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ECOSYSTEMS

Nutrient Addition Differentially Affects Ecological Processes of *Avicennia germinans* in Nitrogen versus Phosphorus Limited Mangrove Ecosystems

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ABSTRACT

Nutrient over-enrichment is a major threat to marine environments, but system-specific attributes of coastal ecosystems may result in differences in their sensitivity and susceptibility to eutrophication. We used fertilization experiments in nitrogen (N)- and phosphorus (P)-limited mangrove forests to test the hypothesis that alleviating different kinds of nutrient limitation may have different effects on ecosystem structure and function in natural systems. We compared a broad range of ecological processes to determine if these systems have different thresholds where shifts might occur in nutrient limitation. Growth responses indicated N limitation in *Avicennia germinans* (black mangrove) forests in the Indian River Lagoon (IRL), Florida, and P limitation at Twin Cays, Belize. When nutrient deficiency was relieved, *A. germinans* grew out of its stunted form by increasing wood relative to leaf biomass and shoot length relative to lateral growth. At the P-limited site, P enrichment (+P) increased specific leaf area, N resorption, and P uptake, but had no effect on P resorption. At the N-limited site, +N increased both N and P resorption, but did not alter biomass allocation. Herbivory was greater at the P-limited site and was unaffected by +P, whereas +N led to increased herbivory at the N-limited site. The responses to nutrient enrichment depended on the ecological process and limiting nutrient and suggested that N- versus P-limited mangroves do have different thresholds. +P had a greater effect on more ecological processes at Twin Cays than did +N at the IRL, which indicated that the P-limited site was more sensitive to nutrient loading. Because of this sensitivity, eutrophication is more likely to cause a shift in nutrient limitation at P-limited Twin Cays than N-limited IRL.

Key words: *Avicennia germinans*; Belize; fertilization experiment; growth; herbivory; Indian River Lagoon; loss of yield; nutrient resorption; biomass allocation; nutrient over-enrichment

INTRODUCTION

Nutrient over-enrichment is a global threat to marine environments (NRC 2000). Yet, system-specific attributes within estuarine and coastal

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ecosystems may result in large differences in their sensitivity and susceptibility to eutrophication (Cloern 2001). Ulanowicz and Abarca-Arenas (1997) further predicted that different ecological processes within coastal ecosystems may also have different patterns of nutrient limitation. Thus, a major challenge for ecologists is to develop a predictive and holistic understanding of how nutrient loading alters ecosystem function and stoichiometry of coastal systems (Downing 1997; Sterner and Elser 2002). For example, will nitrogen (N)-limited wetlands respond to increased nutrients in a way comparable to phosphorus (P)-limited systems? Nutrient loading, which is usually measured in terms of primary productivity, may also alter faunal communities, trophic linkages and other indirect interactions (Robertson and others 1992). In coastal systems, the complex suite of direct and indirect responses to nutrient over-enrichment includes changes in the distribution and biomass allocation of plants, sediment biogeochemistry, nutrient dynamics, and habitat quality (McKee and others 2002; Pennings and others 2005).

Mangrove forests have been shown to vary naturally from N to P limitation (Boto and Wellington 1983; Chen and Twilley 1999; McKee and others 2002; Feller and others 2003a, b; Lovelock and others 2004). These intertidal wetlands dominate tropical and subtropical coastlines with a specialized flora adapted to waterlogged, saline conditions (Ball 1988) and occur along a gradient from oligotrophic to eutrophic conditions. In nutrient-rich riverine systems or bird rookeries of the Neotropics, the red mangrove, *Rhizophora mangle* L., grows to more than 40 m tall (Golley and others 1975). Whereas in nutrient-poor areas behind the coastal fringe or on offshore islands, *R. mangle* forests are dominated by vast stands of stunted or 'dwarf' trees no more than 1.5 m tall (Lugo 1997; Rodriguez and Feller 2004). Although many factors may influence nutrient cycling in these systems (for example, ion retention, nutrient uptake efficiency, investment in chemical defenses, root turnover rates, detritus burial by crabs, variations in tidal inundation, sediment type, rainfall, climatic disturbances, and topography), mangroves are thought to flourish in such nutrient-poor environments primarily as the result of efficient mechanisms for retaining and recycling nutrients (Twilley and others 1986; Robertson and others 1992).

The objective of this study was to test the hypothesis that alleviating different kinds of nutrient limitation will have different effects on ecosystem structure and function in natural systems (Littler and others 1988; Ulanowicz and Abarca-Arenas 1997; Feller and others 2003a, b; Sundareshwar and others 2003). A comparison of fertilization experiments in N- versus P-limited forests at Twin Cays, Belize and the Indian River Lagoon (IRL), Florida provides a model system to test this hypothesis. At Twin Cays, stunted *R. mangle* in the interior of small mangrove islands were P-limited, and P enrichment (+P) caused dramatic changes in growth, nutrient dynamics, and herbivory (Feller 1995). In the IRL, N enrichment (+N) caused similar responses in stunted *Avicennia germinans* L. (black mangrove) (Feller and others 2003b). In the present study, we investigated the effects of +N and +P on a broad suite of ecological processes in an *A. germinans* forest at Twin Cays and compared these responses to a parallel experiment in the IRL. We addressed the following questions. (1) Does +P to stunted *A. germinans* at Twin Cays lead to increased growth similar to +N at IRL? (2) As nutrient availability increases, do the mechanisms used by *A. germinans* to recycle and conserve the limiting nutrient respond similarly in N and P-limited systems? (3) Does increased nutrient availability cause similar changes in plant nutritive quality and herbivory in *A. germinans* growing under different nutrient limitations? By comparing this range of response variables in N- and P-limited ecosystems, we will determine if different community components and ecological processes within and among mangrove ecosystems have different patterns of nutrient limitation and if these systems have different thresholds for shifts in nutrient limitation.

