbeck (1996). Comparable values for K resorption potential have not been determined.

STATISTICS

Our data were grouped by nutrient treatment (Control, +N, +P) × zone (fringe, scrub) × location (IRL, Twin Cays, Bocas), to compare seven response variables of *R. mangle*, including growth responses, N-, P-, and K-resorption efficiencies, and N-, P-, and K-resorption proficiencies. Three-way factorial analyses of variance (ANOVA) were applied for each response variable. When an ANOVA found significant effects, Tukey's honestly significant difference (HSD) tests were applied to examine pairwise differences within and among the treatment levels. To respect the assumptions of heterogeneity of variances and normality, the response variables were transformed using logarithms and exponentials. To investigate relationships between nutrient content of green and senescent leaves as well as among nutrient resorption proficiencies, we used the Spearman rho (ρ) correlation test on the ranked row values. These analyses were conducted using the R software 2.7.0 (R Development Core Team, 2008).

RESULTS

TREE GROWTH

There was a significant three-way interaction of nutrient enrichment × location × zone on growth rates of *R. mangle* trees (see Table 3; Figure 3). For control trees in the fringe zone, the rate of shoot elongation at IRL was signifi-

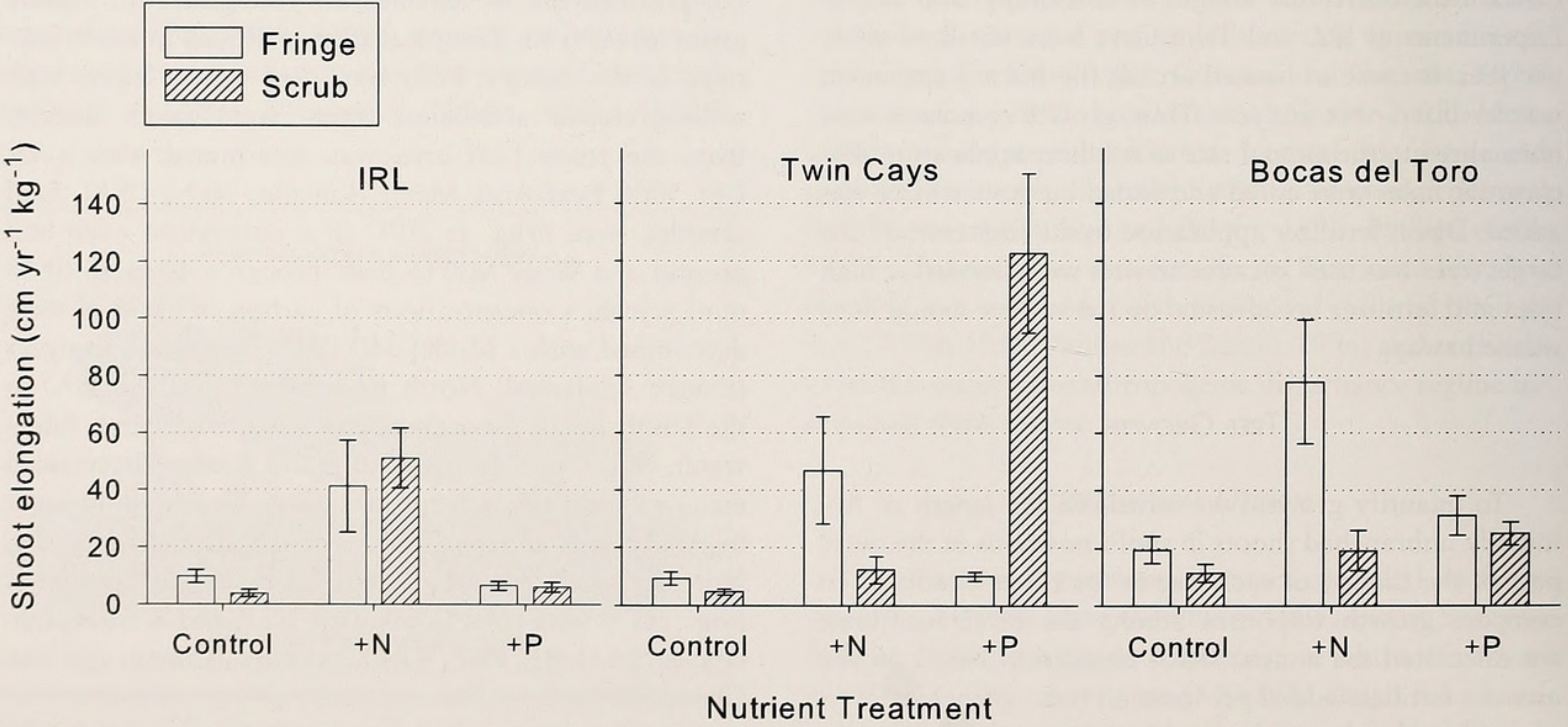

FIGURE 3. *Rhizophora mangle* growth (cm · year^{-1} · kg^{-1}) measured as elongation of individual shoots per year (normalized to fertilizer application at each site) at Indian River Lagoon (IRL), Twin Cays, and Bocas del Toro, in two zones (fringe, scrub), and in response to nutrient enrichment with nitrogen (+N) or phosphorus (+P). (IRL and Twin Cays data from Feller et al., 2003a, 2003b).

cantly lower than at Bocas (HSD adjusted $P < 0.001$) but similar to those at Twin Cays (HSD adjusted $P = 0.070$), which had similar values. There were no significant differences in shoot elongation rates for control trees in the scrub zone among all the locations. +N caused significant increases in shoot elongation rates for fringe and scrub trees at IRL, but only for fringe trees at Twin Cays and Bocas. However, shoot elongation for +N fringe trees in the IRL was lower than observed at Bocas (HSD adjusted $P = 0.089$). +N caused similar increases in shoot elongation in the fringe at Bocas and Twin Cays. In the scrub zone, +P increased growth at Twin Cays (HSD adjusted $P < 0.001$) and Bocas (HSD adjusted $P = 0.095$), although the rates were much higher for Twin Cays (HSD adjusted $P = 0.047$). +P had no effect on growth in either fringe or scrub zones at IRL. The +N treatment had no effect on growth rates in the scrub zones at Twin Cays and Bocas.

