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## Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida

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**Abstract** The objectives of this study were to determine effects of nutrient enrichment on plant growth, nutrient dynamics, and photosynthesis in a disturbed mangrove forest in an abandoned mosquito impoundment in Florida. Impounding altered the hydrology and soil chemistry of the site. In 1997, we established a factorial experiment along a tree-height gradient with three zones, i.e., fringe, transition, dwarf, and three fertilizer treatment levels, i.e., nitrogen (N), phosphorus (P), control, in Mosquito Impoundment 23 on the eastern side of Indian River. Transects traversed the forest perpendicular to the shoreline, from a *Rhizophora mangle*-dominated fringe through an *Avicennia germinans* stand of intermediate height, and into a scrub or dwarf stand of *A. germinans* in the hinterland. Growth rates increased significantly in response to N fertilization. Our growth data indicated that this site is N-limited along the tree-height gradient. After 2 years of N addition, dwarf trees resembled vigorously growing saplings. Addition of N also affected internal dynamics of N and P and caused increases in rates of photosynthesis. These findings contrast with results for a *R. mangle*-dominated forest in Belize where the fringe is N-limited, but the dwarf zone is P-limited and the transition zone is co-limited by N and P. This study demonstrated that patterns of nutrient limitation in mangrove ecosystems are complex, that not all processes respond similarly to the same nutrient, and that similar habitats are not limited by the same nutrient when different mangrove forests are compared.

**Keywords** Disturbance · Fertilization · Experiment · Phosphorus · Photosynthesis · Resorption

### Introduction

Tropical and subtropical mangroves support adjacent marine communities and ecosystems, including seagrass beds and coral reefs. However, little is known about the intra-wetland processes that regulate those interactions. In salt marshes, ecological processes such as primary production and decomposition have been shown experimentally to be nitrogen (N)-limited (Valiela and Teal 1979). The few mangrove wetlands where fertilization experiments have been conducted appear to be either phosphorus (P)-limited (Feller 1995; Koch and Snedaker 1997) or differentially N- or P-limited across tidal gradients (Boto and Wellington 1983; Feller et al. 2003). Several studies have found that mangrove ecosystems have high capacity as a sink for excess nutrients and other pollutants (e.g., Nedwell 1975; Odum and Johannes 1975; Silva et al. 1990; Corredor and Morell 1994; Tam and Wong 1999). However, relatively few studies have evaluated what types of changes might occur within mangrove ecosystems in response to the ongoing process of eutrophication of the coastal zone, which are often immediately next to oligotrophic, but highly diverse, marine ecosystems (Feller et al. 1999, 2003).

The purpose of this long-term study is to examine how nutrient enrichment influences ecological processes in a mangrove system that developed in an area impacted by anthropogenic disturbance. We selected a study site in an abandoned mosquito impoundment along the Indian River Lagoon (IRL), Florida. In March 1997, we set up a fertilization experiment to determine the effects of increased nutrient availability on soil chemistry and plant growth, internal nutrient dynamics, and photosynthesis across the ecotones connecting the mangrove forests with the open water and with interior areas along a tree-height gradient. Results from this study will be compared to a parallel investigation of a pristine mangrove ecosystem on

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offshore islands in Belize associated with the Mesoamerican Barrier Reef (Feller et al. 1999, 2003; McKee et al. 2002). This study aims to test two hypotheses. H1: Essential nutrients are not uniformly distributed within mangrove ecosystems. Based on a fertilization experiment in Belize, soil fertility within mangrove forests is heterogeneous and can switch from conditions of N to P limitation along narrow spatial gradients (Feller et al. 2003). This hypothesis predicts spatial variation in plant responses (e.g., growth and photosynthesis) in response to enrichment with N and P. H2: As the availability of a limiting nutrient increases, internal nutrient dynamics and the mechanisms used by plants to use, 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; Feller et al. 1999). This hypothesis predicts that under N-limiting conditions, N will be tightly conserved via efficient internal nutrient use and cycling mechanisms. Similarly, under P-limiting conditions, P will be more efficiently used and tightly conserved.

## Materials and methods

### Study site

Our study was conducted at Mosquito Impoundment 23 (MI 23), a 122-ha stand of coastal mangroves located in the Avalon State Recreation Area on the lagoonal side of North Hutchinson Island, St. Lucie County, Florida (27°33'N, 80°20'W). This impoundment was originally constructed in 1966 to control populations of *Aedes taeniorrhynchus* and *A. sollicitans*, and was maintained until 1974 when its dike was breached (Rey and Kain 1991). No records are available on the pre- or post-impoundment vegetation in this area (Rey et al. 1986). Impounding, which involved construction of a dike around a wetland with material excavated from the perimeter to control flooding and water depth, altered the wetland's hydrology and pore water chemistry (Carlson et al. 1983; Rey et al. 1986, 1990, 1992). In MI 23, water connection for exchange and circulation with the IRL is through the breach and two 30" diameter culverts (James David, unpublished data). This site has not been managed for mosquito control since 1974. The soil contains dredged sand and shell fragments and has little structure.