MATERIALS AND METHODS

Study Sites

The vegetation at Twin Cays and the IRL was dominated by *R. mangle*, *A. germinans*, and *Laguncularia racemosa* (L.) Graetn.f (white mangrove). Twin Cays is a peat-based, 92-ha archipelago, 12 km off shore (16°50′N, 88°06′W) and receives no terrigenous inputs of freshwater or sediments (Macintyre and others 2004). Since 1980, these islands have been the primary study site for the Smithsonian Marine Field Station on nearby Carrie Bow Cay (Rützler and others 2004). The IRL site is in a 122-ha stand of mangroves in the Avalon State Park on the lagoon side of North Hutchinson Island, St. Lucie County, Florida (27°33′N, 80°20′W), in an abandoned mosquito control impoundment. The soil is composed primarily of sand. Descriptions of forest structure, hydro-edaphic conditions, growth, nutrient dynamics, and photosynthesis in the IRL site were previously reported (Feller and others 2003b; Lovelock and Feller 2003).

Experimental Design

Fertilization experiments were set up at Twin Cays and IRL in January 1997. Both sites were characterized by tree-height gradients perpendicular to the shoreline (Feller and others 2003a, b). At Twin Cays, the experiment was placed in a 0.21-ha stand dominated by old growth *A. germinans* of uniformly low stature trees in the interior of the island. This stand was surrounded by almost pure *R. mangle*, with a fringe stand (5–6 m tall) to the north, a moribund stand (3–4 m tall) to the west, and a shallow, sparsely vegetated pond to the east. The area was flooded and drained by tidal water that entered through a creek system opening onto the main channel of Twin Cays. At IRL, the experiment was in a 0.5-ha stand dominated by stunted *A. germinans* and scattered *L. racemosa* in the interior of an abandoned mosquito impoundment. This site was adjacent to a narrow *R. mangle* fringe (5–6 m tall) to the west along the open water and a coastal scrub forest to the east. Tidal exchange was through culverts into a man-made canal around the perimeter of the impoundment. We used the point-centered quarter method (Cintrón and Shaeffer Novelli 1984) to characterize forest structure at both locations.

Our experimental design was a 3 × 2 factorial (nutrient enrichment × location) analysis of variance (ANOVA) that involved three levels of the nutrient treatment (control, +N, +P) and two locations (Twin Cays, IRL). To minimize the disturbance to the system, we fertilized individual trees rather than plots, which would require heavier and more extensive applications of fertilizers. At Twin Cays, we selected 8 replicate trees, approximately 10 m apart, for a total of 24 trees. For the IRL site, we used 9 replicate trees (27 total) previously described in Feller and others (2003b). Nutrient treatment was randomly assigned within each site. The three nutrient treatment levels were as follows: +N, as granular urea (NH^{+}_{4}, 45:0:0); +P, as triple superphosphate (P_2O_5, 0:45:0); and control (no fertilizer added), as described in Feller (1995). A dose (150 g) of fertilizer was placed in each of two holes (7 cm diameter × 30 cm deep), cored into the substrate on opposing sides of a tree beneath the dripline of the canopy. Each hole was sealed with a peat plug. 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 our study site is flooded at high tides, and fertilizer broadcasted on the surface would be washed away. This method is also consistent with natural patterns in these offshore mangrove islands, where nutrients are delivered by tidally driven subsurface hydrology and sheet flow rather than overland runoff. Trees at both sites were fertilized twice a year at approximately 6-month intervals from January 1997 through April 2001.

Hydro-edaphic Conditions

Measurements of soil and porewater were conducted approximately 1 m from the bole of each experimental tree at Twin Cays and IRL. Data for the IRL site were previously reported in Feller and others (2003b). Soil redox potentials at 1 and 15 cm depths were measured with bright platinum electrodes equilibrated in situ for 1 h (McKee and others 1988). Interstitial water was collected from a depth of 15 cm with a probe attached to a suction device. A portion of the sample was filtered (0.45 μ) and frozen until analysis of PO_4^- and NH_4^+ concentrations on a LACHAT system (QuickChem 8000 Series FIA, Zellweger Analytics, Milwaukee, Wisconsin, USA). Analytical procedures were checked by use of external standards and blanks as specified by the instrument manufacturer. An unfiltered aliquot of each water sample was added to an equal volume of an antioxidant buffer and was analyzed for sulfide with a sulfide micro-electrode. Additional unfiltered aliquots were used to measure pH and salinity.

Growth Responses and Biomass Allocation

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 both sites at 6-mo intervals. The shoots were labeled with small aluminum tags affixed to the twig with vinyl-coated wire. Leaves in the apical position on each shoot were labeled with waterproof ink on their abaxial surfaces to define the starting point of each measurement period. To determine biomass allocation, we harvested the tagged shoots at the end of 4 y and measured shoot length and biomass, number of nodes, and leaf area and biomass. We used mean leaf area and biomass of fully expanded leaves to estimate annual leaf area and biomass production per shoot.

Leaf Nutrient Dynamics

To assess internal nutrient dynamics, we measured N and P concentrations in green and senescent leaves and calculated nutrient resorption efficiency. Resorption efficiency was calculated as (Chapin and Van Cleve 1989):

$$\text{resorption efficiency} = \frac{[\mathrm{N}] \text{ or } [\mathrm{P}]_{\text{green leaf}} - [\mathrm{N}] \text{ or } [\mathrm{P}]_{\text{senescent leaf}}}{[\mathrm{N}] \text{ or } [\mathrm{P}]_{\text{green leaf}}} \times 100. \quad (1)$$

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, Nebraska, 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 Perkin-Elmer 2400 CHN Analyzer at the Smithsonian Environmental Research Center, Edgewater, MD. Concentrations of P were determined using an inductively coupled plasma spectrophotometer (ICP) by Analytical Services, Pennsylvania State University, Pennsylvania, USA.

Herbivory

We measured herbivory by leaf-mass consumers (that is, folivores) and leaf gallers. The folivores were primarily crickets and caterpillars that fed on expanded leaves and caused holes, marginal bites, and scrapes. To calculate rates of damage by folivores, we selected ten leaves in penapical positions with no pre-existing damage. After 6 months, the leaves were harvested and photographed, and the percent leaf area damage was quantified with image analysis software (SPSS, SigmaScan Pro4®). Because rates of folivory from this sampling effort were at or near zero, we also measured the damage that accumulated over the entire leaf lifespan. For this method, we collected and recorded images of ten senescing leaves in basal positions from shoots in the outer part of the canopy of each experimental tree.