NUTRIENT CONSERVATION

The impact of fertilization on N-, P-, and K-resorption efficiencies varied by location and zone (Figure 4a–c). For N-resorption efficiency (NRE), there was a significant three-way interaction among location, zone, and nutrient enrichment (see Table 3; Figure 4a). Values ranged from 26% to 68%. In control trees at all locations, NRE was consistently highest for the fringe. At IRL, +N caused a slight decline in values for fringe but not scrub trees. At Twin Cays, +N had no effect on NRE in the fringe where growth was N limited. However, +P caused an approximately 40% increase in NRE for the P-limited scrub trees (HSD adjusted $P < 0.001$). Although +N had no effect on the growth of scrub trees at Twin Cays, it did result in a slight increase in NRE. Overall, values for NRE were lowest at Bocas.

There were significant two-way interactions among nutrient enrichment × location and nutrient enrichment × zone on P-resorption efficiencies. However, the three-way interaction among nutrient enrichment × location × zone was not significant (see Table 3, PRE; Figure 4b). PRE values ranged from 36% to 80%. Overall, IRL had the lowest PRE. Here, values for control fringe and scrub trees were approximately half those at Twin Cays and Bocas where values were similar. +N caused a slight increase in PRE for IRL fringe and scrub trees. At Twin Cays and Bocas, +N had no effect in either zone, but +P caused an approximately 50% decrease in PRE for scrub trees and an approximately 25% decrease for fringe trees.

For K-resorption efficiency (KRE), we found a significant three-way interaction of nutrient enrichment × location × zone (see Table 3; Figure 4c). In the IRL, values were uniformly low but positive in both zones, and nutrient enrichment had no effect. For control fringe trees at all locations, KRE was consistently positive. Overall, the lowest KRE values occurred at Twin Cays. The negative values for senescent foliage from control scrub trees at Twin Cays and Bocas indicated that K accumulated in leaves rather than being resorbed by the plant during senescence. At Twin Cays and Bocas, +P caused a significant increase in KRE by scrub trees, but had little effect on fringe trees. However, +N had no significant effect on KRE in either zone.