The mangrove stand was dominated by *Avicennia germinans* L. (black mangrove) with scattered *Laguncularia racemosa* Gaertn.f. (white mangrove) in the interior with *Rhizophora mangle* L. (red mangrove) confined to the periphery immediately alongside the canal. This site is characterized by a tree-height gradient, perpendicular to the shoreline. To quantify forest structure, we used the point-centered quarter method (Cintrón and Schaeffer-Novelli 1984). Measurements were taken at 20 points at regular intervals along four transects.

### Experimental design

The experimental design was a randomized complete block with a factorial treatment arrangement. Transects along the tree-height gradient were replicated in three blocks, 100–150 m apart, along the western side of MI 23. In each block, three transects, 25–50 m long and ~10 m apart, were oriented perpendicular to the shoreline and subdivided into fringe, transition, and dwarf zones. Two species were targeted for fertilizer treatment: *R. mangle* in the fringe zone and *A. germinans* in the transition and dwarf zones.

Three replicate trees were selected within each zone. Trees were fertilized with 300 g of N fertilizer as urea (45:0:0), or P fertilizer as P<sub>2</sub>O<sub>5</sub> (0:45:0), as described in Feller (1995). Nutrient treatment for each transect within each block was assigned randomly. A total of 81 trees (3 nutrient treatments × 3 zones × 3 blocks × 3 trees per zone) were treated and measured at 6-month intervals for 2 years. Doses (150 g) of fertilizer were placed in small holes (3 cm diameter × 30 cm deep), cored into the substrate beneath the drip line on opposing sides of the canopy of each tree, and sealed. We used this method rather than surface broadcasting to assure that the fertilizers were available to tree roots rather than lost in tidal flushing. For controls, holes were cored and sealed, but no fertilizer was added.

### Plant growth and nutrient dynamics

As a bioassay of the effects of nutrient treatment on plant growth, we tracked the responses of five, initially unbranched, shoots (first order) in sunlit positions in the outer part of the canopy of each tree. To distinguish the growth produced over an interval, we labeled the leaves in the apical position on each of these shoots at each sampling period. Stem growth and leaf production were measured from the previously marked apical position to the base of the current apical bud along the main axis and any shoots. Demographic growth analysis was used to determine effect of nutrient enrichment on plant growth rates (McGraw and Garbutt 1990). Demographic absolute growth rates (DAGR) were calculated for monthly increases in stem growth for year 1 (March 1997–March 1998) and year 2 (March 1998–March 1999). Demographic relative growth rates (DRGR) were calculated for monthly rates of leaf production for year 1 and year 2, using the formula:

$$\frac{\ln(\text{No. leaves})_{\text{time1}} - \ln(\text{No. leaves})_{\text{time0}}}{\text{time1} - \text{time0}} = \text{DRGR}(\text{leaves}/\text{mo}). \quad (1)$$

To determine the effects of nutrient enrichment on internal nutrient dynamics, we measured nutrient concentrations in green and senescent leaves and calculated nutrient resorption efficiency for each experimental tree. Resorption efficiency (RE) was calculated for each experimental tree as the percentage of N or P recovered from senescing leaves before leaf fall (Chapin and Van Cleve 1989):

$$\frac{\text{NorP}(\text{mg} \cdot \text{cm}^{-2})_{\text{greenleaves}} - \text{NorP}(\text{mg} \cdot \text{cm}^{-2})_{\text{senescentleaves}}}{\text{NorP}(\text{mg} \cdot \text{cm}^{-2})_{\text{greenleaves}}} \times 100 = \text{RE}(\%). \quad (2)$$

Leaf samples for analyses were harvested in January 1999. 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 from a penapical stem position and fully senescent yellow leaves with a well-developed abscission layer from a basal position on first-order branches. Senescent leaves were collected by hand directly from the trees to eliminate nutrient loss via leaching and leaf loss by tidal flushing. We assumed that yellow leaves that could be removed from a stem with only slight pressure represented senescent leaf litter. Leaf area was determined with a Li-Cor 3000 Portable Area Meter (Li-Cor, Lincoln, Neb.). Leaf samples were dried at 70°C in a convection oven and ground in a Wiley Mill to pass through a 40 (0.38mm) 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. Phosphorus (P) concentration was determined using an inductively coupled plasma spectrophotometer by Analytical Services, Pennsylvania State University, State College, Pa., USA.