The leaf gallers were two species of psyllids (Homoptera: Psyllidae: *Telmapsylla* sp. and *Leuronota* sp.) that fed on expanding leaves and thereby caused a reduction in leaf size (that is, loss of yield). Following emergence of the psyllid adults, a galled leaf continued to develop, but the resulting mature leaf was misshapen and smaller than ungalled leaves. To measure the effects of nutrient enrichment on this loss of yield, we determined the proportion of misshapen leaves per harvested shoot. To quantify the effect on leaf size, we measured 115 pairs of fully mature leaves with one member previously galled and one member ungalled. These values were used to calculate the leaf area per shoot and the loss of yield.

Statistical Analysis

Our data were grouped by nutrient treatment (control, +N, +P) and location (Twin Cays, IRL) and were analyzed as a two-way analysis of variance (ANOVA) using SigmaStat 3.1 (2004 SYSTAT Software, Inc.). When an ANOVA found a significant effect, we used the Holm–Sidak test to examine pairwise differences within and among the treatment levels. The normality assumption was tested with the Kolmogorov–Smirnov test, and the equal variance assumption was tested with the Levene median test. For heterogeneous variances, continuous data were transformed using logarithms and non-continuous data (counts) using the square root. Regression procedures were used to examine the associations between and among plant, edaphic, and herbivory variables. To examine broad patterns in the responses by *A. germinans* to nutrient enrichment at the two sites, we used principal components analysis (PCA) to ordinate the 20 variables measured in this study (PC-Ord 5.0, MjM Software Design, Gleneden Beach, Oregon, USA).

RESULTS

Forest Structure

Stunted *A. germinans* (1.0–1.4 m tall) dominated both sites. The Twin Cays stand was open with a tree density of 2,000 stems per ha compared to a much denser canopy at IRL of approximately 40,000 stems per ha. However, the trees were older with larger stem diameters at Twin Cays with a basal area almost half that of the IRL site.

Hydro-edaphic Conditions

The soil at Twin Cays was peat, consisting mainly of fine roots and root fragments, and characterized by low bulk density (Table 1). By comparison, the IRL site was characterized by sandy soil with a high bulk density. Porewater salinity was similar and slightly hypersaline at both sites. Soils at Twin Cays were more reduced with higher sulfide concentrations. Porewater concentrations of NH_4-N and PO_4-P at control trees also indicated high availability of N as compared to P at Twin Cays. Nutrient treatments had minor effects on salinity, pH, and redox potentials, but significantly affected porewater concentrations of N or P.

Plant Growth

There was a significant nutrient enrichment × location interaction on growth rates of *A. germinans* ($F_{2,45}$= 109, $P \leq 0.0001$). Shoot elongation for control trees was similar for the two locations. However, +P and +N caused dramatic increases in shoot elongation at Twin Cays and IRL, respectively (Figure 1A). The growth of +P trees at Twin Cays was significantly lower than growth of the +N trees at the IRL. The +N treatment had no effect on growth rates at Twin Cays, and +P had no effect at IRL.

Nutrient enrichment also altered the distribution of biomass in tree canopies at both locations (Table 2). The leaf area ratio (LAR, cm^2/g, that is, the ratio of leaf area to total biomass) and specific leaf area (SLA, cm^2/g, that is, the ratio of leaf area to leaf biomass) at Twin Cays were significantly lower than at IRL for all nutrient enrichment levels. +P caused a significant decrease in LAR and increase in SLA at Twin Cays, but +N had no effect on either ratio at IRL. At Twin Cays, SLA was correlated with shoot growth (r = 0.691, $F_{1,22}$= 20.113, P = 0.000). The shoot weight ratio (SWR, g/g, that is, stem biomass to total biomass) and stem length to stem biomass ratio (SL:SB, cm/g) for control trees were higher at Twin Cays than IRL. The SWR values for control trees indicated that the woody portion of the shoots made up 20% of the total biomass at Twin Cays compared to 7% at IRL. But, the proportion allocated to wood biomass increased by more than twofold (~40% of total biomass) in response to +P at Twin Cays and by fourfold (~28%) in response to +N at IRL. Both SL:SB and the leaf area to shoot length ratio (LA:SL, cm^2/g) decreased in response to +P at Twin Cays and +N at IRL.

Nutrient Dynamics

Nutrient enrichment had striking and complex effects on the dynamics of leaf N and P that varied by location (Figure 2A–L). For control trees, the values were higher for %N and lower for %P at Twin Cays than IRL (Figure 2A–D). Values for %N decreased in response to +P at Twin Cays and increased in response to +N at IRL. At Twin Cays, +P also caused a marked increase in %P in green but not senescent leaves. The N% of green leaves and porewater salinity were correlated at the two locations (r = 0.398, $F_{1,49}$ = 9.030, P = 0.004). The C:N ratios of senescent leaves from control trees were over three times higher at IRL with signifi-

Table 1. Summary of Porewater and Soil Variables at Twin Cays and Indian River Lagoon (IRL) to Nutrient Enrichment (control, +N, +P)