Fertilization also had striking and complex effects on resorption proficiencies, measured as the $\%N_{\text{senesced leaf}}$, $\%P_{\text{senesced leaf}}$, and $\%K_{\text{senesced leaf}}$, that varied by location and zone (Table 3; Figure 5a–c). Concentrations of N, P, and K in senesced leaves were positively associated with their concentrations in green leaves (Spearman ρ values for N, P, and K = 0.52, 0.87, and 0.65, respectively, all significantly different than 0 with $P < 0.0001$). There was no relationship between $\%N_{\text{senesced leaf}}$ and $\%P_{\text{senesced leaf}}$ (Spearman $\rho = 0.03$, $P = 0.66$), but $\%K_{\text{senesced leaf}}$ was significantly correlated with $\%N_{\text{senesced leaf}}$ (Spearman $\rho = 0.19$, $P = 0.02$) and with $\%P_{\text{senesced leaf}}$ (Spearman $\rho = -0.43$, $P < 0.0001$). For NRP, there was a significant three-way interaction among location, zone, and nutrient enrichment (see Table 3; Figure 5a). The $\%N_{\text{senesced leaf}}$ ranged from a low of 0.28% for +P scrub trees at Twin Cays to a high of 0.91% in +N fringe trees at Bocas. For control trees from the fringe and scrub zones, values were similar at IRL and Bocas but were significantly lower at Twin Cays, which indicated increased NRP. +N caused an increase of 20% in $\%N_{\text{senesced leaf}}$ from the fringe at IRL but had little effect on fringe trees at the other locations. In the scrub zone, +N had no effect on $\%N_{\text{senesced leaf}}$ at IRL and Twin Cays, but significantly higher values at Bocas resulted in a decrease in NRP. +P had little effect on either fringe or scrub zones at IRL and Bocas, but it caused a dramatic decrease in $\%N_{\text{senesced leaf}}$ and a corresponding increase in NRP in scrub trees at Twin Cays.

We found the highest levels of $\%P_{\text{senesced leaf}}$ (~0.06%) in the control trees in both zones at IRL, which indicated low PRP compared to Twin Cays and Bocas. Fertilization with +N or +P had no detectable effect on these levels at IRL (Figure 4b; all HSD adjusted $P > 0.5$). Very low levels (~0.01%) of $\%P_{\text{senesced leaf}}$ in both zones at Twin Cays and Bocas indicated high PRP in the range of maximal P resorption (Figure 6). +N had no effect on values in either zone at Twin Cays or Bocas. +P caused the most dramatic increase in $\%P_{\text{senesced leaf}}$, with a concomitant decrease in