## Photosynthesis

Rates of photosynthetic electron transport on experimental trees were measured with a PAM 2000 chlorophyll fluorescence system (H. Walz, Effeltrich, Germany) during a sunny morning under light conditions saturating for photosynthesis in March 2000. These rates of photosynthetic electron transport correlate with rates of photosynthetic CO<sub>2</sub> assimilation (Genty et al. 1989; Krall and Edwards 1992; Lovelock and Winter 1996), although the relationship between photosynthetic electron transport and CO<sub>2</sub> fixation for different plant species may differ and vary between 8 and 16 electrons transported per mole of CO<sub>2</sub> assimilated (Krall and Edwards 1992; Lovelock and Winter 1996). In the dwarf and transition zones, rates of photosynthetic electron transport were calculated as an average of three measurements made on three most recently fully expanded leaves per plant. Mean light levels during the measurements were 1,200  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  and mean leaf temperatures were 33°C. In the fringe, the height of the canopy prevented in situ measurements of leaves developed in direct sunlight (comparable to those in the dwarf and transition zones). Thus, branches were picked using a saw on an extendable arm and transported to the laboratory. The most recently fully expanded leaf from each branch was placed in a chamber at 100% relative humidity, saturating CO<sub>2</sub> (supplied by breathing into the plastic chamber) and at 1,500  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , supplied by the white actinic light source of the PAM 2000. Rates of photosynthetic electron transport were measured with the PAM 2000 on one leaf per plant. In September 1998 and June 1999, we measured rates of photosynthetic CO<sub>2</sub> fixation under light conditions saturating for photosynthesis in dwarf trees with a Li-Cor 6400 portable gas exchange system (Li-Cor, Lincoln, Neb., USA). Photosynthetic nutrient use efficiency (PNUE) was calculated as photosynthetic CO<sub>2</sub> assimilation (A) divided by the leaf N concentration (Field et al. 1983).

## Hydro-edaphic measurements

Measurements of soil and porewater were conducted at each experimental tree approximately 1 m from the bole. Soil samples were collected with a piston-type corer for determination of 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 with a probe attached to a suction device as described in McKee et al. (1988). A portion of the sample was filtered (0.45  $\mu$ ) and frozen until analysis of PO<sub>4</sub><sup>2-</sup> and NH<sub>4</sub><sup>+</sup> concentrations on a LACHAT system (QuickChem 8000 Series FIA, Zellweger Analytix, Milwaukee, Wis., USA). Analytical procedures were

checked by use of external standards and blanks as specified by 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 McKee et al. 1988). Additional unfiltered aliquots were used to measure pH and salinity.

## Statistical analysis

Our data were analyzed by a factorial analysis of variance (ANOVA, fixed effects model) in a randomized complete block experimental design, using Systat 8.0 (Wilkinson 1996) or JMP 4.0 (SAS Institute, Cary, N.C., USA). Grouping factors were nutrient treatment (Control, N, P)  $\times$  zone (fringe, transition, dwarf), in three blocks (1, 2, 3) to look for differences in variables based on harvested materials and measurements in this experiment. Physicochemical data were analyzed with repeated-measures ANOVA over four sample dates: April 1997, October 1998, March 1999, and March 2000. When significant main effects or interactions occurred, comparisons were conducted with 1 *df* contrast analysis. To analyze treatment effects on plant growth rates, we used repeated-measures ANOVA over two 1-year periods. When an ANOVA found a significant main effect or interaction between nutrient treatment and zone, we used Fisher's Least Significant Difference post hoc hypothesis test to examine pairwise differences within and among the treatment levels. To analyze for heteroscedasticity, probability plots of variables and ANOVA residuals were examined. For heterogeneous variances, we transformed continuous data using logarithms and transformed noncontinuous data (counts) using the square root.

## Results

### Forest structure

The height of the canopy at MI 23 was tallest in the fringe along the water's edge and decreased to landward (Table 1). The fringe zone was a dense but narrow stand (2–5 m wide) of uniformly tall trees (3.5–6 m), dominated by *R. mangle* with *L. racemosa* and *A. germinans* intermixed. The transition zone was 5–10 m wide and dominated by 1–3 m tall saplings of *L. racemosa* and *A. germinans*. The interior of the impoundment was 70–100 m wide and was an open stand of stunted trees (~1 m tall), dominated by *A. germinans*, referred to as the dwarf zone. Tree density and basal area ( $\text{m}^2 \cdot 0.1 \text{ ha}^{-1}$ ) were highest in the fringe zone, with basal area 10–30 times greater than in the dwarf and transition zones, respec-

**Table 1** Forest stand characteristics of the fringe, transition, and dwarf zones at Mosquito Impoundment 23, Fort Pierce, Fla.