	Twin Cays			IRL			ANOVA		
	Control	+N	+P	Control	+N	+P	Treatment	Location	Treatment × Location
Porewater									
Salinity mg/l	57 ± 3	60 ± 2	59 ± 3	49 ± 1	57 ± 2	55 ± 1	3.52^{*}	7.13^{**}	0.67^{NS}
pH	6.40 ± 0.1	6.50 ± 0.1	6.40 ± 0.1	6.80 ± 0.03	6.90 ± 0.04	6.6 ± 0.04	5.88^{**}	58.7^{****}	1.49^{NS}
Sulfide (mM)	1.26 ± 0.22	1.65 ± 0.31	1.09 ± 0.31	0.08 ± 0.02	0.11 ± 0.04	0.04 ± 0.01	1.61^{NS}	74.9^{****}	1.03^{NS}
NH_4-N (uM)	252 ± 63	560 ± 132	92 ± 54	16 ± 3	3349 ± 1166	15 ± 3	7.73^{**}	3.42^{NS}	4.85^{*}
PO_4-P (uM)	4.53 ± 0.88	6.74 ± 0.96	4.79 ± 0.56	22.03 ± 1.82	30.98 ± 8.82	184.87 ± 28.12	21.8^{****}	43.1^{****}	22.3^{****}
Soil									
% Organic matter	74 ± 0.8	75 ± 0.8	75 ± 0.4	1.93 ± 0.16	1.99 ± 0.12	1.89 ± 0.09	0.65^{NS}	37849^{****}	0.54^{NS}
Bulk density (g/cm^3)	0.18 ± 0.01	0.19 ± 0.01	0.19 ± 0.01	1.17 ± 0.03	1.20 ± 0.02	1.15 ± 0.04	0.43^{NS}	1836^{****}	0.39^{NS}
Eh 1 cm (mV)	−85 ± 19	−105 ± 32	43 ± 63	192 ± 26	193 ± 18	173 ± 15	2.50^{NS}	87.8^{****}	4.48^{*}
Eh 15 cm (mV)	−93 ± 27	−123 ± 36	−12 ± 46	95 ± 27	74 ± 23	49 ± 12	1.11^{NS}	39.6^{****}	3.47^{*}

Values are the mean ± SE; N = 8 and 9, respectively.
*Results of ANOVA are given with F-ratios and significance indicated by * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, **** ≤ 0.0001, NS = not significant.*

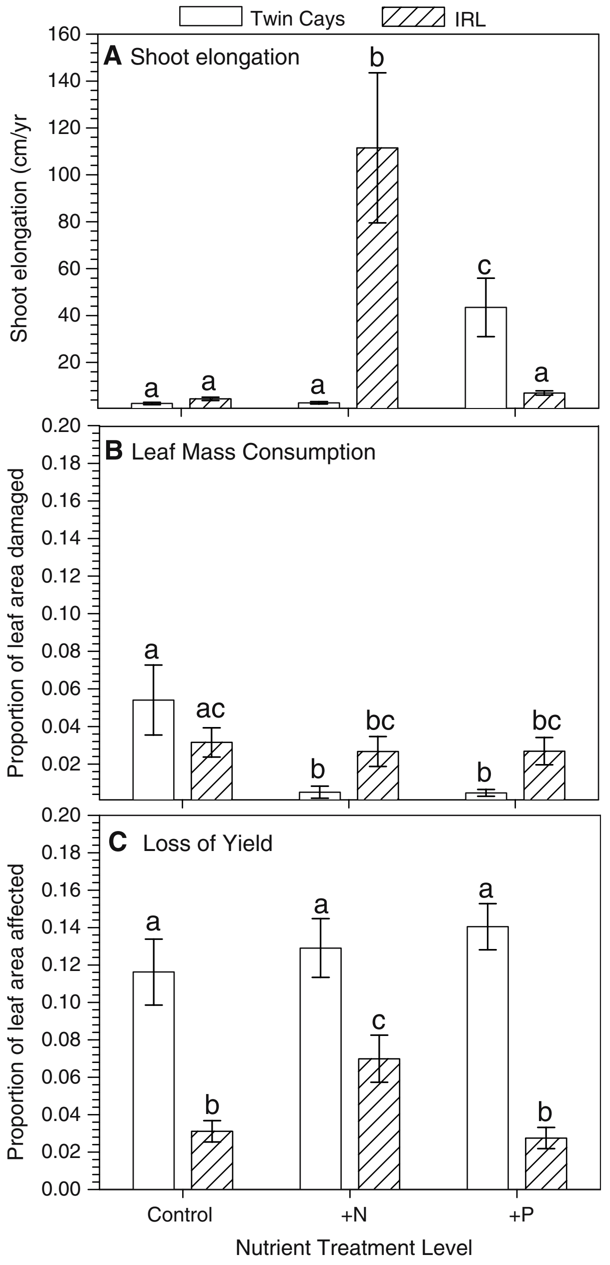

Figure 1. Comparison of the effects of nutrient enrichment (Control, +N, +P) on *Avicennia germinans* for **A** stem elongation (cm/year), **B** herbivory by leaf mass consumers (folivores), and **C** herbivory by the loss of yield that resulted from feeding by two psyllids at Twin Cays, Belize, and the Indian River Lagoon (IRL), Florida. Values are means (±1 SE). The *same lowercase letter* indicates that treatment means are not significantly different ($P < 0.05$); $N = 51$ trees.

cantly lower values in response to +N (Figure 2E, F). At Twin Cays, +P caused C:N values to increase by a factor of 2.5 relative to control trees. The C:P ratios of senescent leaves at Twin Cays were over twice as high as IRL (Figure 2J), but values decreased significantly in the +P trees. There was also a significant nutrient enrichment × location interaction for N resorption efficiency (Figure 2K, L). Control and +N trees at Twin Cays had very low N resorption, but values increased dramatically in response to +P. This contrasted with the IRL where N resorption efficiency increased in response to +N. P% of green leaves was correlated with N resorption efficiency at the two locations ($r = 0.520$, $F_{1,51}$= 18.147, $P < 0.001$). Other than a slight increase in the +N trees at IRL, P resorption efficiency did not vary by nutrient enrichment or location (Figure 2L).

Herbivory

Short-term rates of folivory were very low at both sites with no difference among nutrient enrichment levels ($P > 0.05$). The folivory that accumulated over the entire leaf lifespan was also low and variable with a slight but significant difference among nutrient levels ($F_{2,48}$= 4.400, $P = 0.018$), but not between locations ($P > 0.05$; Figure 1B). Overall, folivory correlated with SLA ($r = 0.380$, $F_{1,43}$= 7.768, $P = 0.008$), but not with leaf N, P, or C:N ratios ($P > 0.5$).