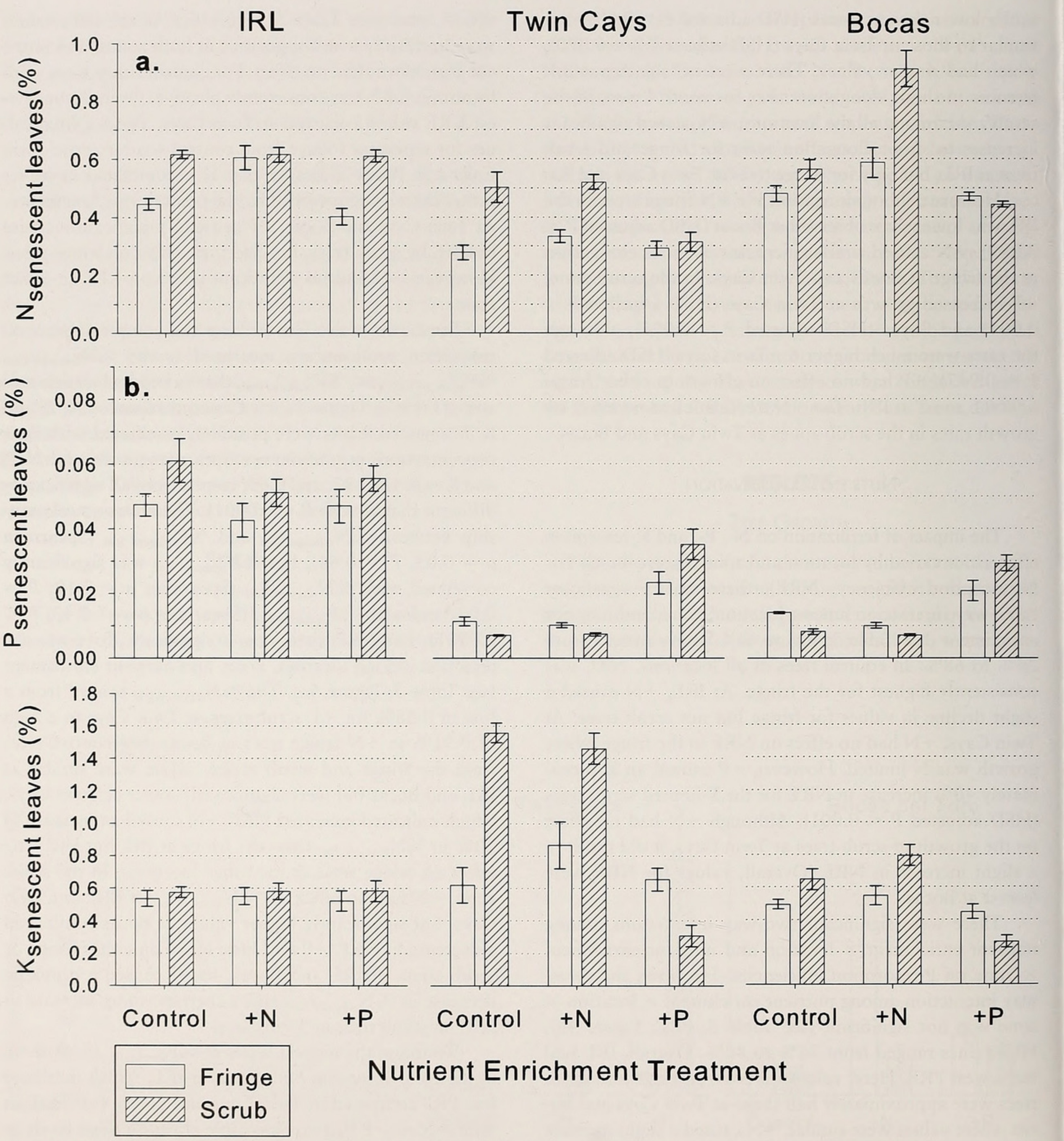

FIGURE 4. Resorption efficiencies for (a) nitrogen (N), (b) phosphorus (P), and (c) potassium (K) at Indian River Lagoon (IRL), Twin Cays, and Bocas del Toro (Bocas) in two zones (fringe = open bars, scrub = hatched bars), and in response to nutrient enrichment with nitrogen (+N) or phosphorus (+P). (IRL and Twin Cays data from Feller et al., 2003a, 2003b).