Zone	Species	Tree height (m) (mean $\pm$ 1 SE)	Stand density (stems $\cdot$ 0.1 ha <sup>-1</sup> )	Basal area (m <sup>2</sup> $\cdot$ 0.1 ha <sup>-1</sup> )	Relative density (%)	Relative dominance (%)	Relative frequency (%)
Fringe	<i>Rhizophora mangle</i>	3.9 $\pm$ 0.1 (N=53)	3,953	6.4	66.3	56.0	48.8
	<i>Laguncularia racemosa</i>	3.2 $\pm$ 0.3 (N=18)	1,343	3.9	22.5	33.8	33.3
	<i>Avicennia germinans</i>	3.8 $\pm$ 0.3 (N=9)	671	1.2	11.2	10.2	17.9
Transition	<i>Rhizophora mangle</i>	–	0	0	0	0	0
	<i>Laguncularia racemosa</i>	1.9 $\pm$ 0.4 (N=14)	2222	0.22	83.8	85.6	67.7
	<i>Avicennia germinans</i>	2.0 $\pm$ 0.3 (N=66)	431	0.04	16.2	14.4	33.3
Dwarf	<i>Rhizophora mangle</i>	–	0	0	0	0	0
	<i>Laguncularia racemosa</i>	–	0	0	0	0	0
	<i>Avicennia germinans</i>	1.0 $\pm$ 0.04 (N=81)	3,725	1.1	100	100	100

**Table 2** Summary of hydro-edaphic conditions measured across the tree-height gradient by treatment (*Control*, unfertilized, N, nitrogen fertilized, P, phosphorus fertilized). Values are the mean±1 SE) of replicate (N=9) measurements taken four times during the study (April 1997, October 1998, March 1999, and March 2000)

Soil	Fringe			Transition			Dwarf		
	Control	N	P	Control	N	P	Control	N	P
	Bulk density (g cm <sup>-3</sup> )	0.52 (0.09)	0.52 (0.10)	0.54 (0.11)	1.06 (0.04)	1.02 (0.04)	1.09 (0.03)	1.17 (0.03)	1.20 (0.02)
Organic matter (%)	14.6 (2.7)	17.3 (3.9)	14.7 (2.9)	3.3 (0.5)	3.9 (0.2)	3.4 (0.3)	1.9 (0.2)	2.0 (0.1)	1.9 (0.1)
Eh <sub>1</sub> cm (mV)	155 (21)	171 (24)	202 (24)	223 (21)	183 (23)	170 (28)	192 (23)	193 (20)	173 (26)
Eh <sub>15</sub> cm (mV)	30 (22)	90 (26)	51 (26)	89 (25)	35 (26)	72 (27)	95 (25)	74 (22)	49 (20)
Porewater									
Salinity (ppt)	39 (1)	40 (1)	40 (1)	41 (1)	43 (1)	42 (1)	49 (2)	57 (2)	55 (2)
pH	6.61 (0.05)	6.61 (0.05)	6.62 (0.04)	6.74 (0.04)	6.70 (0.04)	6.64 (0.04)	6.83 (0.04)	6.88 (0.05)	6.62 (0.06)

tively. Stem density and height in the transition zone were higher than in the dwarf zone, but basal area in the dwarf zone was approximately five times greater than in the transition zone.