The most significant mode of herbivory was loss of yield caused by leaf-galling psyllids ($F_{1,114} = 53.032$, $P < 0.001$). Leaves galled by *Telmasylla* sp. and *Leuronota* sp. were 37.3 ± 2.2% smaller than ungalled leaves. Higher proportions of the total leaves on the fertilized trees were galled at Twin Cays than at IRL ($F_{1,45}$= 85.750, $P < 0.001$). At Twin Cays, 34.2 ± 2.3% of the leaves were galled, but with no difference by nutrient enrichment. At IRL, the +N trees had a significantly higher percentage of galled leaves (18.7 ± 3.4%) than did the control (8.3 ± 1.5%) or +P trees (7.4 ± 1.5%). The loss of yield was two to four orders of magnitude greater than damage by folivores (Figure 1C). There was a significant nutrient enrichment × location interaction on loss of yield ($F_{2,45}$= 3.918, $P = 0.027$). Values were significantly higher at Twin Cays with no significant differences among the nutrient enrichment levels. This contrasts with the IRL where +N resulted in a significant increase in psyllid damage. Of the leaf variables measured in this study, loss of yield was best predicted from a linear combination of C:N ($r^2 = 0.378$; $F_{1,45}$= 27.365, $P < 0.001$) and SLA ($r^2 = 0.483$; $F_{1,45} = 27.365$, $P = 0.005$).

Results from the PCA summarized the 20 response variables that we measured and identified two axes with eigenvalues that accounted for 64% of the variation. Component loading indicated that

Table 2. Biomass Allocation Ratios for *Avicennia germinans* at Twin Cays and IRL to Nutrient Enrichment (control, +N, +P)

		Nutrient enrichment treatment		
Biomass allocation ratio		Control	+N	+P
LAR (cm^2/g)	Twin Cays	$29.43 \pm 1.13^{a*}$	$29.23 \pm 1.02^{a*}$	$23.52 \pm 1.22^{b*}$
	IRL	38.49 ± 1.40^{ab}	34.31 ± 1.68^{a}	42.33 ± 2.15^{b}
SLA (cm^2/g)	Twin Cays	$36.53 \pm 0.67^{a*}$	$37.76 \pm 0.98^{a*}$	43.33 ± 1.27^{b}
	IRL	45.77 ± 0.89^{a}	48.44 ± 1.32^{a}	45.44 ± 1.46^{a}
LWR (g/g)	Twin Cays	$0.80 \pm 0.02^{a*}$	0.77 ± 0.03^{a}	$0.54 \pm 0.019^{b*}$
	IRL	0.93 ± 0.01^{a}	0.69 ± 0.04^{b}	0.93 ± 0.01^{a}
SWR (g/g)	Twin Cays	$0.20 \pm 0.02^{a*}$	0.23 ± 0.02^{a}	$0.46 \pm 0.03^{b*}$
	IRL	0.07 ± 0.01^{a}	0.31 ± 0.04^{b}	0.07 ± 0.01^{a}
SL:SB (cm/g)	Twin Cays	$29.13 \pm 0.99^{a*}$	$27.45 \pm 1.63^{a*}$	$15.35 \pm 0.92^{b*}$
	IRL	21.20 ± 1.41^{a}	11.93 ± 1.66^{b}	20.45 ± 1.56^{a}
LA:SL (cm^2/cm)	Twin Cays	28.62 ± 4.21^{a}	$26.32 \pm 4.36^{a*}$	$17.29 \pm 1.86^{b*}$
	IRL	26.40 ± 0.00^{a}	12.05 ± 1.90^{b}	35.47 ± 6.04^{a}

Leaf area ratio (LAR) = leaf area (cm^2)/leaf + stem (g); leaf weight ratio (LWR) = leaf (g)/leaf + stem (g); shoot weight ratio (SWR) = stem (g)/leaf + stem (g); specific leaf area (SLA) = leaf area (cm^2)/leaf (g); stem length (cm):stem (g) (SL:SB) = stem length (cm)/stem (g); leaf area (cm^2):stem length (g) (LA:SL) = leaf area (cm^2)/stem length (cm). Values are means (±: 1SE). In a row, values with the same lowercase letter are not significantly different. An asterisk indicates significant difference between locations for each nutrient treatment level. N = 8 trees per treatment level at Twin Cays and 9 trees per treatment at IRL.

Axis I represented 11 of the 12 that variables were highly correlated (that is, component loadings >0.65) with leaf nutrients in roughly equal proportions, while Axis II represented primarily growth and biomass allocation (Table 3). When scores on these axes were plotted in Figure 3, Twin Cays and IRL trees differed dramatically in terms of leaf nutrients (that is, groups are widely separated along Axis I), but were relatively similar in terms of growth/biomass allocation (that is, groups are similar on Axis II). At Twin Cays, +P caused shifts along both axes, whereas at IRL, +N caused a shift mainly along Axis II. When nutrient limitation was alleviated, regardless of nutrient identity (N or P), trees at Twin Cays and IRL changed in growth/biomass allocation (shifts up along Axis II), and the differences in leaf nutrient characteristics between the two locations almost disappeared as the groups converged along Axis I.

DISCUSSION

The results from this study demonstrated that the system-specific attributes of N or P limitation were important in these mangrove ecosystems and led to large differences in their sensitivity and susceptibility to nutrient loading. Although stunted *A. germinans* of similar height dominated both experimental locations, the Twin Cays site was more open with greater basal area per tree. From leaf scar counts, leaf production rates, and tree architecture, we estimate that the stunted trees in the interior of Twin Cays were 50–100 years old (Feller 1995). In comparison, the trees in the IRL location were less than 30 years old (Rey and others 1986). The two locations also differed in substrate types, that is, soil at IRL consisted of terrigenous sand whereas the soil at Twin Cays site was peat, composed primarily of roots (Macintyre and others 2004). Under control conditions, porewater N:P availability was indicative of P limitation at Twin Cays (molar ratio = 132) and N limitation at IRL (molar ratio = 1.7). Addition of N or P fertilizer generally increased porewater concentrations of NH_4 and PO_4. However, since porewater concentrations were also affected by root uptake, the patterns reflected growth stimulation by +N or +P relative to limiting nutrient.