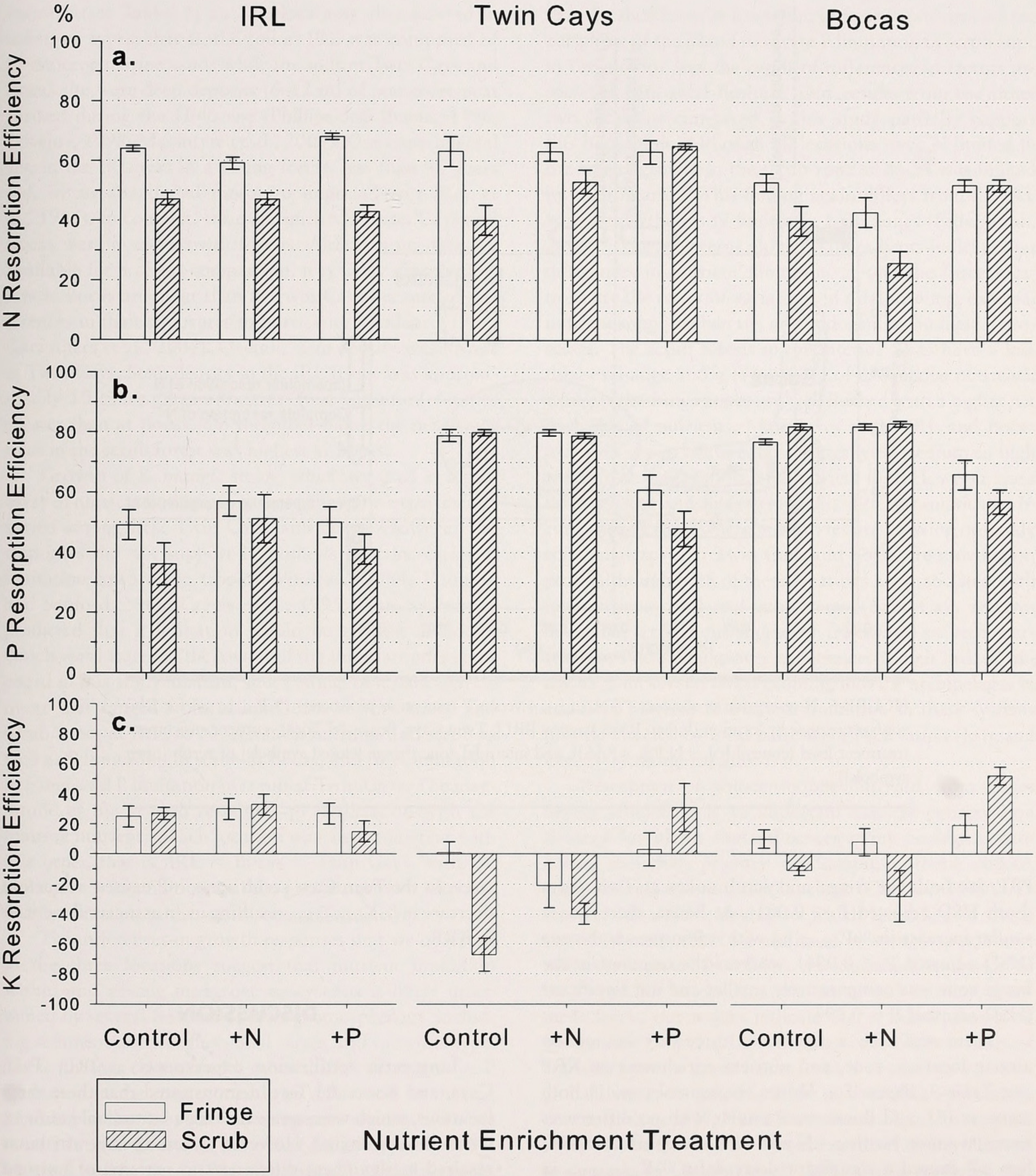

FIGURE 5. Resorption proficiencies for (a) nitrogen, (b) phosphorus, and (c) potassium at Indian River Lagoon (IRL), Twin Cays, and Bocas del Toro (Bocas) in two zones (fringe, scrub), and in response to nutrient enrichment with nitrogen (+N) or phosphorus (+P).