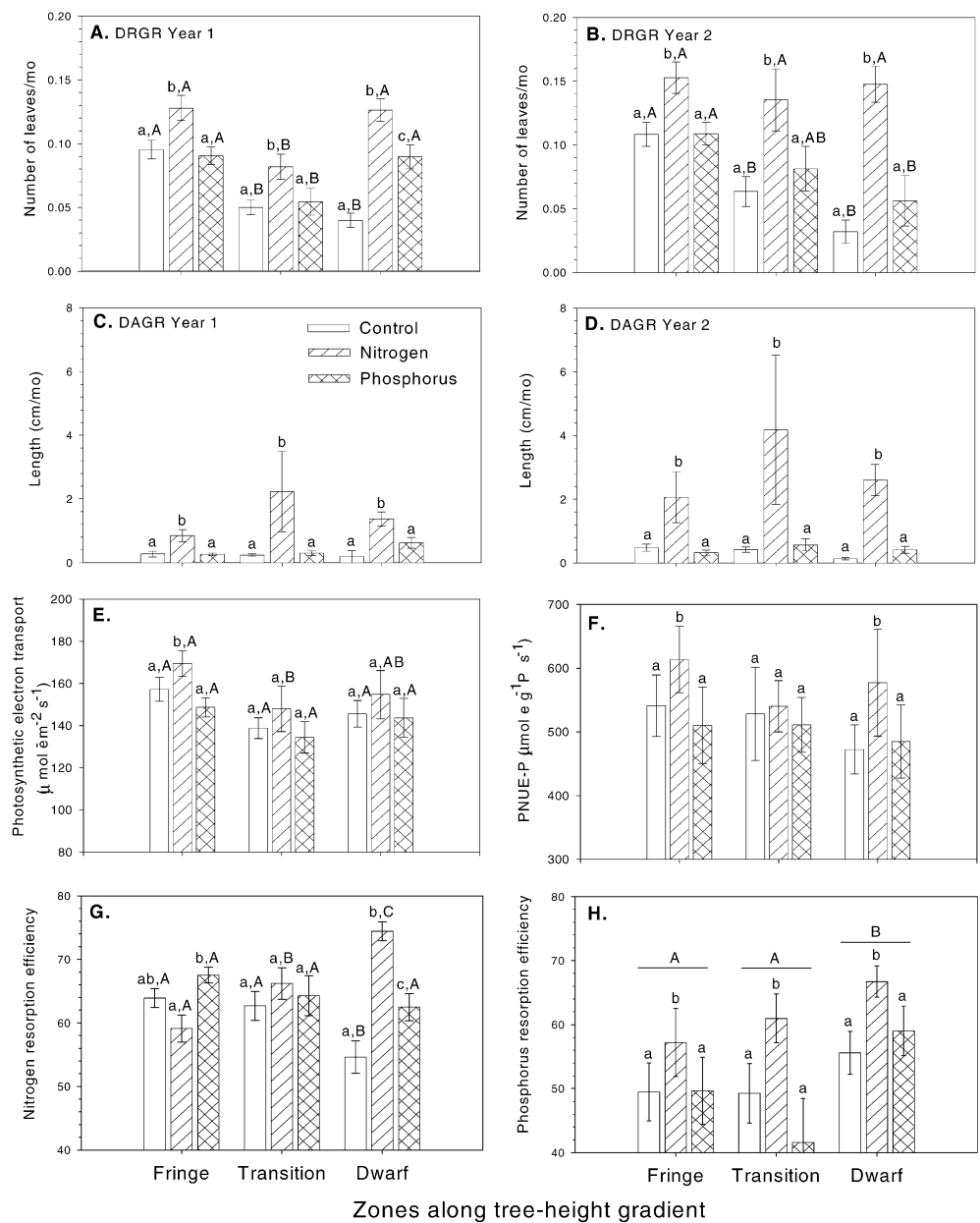
#### Hydro-edaphic conditions

The soil at MI 23 had a high bulk density and a low organic matter content that varied with zone ( $F_{2, 70}=102.1$ ,  $P=0.0001$ ;  $F_{2, 70}=61.8$ ,  $P=0.0001$ ), but not treatment (Table 2). Organic matter content was higher in the fringe compared to transition and dwarf zones ( $F_{1,70}=122.1$ ,  $P=0.0001$ , 1 *df* contrast). Soil bulk density was lowest in the fringe and significantly higher in transition and dwarf zones ( $F_{1, 70}=198.2$ ,  $P=0.0001$ , 1 *df* contrast). Soil redox potentials indicated slightly reducing conditions in all three zones that fluctuated over time ( $F_{3, 70}=63.5$ ,  $P=0.0001$ ;  $F_{3, 70}=29.9$ ,  $P=0.0001$  for 1 and 15 cm depths, respectively). There was no clear temporal pattern or significant differences in redox potential across zones or with treatment. The dwarf zone remained hypersaline throughout the study compared to the fringe and transition zones, which were not different ( $F_{1, 70}=3.3$ ,  $P=0.001$ ) (Table 2). Addition of N and P resulted in higher salinity in all three zones ( $F_{2, 72}=8.9$ ,  $P=0.001$ ). Sulfide was low overall, consistent with redox potentials, and was lower in the dwarf compared to fringe and transition zones ( $F_{2, 72}=10.3$ ,  $P=0.002$ , 1 *df* contrast). Porewater pH varied only slightly across zones and treatments (Table 2). Porewater concentrations of PO<sub>4</sub>-P and NH<sub>4</sub>-N did not vary significantly across zones, but did show large differences with treatment, as expected ( $F_{2,72}=49.1$ ,  $P=0.0001$ ;  $F_{2, 72}=14.9$ ,  $P=0.0001$ , respectively).