At Twin Cays, +P stimulated the growth of *A. germinans*, which indicated that this site was P-limited. These results contrasted with the IRL where a previous experiment determined that location to be N-limited (Feller and others 2003b). At both sites, we found that experimentally alleviating nutrient limitation reduced the structural distinctions between dwarf and taller growth forms of this species, similar to results reported for *R. mangle* (Lovelock and others 2006a). Addition of the limiting nutrient also altered *A. germinans* allocation of biomass to leaves relative to stems (Table 2). At Twin Cays, +P resulted in a significant increase in allocation to shoot biomass. Similarly, +N caused a significant increase in shoot biomass of trees at IRL. At both locations, the ratio of leaf area

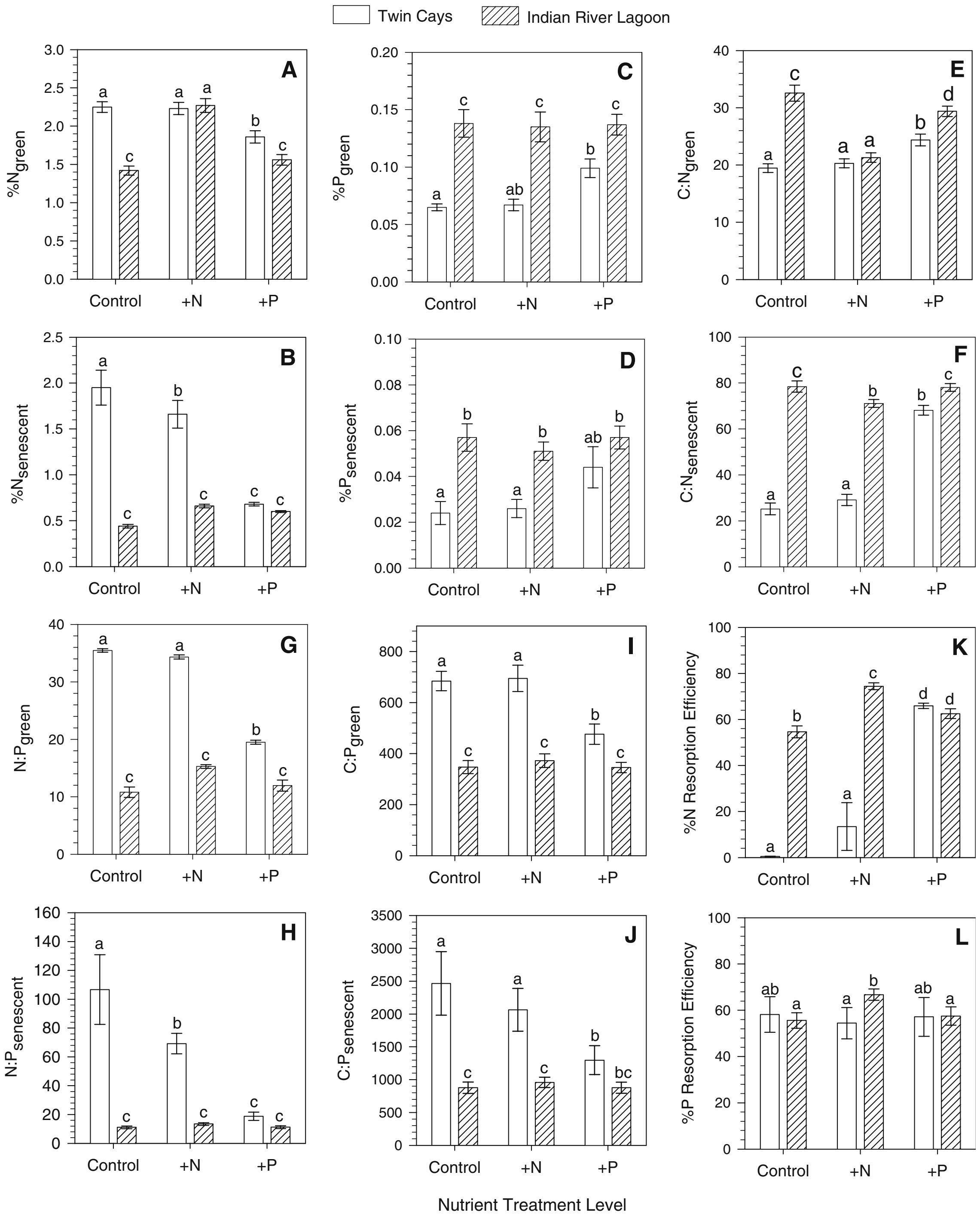

Figure 2. **A–D** Nitrogen and phosphorus content in green and senescent leaves; **E–J** C:N, N:P, and C:P ratios of green and senescent leaves; and **K–L** N and P resorption efficiencies based on percent of dry mass for dwarf *A. germinans* at Twin Cays, Belize, and the IRL, Florida, in response to nutrient enrichment (Control, +N, +P). Values are means (±1 SE). The *same lowercase letter* indicates that means are not significantly different ($P < 0.05$); $N = 51$ trees.

to total biomass of the stems was highest in control trees, which suggests that under nutrient-limiting conditions resource allocation to leaf area was maximized. The LWR for control trees at Twin Cays and IRL indicated that approximately 79 and 58%, respectively, of the shoot biomass was invested in leaves. However, when supplemented with the limiting nutrient, the proportion of resources going

Table 3. Component Loading of the First Two Principal Components for the 20 Key Response Variables in *A. germinans* at Twin Cays, Belize and IRL, Florida, in Response to 4 years of + N or +P Enrichment

	Eigenvectors	
Response variables	PC I	PC II
N:P$_{green}$	−0.96*	0.01
N:P$_{senescent}$	−0.96*	−0.12
C:N$_{senescent}$	0.92*	0.11
C:P$_{green}$	−0.90*	−0.04
%N$_{senescent}$	−0.88*	−0.20
%P$_{green}$	0.87*	0.04
C:P$_{senescent}$	−0.81*	−0.05
%P$_{senescent}$	0.80*	0.04
SLA	0.79*	0.29
C:N$_{green}$	0.72*	−0.40
%N$_{green}$	−0.66*	0.40
N resorption	0.64	0.38
Loss of yield	−0.64	0.44
LAR	0.59	−0.58
SL:SB	−0.52	−0.46
LWR	0.25	−0.90*
Growth	0.16	0.72*
Folivory	−0.09	−0.35*
LA:SL	−0.02	−0.71
P resorption	0.00	0.14

Nutrient ratios are based on mass. Asterisks mark loadings ≥ 0.65.