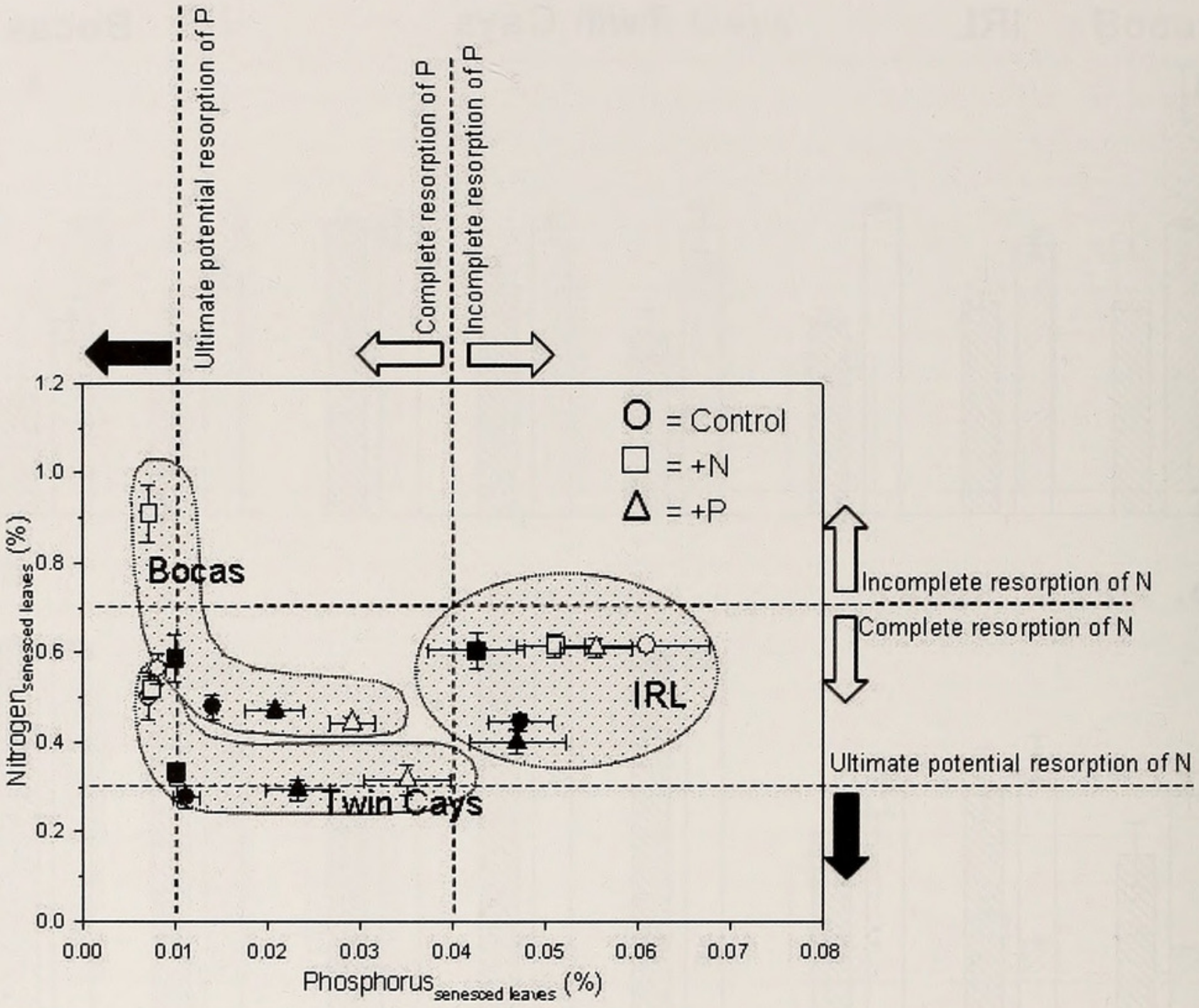

FIGURE 6. N-resorption proficiency (%N$_{\text{senesced leaf}}$) versus P-resorption proficiency (%P$_{\text{senesced leaf}}$) for *Rhizophora mangle* by location (Indian River Lagoon [IRL], Twin Cays, Bocas del Toro), nutrient enrichment treatment level (control [○], +N [□], +P [△]), and intertidal zone (fringe [closed symbols] or scrub [open symbols]).

PRP, for both the fringe and scrub zones at Twin Cays (both HSD adjusted $P < 0.001$). At Bocas, there was a similar increase in %P$_{\text{senesced leaf}}$ with +P in the scrub zone (HSD adjusted $P < 0.001$), whereas the response in the fringe zone was comparatively smaller and not significant (HSD adjusted $P = 0.694$).

There was also a significant three-way interaction among location, zone, and nutrient enrichment on KRP (see Table 3; Figure 5c). Values for control trees in both zones at IRL and Bocas were similar with no differences between zones. Neither +N nor +P had any effect at IRL, but +P caused a significant decrease in %K$_{\text{senesced leaf}}$ in both zones at Bocas. The %K$_{\text{senesced leaf}}$ ranged from a low of 0.26% for +P scrub trees at Bocas to a high of 1.56% in control scrub trees at Twin Cays, which was more than double the K concentrations in senescent foliage of fringe trees. In the Twin Cays scrub zone, +P caused a fourfold decrease in %K$_{\text{senesced leaf}}$, resulting in an associated increase in KRP.