#### Plant growth

Nutrient treatment and zone had significant effects on growth rates (Fig. 1A–D). During both years, the N fertilizer caused a significant increase in leaf production (Fig. 1A, B) and shoot growth in each zone (Fig. 1C, D). For control trees, leaf production was highest for *R. mangle* in the fringe. Leaf production and shoot growth were significantly greater in year 2 than in year 1 ( $F_{1, 70}=9.9$ ,  $P=0.002$ ;  $F_{1, 70}=11.4$ ,  $P=0.001$ , respectively). The P fertilizer had no effect on growth, except in the dwarf zone where leaf production increased slightly in year 1 (Fig. 1A). However, in year 2, adding P had no detectable effect on leaf production (Fig. 1B). Growth rates in years 1 and 2 were similar for the control and P-fertilized trees, but increased significantly in year 2 for the N-fertilized trees ( $F_{1, 70}=8.49$ ,  $P=0.001$ ). Data from both years indicated N-limited growth by *R. mangle* in the fringe zone and *A. germinans* in the transition and dwarf zones. During year 1, a significant block effect for DRGR ( $F_{2, 70}=7.6$ ,  $P=0.001$ ) showed that plant growth rates were not uniform at the three replicate sites.

**Fig. 1** Effects of nutrient enrichment on demographic relative growth rates based on new leaves during (A) year 1 and (B) year 2; and absolute relative growth rates based on new shoot growth during (C) year 1 and (D) year 2; (E) N-resorption efficiency, (F) P-resorption efficiency, (G) efficiency maximum rates of photosynthetic electron transport, and (H) photosynthetic P use efficiency (photosynthetic electron transport rate per unit P) in fertilized mangrove trees by treatment (*Control* unfertilized, *N* nitrogen fertilized, *P* phosphorus fertilized) and zone along a tree-height gradient (fringe, transition, dwarf). Values are means  $\pm$ SE. Within a zone the same lowercase letter indicates that treatment means are not significantly different; among zones the same uppercase letter indicates that treatment means are not significantly different ( $P < 0.05$ ).  $N = 81$  trees (3 nutrient treatments  $\times$  3 zones  $\times$  3 blocks  $\times$  3 replicate trees)



## Nutrient dynamics

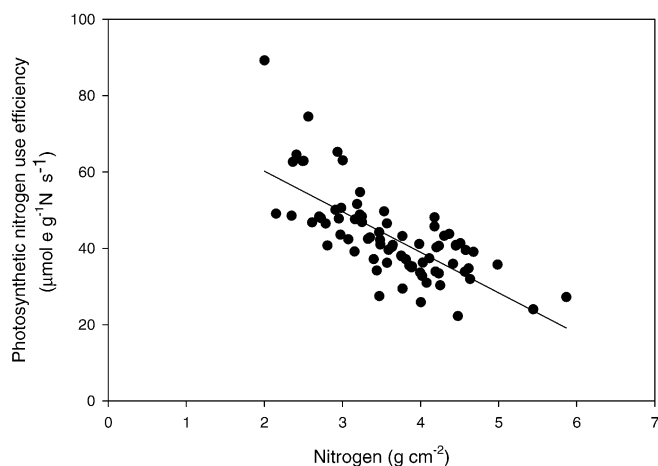
Nutrient enrichment and zone, but not block, had complex effects on the within-plant dynamics of N and P (Table 3). The N concentration of green leaves [ $N_G$ ] from N-fertilized trees was significantly higher in all zones, and *A. germinans* had significantly higher [ $N_G$ ] than *R. mangle* for all treatments (Table 3). In the dwarf zone, adding N caused a 60% increase in [ $N_G$ ], compared to ~30% in fringe or transition zone. Nutrient treatment and zone also had significant effects on the N concentration of senescent leaves [ $N_S$ ], with significant nutrient  $\times$  zone interactions (Table 3). In controls, [ $N_S$ ] was higher in *A. germinans* (transition and dwarf zones) than in *R. mangle* (fringe). Adding N caused a 36% increase in [ $N_S$ ] in *R. mangle*, compared to 7% and 12% in *A. germinans* in the

transition and dwarf zones, respectively (Table 3). The P fertilizer had little effect on [ $N_G$ ] or [ $N_S$ ]. However, the N and P fertilizers altered N resorption efficiency, with a significant nutrient  $\times$  zone interaction ( $F_{4,70} = 8.8$ ,  $P = 0.001$ ; Fig. 1G). For controls, N resorption was significantly lower in dwarf trees compared to fringe or transition trees. The greatest response was in the dwarf zone where adding N caused ~40% increase in N resorption.