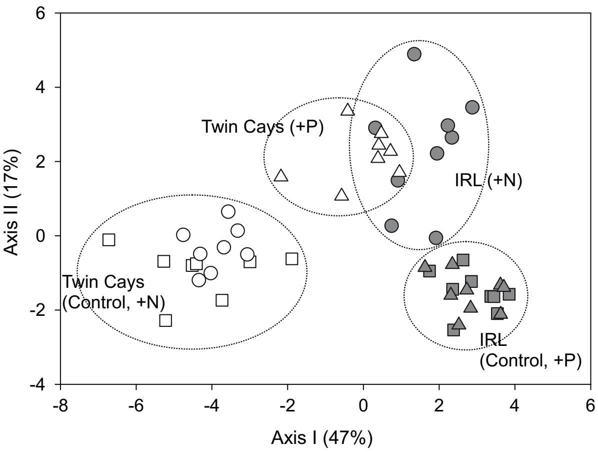

Figure 3. Principal components analysis of 20 key response variables for *A. germinans* trees at Twin Cays, Belize and IRL, Florida, in response to nutrient enrichment. *Symbols* represent three nutrient enrichment levels: control (*squares*); +N (*circles*); +P (*triangles*) at Twin Cays (*open symbols*) and IRL (*closed symbols*).

to woody biomass increased. The ratio of leaf area to stem length (LA:SL) also decreased at both locations when nutrient limitation was alleviated. This increase in woody biomass in response to nutrient enrichment was mainly due to shoot elongation rather than increases in girth, as evidenced by a large decrease in the ratio of shoot biomass to shoot length. These results suggest that when nutrient deficiency is relieved, the dwarf *A. germinans* trees will shift strategies and will grow out of their stunted form by increasing investment in wood relative to leaf biomass and stem length relative to lateral growth.

In many plant species, increases in growth rates with relief of nutrient limitations are achieved through greater investment in leaf tissue and reduced investment in stems and roots (Poorter and Nagel 2000). However, growth enhancements at both Twin Cays and IRL were associated with reduced investment in leaves relative to stem tissue in terminal twigs (Table 2). How then are elevated growth rates achieved? We identify four processes by which growth rates were enhanced despite declining investment in leaf area compared to stem tissue in terminal twigs. (1) Enhanced SLA, which occurred in both Twin Cays and IRL (Table 2), reduced construction and respiration costs. A comparison of SLA for control trees at the two locations indicated that the Twin Cays trees were more sclerophyllous than the IRL trees, and that addition of the limiting nutrient had a greater effect on the ratio of leaf area to leaf biomass of *A. germinans* at Twin Cays than at the IRL. At Twin Cays, SLA correlated significantly with relative growth rates, which is consistent with studies in other nutrient-poor habitats (Maranon and Grubb 1993; Poorter and De Jong 1999). However, at IRL, SLA and growth rates were not significantly correlated. Thus, other factors (below) must contribute to growth enhancements. (2) Maximum photosynthetic rates per unit leaf area increased with relief of nutrient limitation. Enhancement of photosynthesis above that of controls was more pronounced for P-limited plants at Twin Cays compared to N-limited plants at IRL, where enhancements appeared to be seasonal (Lovelock and Feller 2003; Lovelock and others 2006b). (3) With addition of limiting nutrients and increased investment in shoot elongation and the number of shoots (modules), self-shading due to short internodes was reduced while total plant leaf area increased. (4) Additionally, although not measured, investment in roots would also be expected to decline with relief of nutrient limitation, thereby reducing the cost of this component (Poorter and Nagel 2000). The alternate states of N or P limitation may affect allocation to roots in different ways. One prediction, based on relative sensitivities of SLA and photosynthetic rates at Twin

Cays and IRL, is that relief of N limitation reduces investment in roots, whereas relief of P limitation should do so to a lesser extent. However, this hypothesis remains to be tested directly.

Nutrient enrichment also resulted in complex changes to internal nutrient cycling and conservation patterns in *A. germinans* that varied by location. Shaver and Mellilo (1984) predicted that under nutrient-limiting conditions the limiting nutrient would be more tightly conserved via efficient internal recycling mechanisms than under nutrient-replete conditions. However, we found that, regardless of whether N or P was limiting, the resorption of P was incomplete in this species and did not reach maximal physiological levels (Killingbeck 1996). At P-limited Twin Cays, +P caused increased P uptake but had no detectable effect on P resorption efficiency. In contrast, +P did alter how efficiently N was acquired, used, and conserved by *A. germinans*. Under control conditions, the %N in senesced leaves was approximately 2.0% and N resorption was less than 1%. When compared to the 77 species of woody plants summarized by Killingbeck (1996), these values indicated extremely low N resorption proficiency for *A. germinans* in these naturally occurring P-limiting conditions. They also contrast with previous findings for *R. mangle* at Twin Cays where +P caused a decrease in P resorption efficiency from approximately 80 to approximately 30% and an increase in N resorption efficiency from approximately 40 to approximately 65% (Feller and others 1999). Similarly, +N influenced internal P dynamics at our N-limited location at IRL. Comparable results have been reported in other plant systems where both increased N and P stimulated growth (or other processes) because the N supply influenced P dynamics, and vice versa (Güsewell and others 2003; Güsewell 2004). This pattern differs in the IRL where +N also caused an increase in both N and P resorption efficiency. At Twin Cays, however, N resorption increased dramatically in response to +P and thus converged on values similar to control trees at IRL. Leaf %N for the Twin Cays trees also indicated that +P resulted in a decrease in N uptake, which contrasted with the N-limited IRL site where +N decreased N uptake (Feller and others 2003b). In addition, +P dramatically altered the N:P and C:N ratios of senescent leaves, which suggests that P loading may decrease, rather than increase, nutrient cycling in P-limited *A. germinans* forests through its influence on litter quality.