DISCUSSION

Long-term fertilization experiments at IRL, Twin Cays, and Bocas del Toro demonstrated that these three locations, which were arrayed along a latitudinal gradient, were nutrient limited. However, system-specific attributes resulted in significant differences in patterns of nutrient limitation and responses to fertilization. Although the mangrove ecosystems at these locations exhibited similar tree-height gradients dominated by *Rhizophora mangle*, they differed in several hydrogeomorphic and structural features (see Tables 1, 2). The locations also differed in substrate types; that is, the soil at IRL was composed of Pleistocene marine sands while the soils at Twin Cays and Bocas site were deep deposits (6–12 m) of mangrove peat formed during the Holocene (Phillips and Bustin, 1996; Lovejoy, 1998; Macintyre et al., 2004). Our experimental site in the IRL was in a young forest, less than 40 years old, in an abandoned mosquito impoundment (Rey et al., 1986). In contrast, the experiments at Twin Cays and Bocas were in old-growth forests. Although no data are available for a direct comparison, it is likely that the forests at Bocas are older than at Twin Cays because of differences in their exposures to hurricanes (Stoddart, 1963; Carruthers et al., 2005). Overall, stem density was lowest at Twin Cays. Stem density in the IRL fringe was approximately 10 times greater than at Twin Cays and 4 times greater than at Bocas. On the other hand, the density of trees in the scrub forest was highest at Bocas.

Growth of *R. mangle* stems, which we used as a bioassay of nutrient limitation in our fertilization experiments, varied among IRL, Twin Cays, and Bocas. However, the responses did not support Hypothesis 1 of increasing P limitation toward the tropics (Vitousek, 1984; Vitousek and Sanford, 1986; Crews et al., 1995). This hypothesis predicted that P limitation would be greatest at Bocas, which was located at the lowest of the three latitudes compared in this study. Instead, shoot elongation indicated an order that ranged from N limitation in both fringe and scrub zones at IRL, to N limitation in fringe and scrub as well as P limitation in scrub at Bocas, and to N limitation in fringe and P limitation in scrub at Twin Cays. The magnitude of the growth responses to fertilization with the limiting nutrient at each location was also consistent with this order, that is, IRL < Bocas < Twin Cays, with the most severe P limitation and the greatest growth response to P fertilization in the scrub zone at Twin Cays.

The differences in growth responses that we observed at the three locations suggest that nutrient limitation within and among mangrove ecosystems is likely determined by several features of their geomorphology, including sediment/nutrient flux, tidal range, and substrate type. These findings contrast with other studies that attribute P limitation in the tropics mainly to differences in the age of soils between tropical and temperate regions, with the most P-limited forests on the oldest soils (Vitousek, 1984; Vitousek and Sanford, 1986; Crews et al., 1995; Güsewell, 2004; McGroddy et al., 2004; Reich and Oleksyn, 2004; Kerkhoff et al., 2005).

Based on findings from Twin Cays (Feller, 1995; Feller et al., 2003a, 2007), McKee et al. (2002) hypothesized that the shift from N limitation in fringe zone around the periphery of the island to severe P limitation in scrub zone in the interior was the result of differences in factors associated with tidal flushing. Our results from the other two locations compared in this study partially support this hypothesis. Although all locations were N limited in the fringe, growth in the scrub zone at Bocas was limited by both N and P. This finding again differs from the IRL where growth was N limited in both zones (Feller et al., 2003b). These patterns along tidal gradients indicate that differences in nutrient limitation among the three locations are the result of variations in tidal flushing, external nutrient supply, substrate, and endogenous biological processes. The scrub forests in the interior areas have a low tidal exchange and a low supply of exogenous nutrients, whereas the fringe zones are well flushed with a higher net exchange of nutrients. Mangroves at the IRL and Bocas locations are in continental settings with medium to high relief, freshwater inflow, and nutrient flux. However, their tidal regimes and underlying soils differ dramatically. In contrast with IRL where mangroves are growing on sandy soils, mangroves at Twin Cays and Bocas are growing on peat. Although both of these locations are associated with low-nutrient coral reef ecosystems, Twin Cays receives negligible terrigenous inputs of freshwater or sediments whereas Bocas mangroves experiences a high flux of nutrients from several rivers draining into the archipelago. In addition, patterns of nutrient limitation in these systems may be affected by local patterns of N_2 fixation (Joye and Lee, 2004; Borgatti, 2008).