Zone, but not nutrient treatment, had a highly significant effect on P concentration of green [ $P_G$ ] and senescent [ $P_S$ ] leaves (Table 4). The *R. mangle* in the fringe had much lower [ $P_G$ ] and [ $P_S$ ] than the *A. germinans* in the transition and dwarf zones (Table 3). Values for transition and dwarf zone trees were similar. Nutrient treatment and zone had significant effects on P-resorption

**Table 3** Percent nitrogen and phosphorus in green ( $[N_G]$ ,  $[P_G]$ ) and senescent ( $[N_S]$ ,  $[P_S]$ ) leaves from *Rhizophora mangle* in the fringe zone and *Avicennia germinans* in the transition and dwarf zones in response to treatment (Control, unfertilized, N, nitrogen fertilized, P, phosphorus fertilized). Values are means $\pm$ (1 SE).  $N = 27$  trees per treatment level and 27 trees per zone. Data were arcsine square-root transformed prior to analysis

Zone	Fringe				Transition				Dwarf				
	Control		N		Control		N		Control		N		P
$[N_G]$	1.26 (0.05)	1.56 (0.07)	1.26 (0.08)	1.66 (0.06)	2.17 (0.01)	1.60 (0.06)	2.17 (0.01)	1.42 (0.06)	2.27 (0.09)	1.58 (0.05)			
$[N_S]$	0.44 (0.02)	0.60 (0.04)	0.40 (0.03)	0.57 (0.01)	0.61 (0.04)	0.52 (0.04)	0.61 (0.04)	0.59 (0.02)	0.66 (0.02)	0.60 (0.01)			
$[P_G]$	0.097 (0.003)	0.104 (0.002)	0.096 (0.005)	0.147 (0.008)	0.134 (0.006)	0.147 (0.011)	0.135 (0.013)	0.138 (0.012)	0.135 (0.013)	0.137 (0.009)			
$[P_S]$	0.047 (0.003)	0.043 (0.005)	0.047 (0.005)	0.071 (0.009)	0.055 (0.011)	0.075 (0.005)	0.051 (0.004)	0.057 (0.006)	0.051 (0.004)	0.057 (0.005)			



**Fig. 2** The relationship between leaf nitrogen concentration per unit area ( $\text{g cm}^{-2}$ ) and photosynthetic N use efficiency ( $\mu\text{mol e g}^{-1}\text{N s}^{-1}$ ) in fertilized mangroves at MI 23.  $N=81$

efficiency ( $F_{2, 68}=5.7$ ,  $P=0.01$ ;  $F_{2, 68}=3.9$ ,  $P=0.02$ , respectively), with no significant interactions between these factors (Fig. 1H). Adding N caused a significant overall increase in P resorption efficiency, with values 10%–20% greater in N-fertilized trees than in control or P-fertilized trees. Phosphorus resorption was significantly higher in the dwarf zone than in the transition ( $P=0.01$ ) or fringe ( $P=0.03$ ) zones.

### Photosynthesis

Nutrient enrichment had a significant effect on maximum rates of photosynthetic electron transport across zones and blocks ( $F_{2, 52}=12.2$ ,  $P=0.02$ , Fig. 1E). Adding N enhanced photosynthetic electron transport of leaves relative to controls, while adding P did not. Photosynthetic  $\text{CO}_2$  fixation was enhanced in N-fertilized plants in the dwarf zone in September, but not in June. However, the magnitude of the effect was influenced by block at both measurement times (September 1998,  $F_{2, 18}=11.0$ ,  $P=0.001$ ; June 1999,  $F_{2, 18}=10.7$ ,  $P=0.001$ ), with block 2 having higher rates of photosynthesis than blocks 1 or 3.

Nitrogen concentrations of the leaves used for measurement of photosynthetic electron transport were enhanced in response to the N fertilizer ( $F_{2, 52}=10.8$ ,  $P=0.02$ ), while leaf P concentrations were not affected by fertilizer treatments. The utilization of nutrient resources for photosynthetic processes was also significantly affected by fertilizer treatments. Adding N enhanced PNUE-P compared to controls (Fig. 1F,  $F_{2, 52}=21.5$ ,  $P=0.01$ ). Fertilizer treatments did not significantly alter the photosynthetic N use efficiency, but over all trees, PNUE-N was negatively correlated with N concentrations in leaves (Fig. 2).