At both Twin Cays and IRL, N dynamics in *A. germinans* leaves were correlated with porewater salinity and leaf %P. Salt resistance is an energy- and nutrient-requiring process because it involves salt tolerance, excretion, and exclusion (Kozlowski 1997). In halophytes such as *A. germinans*, *Spartina alterniflora*, and *Sarcobatus vermiculatus*, the N-rich, osmotically compatible solute, glycine betaine is used in osmoregulation and results in improved water status of tissues (Popp and others 1988). The N required for the synthesis of glycine betaine may increase the N demand and intensify nutrient limitation for *A. germinans* especially under hypersaline conditions (Bradley and Morris 1992; Drenovsky and Richard 2004). Thus, the increased growth by the stunted *A. germinans* at Twin Cays and IRL in response to +P or +N, respectively, may have been in part due to improved osmoregulation as well as relief from nutrient limitation.

Nutrient enrichment also altered herbivory, but the pattern differed by location and functional group of herbivores, that is, folivores and leaf gallers. In some systems, folivores can consume up to 20% of the leaf area and have a major impact on primary production (Cyr and Pace 1993). Here, the folivores that feed externally on leaves accounted for a small fraction of the leaf area. Of the leaf parameters measured, only SLA was correlated with folivory. Despite significant differences in chemical content and nutrient ratios of leaves in response to nutrient enrichment, these variables explained very little of the leaf damage. Thus, these data indicated that increased nutrient availability had little effect on rates of folivory. In contrast, the loss of yield caused by gall-forming psyllids was the most significant form of herbivory in *A. germinans* at both IRL and Twin Cays where it caused a reduction in leaf area by 2–6% and 12–14%, respectively. This type of injury, which is seldom measured in natural systems (Peterson and Higley 2001), has not been measured in previous herbivory studies in mangroves and may account for the consistently low values that have been reported (Farnsworth and Ellison 1991; Feller 1995). Although reduction in leaf area through loss of yield was greater than damage by all folivores combined at Twin Cays, nutrient enrichment had no effect on the level of damage. In comparison, loss of yield was lower overall at IRL, but +N caused a significant increase. Leaf C:N ratios and SLA explained close to 70% of the loss of yield at the two locations. In contrast with folivores, these data for loss of yield suggested that the changes in leaf nutritive quality caused by nutrient enrichment resulted in altered patterns and rates of herbivory. We predict that nutrient loading will affect patterns of herbivory in mangrove ecosystems, but will depend on system-specific attributes related to nutrient availability and the functional group of herbivores in question.

Our data from two mangrove ecosystems clearly supported the hypothesis that alleviating different kinds of nutrient limitation has different effects on ecosystem structure and function in natural systems (Littler and others 1988; Ulanowicz and Abarca-Arenas 1997; Feller and others 2003a, b; Sundareshwar and others 2003). The response to nutrient enrichment depended on the ecological process measured, the species, and the limiting nutrient. Our results show that a range of ecological processes that spanned growth, nutrient dynamics, and herbivory in two stunted *A. germinans* stands did not necessarily respond similarly to additions of the site-specific limiting nutrient. One-to-one comparisons between P-limited Twin Cays and N-limited IRL showed that the responses by multiple traits and community components to +N or +P depended on relative availability of these nutrients. Of the 20 response variables that we measured at both locations, 9 at IRL showed no significant change relative to controls in response to +N. This contrasts sharply with Twin Cays where all but two of these variables were significantly altered by +P. Although growth was nutrient limited at both locations, this may indicate that P was more strongly limiting at Twin Cays than N was limiting at IRL. We found no indication that +N increased P limitation at Twin Cays or that +P increased N limitation at IRL. On the other hand, excess input of a limiting nutrient can cause a shift in patterns of nutrient limitation in some ecosystems (for example, Aerts and others 1992; Reddy and others 1999). At Twin Cays, +P caused most of the 20 variables to converge toward values for control trees at N-limited IRL. However, at IRL, only 9 of the 20 converged toward values for control trees at P-limited Twin Cays. Multivariate analysis with PCA revealed that leaf nutrient ratios and concentrations were more sensitive to nutrient enrichment than others and that the two systems became more similar in these traits when nutrient limitation was alleviated (Figure 3). They also suggested that P loading at Twin Cays would likely cause a shift from P to N limitation, but that N loading was unlikely to lead to a shift to P limitation at IRL.

Our results indicated that the response of ecological processes to nutrient over-enrichment will depend on site characteristics, the species, and the nature of nutrient limitation. The difference in patterns of nutrient limitation at the two sites was due to a combination of physical and biogeochemical factors. For example, stunted forests at offshore islands such as Twin Cays received a very low supply of exogenous nutrients, but the N:P ratio of the substrate was relatively high due to benthic N_2 fixation (Joye and Lee 2004). There has been little human impact on the nutrient regime at Twin Cays (Rützler and others 2004). Additionally, Twin Cays is in a calcium carbonate setting where adsorption of P by biogenic calcium carbonate may exacerbate P limitation (Fourqurean and others 1992). In contrast, the IRL is a nutrient-rich environment situated in a large coastal catchment adjacent to a highly populated area with extensive agriculture, where it receives continuous input of freshwater runoff from terrigenous sources (Phlips and others 2002).

The disparity in demand for N versus P at Twin Cays and IRL suggested that there may be a fundamental difference in N- versus P-limited systems in their sensitivity and susceptibility to nutrient loading. Fertilization experiments that span the two major biogeographic realms of mangrove distribution (Boto and Wellington 1983; Feller and others 2003a, b; Lovelock and others 2004) have shown that many of these forests exist in at least two states based on patterns of nutrient limitation (that is, N- or P-limited). Although shifts from desired to less desired states may often follow a gradual loss of ecosystem resilience (Folke and others 2004), it is not known how a shift from P to N limitation might affect ecosystem function in mangroves.

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