Resorption of phloem-mobile nutrients from leaves during senescence is an important nutrient conservation strategy for plants that influences many ecological processes, including primary production, nutrient uptake, competition, and nutrient cycling (Chapin, 1980). To resolve the relative degree to which latitude and nutrient enrichment affect the ability of *R. mangle* to conserve nutrients invested in foliage, we examined resorption of N, P, and K. Across location, zone, and nutrient treatment levels, our results indicate that a major control of the nutrient concentrations in senesced leaves was nutrient concentration in green leaves, which is consistent with a global dataset compiled by Kobe et al. (2005). Specifically, concentrations of N, P, and K in senesced leaves were positively associated with their concentrations in green leaves. In contrast to Oleksyn et al. (2003), who predicted that nutrient resorption efficiencies should increase with latitude, we found the lowest efficiencies at IRL, our northernmost location, consistent with Lovelock et al. (2007). We also found the most efficient nutrient conservation for

N and P at Twin Cays, the location positioned at the intermediate latitude. Although the levels to which nutrients were conserved varied by nutrient, location, and zone, the patterns did not fall clearly along a latitudinal gradient. All experimental trees at the three locations, except for the +N trees in the scrub zone at Bocas, had less than 0.7% N concentrations in their senescent leaves, which is within the range of complete resorption in the model proposed by Killingbeck (1996) (see Figure 6). In the Twin Cays fringe and the +P-fertilized scrub trees, the N concentration in senesced leaves was less than 0.3%, which was found to be the maximal level to which N can be reduced in senescent leaves of evergreen species and is regarded by Killingbeck (1996) as the ultimate potential resorption for N. In Killingbeck's model, less than 0.04% $P_{\text{senesced leaf}}$ represents complete resorption of P for evergreens. All experimental trees at Twin Cays and Bocas had values below this threshold and thus exhibited complete P resorption. Moreover, control and +N trees in the scrub and fringe zones at Twin Cays and Bocas had 0.01% $P_{\text{senesced leaf}}$ or less, which is the maximal level to which P can be reduced in senescent leaves in evergreens representing the ultimate potential resorption of P. Comparable levels of $\%P_{\text{senesced leaf}}$ have been reported for mangroves elsewhere (Alongi et al., 2005). In contrast, all the trees at IRL had values for $P_{\text{senesced leaf}}$ greater than 0.04%, which represents incomplete resorption. In contrast to suggestions by Aerts and Chapin (2000), the results presented here indicate there are nutritional controls on nutrient resorption in *R. mangle*. Nutrient enrichment clearly altered resorption of N and P at Twin Cays and Bocas but had no effect at IRL. Enrichment with +P resulted in increases in N and K resorption efficiency and proficiency at Twin Cays and Bocas but had the opposite effect on P resorption. Similarly, +N decreased N resorption, but only in the N-fertilized trees in the scrub zone at Bocas. These findings suggest that P enrichment may have either increased the requirements for N and K in *R. mangle* or it may have increased its physiological capacity to conserve these nutrients during leaf senescence. Increased resorption of N and K in response to +P may also indicate that under P-limiting conditions these nutrients become limiting when P is added to the system. Although we found no relationships between growth and N or P concentrations in green leaves, we did observe a weak but significant relationship between $\%K_{\text{green leaf}}$ and growth rates ($r = 0.230$, $F = 8.723$, $P < 0.01$). These results indicate that K availability may be important to the structure and function of some mangrove forests (Kathiresan et al., 1994), which warrants further study.

In conclusion, our results indicate that nutrient overenrichment of the coastal zone will alter forest structure and nutrient dynamics in mangrove ecosystems. We showed that fertilization altered growth and nutrient conservation in *R. mangle*, but the patterns did not correspond with a latitudinal gradient. Growth was consistently N limited for trees in fringing forests, which have higher water exchange rates compared to scrub forests, supporting the hypothesis of Smith (1984) and McKee et al. (2002) that open systems are more likely to be N limited than P limited. In the IRL, scrub trees in the interior of the forest were also N limited. Patterns of nutrient limitation became more complex at lower latitudes. Phosphorus limitations characterized the scrub zone at Twin Cays whereas both N and P limitations were widespread in the scrub zone at Bocas. Our results clearly indicated that the phenotypic potential of *R. mangle* to resorb N, P, and K from senescing leaves varied as a function of nutrient availability, which was driven by differences in hydrology and substrate along latitudinal and tidal gradients.

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