**Table 4** Results of three-way ANOVAs performed on percent nitrogen (N) and phosphorus (P) concentration in green and senescent leaves from *Rhizophora mangle* and *Avicennia germinans* by nutrient treatment, Nt (Control, unfertilized, N, nitrogen fertilized, P, phosphorus fertilized) and Zone (fringe,

transition, dwarf), blocked at three sites at Mosquito Impoundment 23, Fort Pierce, FL. Values are *F*-ratios. *N*=27 trees per nutrient treatment; *N*=27 trees per zone. Data were arcsine square-root transformed

Source of variation	<i>df</i>	N <sub>green</sub>	N <sub>senescent</sub>	P <sub>green</sub>	P <sub>senescent</sub>
Nutrient (Nt)	2	51.644 ***	14.424***	0.059 <sup>ns</sup>	2.621 <sup>ns</sup>
Zone	2	36.498***	19.399***	25.735***	8.480***
Block	2	0.499 <sup>ns</sup>	0.876 <sup>ns</sup>	0.163 <sup>ns</sup>	1.197 <sup>ns</sup>
Nt × Zone	4	3.414**	2.621 <sup>ns</sup>	0.524 <sup>ns</sup>	0.569 <sup>ns</sup>

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ ; ns, not significant

## Discussion

The tidal forest at MI 23 was characterized by a spatial gradient in both species dominance and tree stature. Tall *R. mangle* dominated a narrow fringe along the man-made channel, but was virtually absent from the interior portions of the forest, which were dominated by stunted *A. germinans* and *L. racemosa*. Such spatial variability of species zonation, primary production, tree stature, and growth rates within a mangrove forest has been correlated with many environmental variables, including salinity, nutrient availability, flooding frequency, oxidation-reduction status of soil, sulfide concentrations, and surface hydrology (MacNae 1968; Lugo and Snedaker 1974; Onuf et al. 1977; Boto and Wellington 1983; Cintrón et al. 1978; 1985; Lugo 1990; Jimenez and Sauter 1991; Clough et al. 1982; McKee 1993; 1995). Growth response to fertilization indicated that the mangrove forest at MI 23 was N-limited along the entire tree-height gradient. These data partially support Hypothesis 1, i.e., that nutrient availability limits growth, but does not shift from N to P limitation.

Results from this study contrast with a parallel investigation of a pristine mangrove ecosystem on offshore islands in Belize (Twin Cays), associated with the Mesoamerican Barrier Reef System (Feller 1995; Feller et al. 1999, 2003; McKee et al. 2002). The Belize site is characterized by a height gradient in *R. mangle* from fringe to interior, whereas the Florida site exhibits a switch in species dominance to landward. In contrast with the Belize site where the soil in dwarf forests is strongly reducing with sulfide accumulation, the Florida interior forest is drained for most of the year and is hypersaline. Both forests were characterized by a distinctive tree-height gradient of relatively tall trees in the fringe, with tree height decreasing to landward. The hinterlands at both sites were dominated by extensive stands of stunted trees but with different dominant species. The dwarf zone in Belize is dominated by *R. mangle* compared to *A. germinans* in MI 23. In contrast with the Belize site where the soil in the interior areas is waterlogged, the hinterland in Florida site is drained for most of the year. These sites also differed in age and disturbance history. The Florida site is heavily disturbed, and the forest is young (<30 years old). The Belize site is pristine and has been a mangrove system for 7,000–10,000 years (Macintyre et al. 1995).

This site also has not witnessed a severe hurricane since 1961 or experienced conspicuous anthropogenic damage throughout its Holocene history (Rützler and Feller 1996).

MI 23 has direct contact with the Indian River Lagoon that receives large amounts of nutrient input from coastal runoff and canals and rivers draining into the IRL from agricultural and urban developments (<http://www.epa.gov/OWOW/oceans/lagoon/impacte.html>). Even with potentially high nutrient inputs, all measurements of growth and productivity were still nutrient limited at MI 23. The N fertilizer caused a significant increase in photosynthetic electron transport, shoot growth, and leaf production in all zones. Additionally, photosynthetic CO<sub>2</sub> fixation was significantly enhanced in the N-fertilized dwarf trees compared to control and P-fertilized trees. Temporal differences in responses to N enrichment were due to patterns of leaf aging (Lovelock and Feller 2003).

The greatest responses to N enrichment occurred in the dwarf and transition zones, while the response of photosynthetic electron transport to the N enrichment was similar across all zones. Infrequent tides sufficient to flood the dwarf and transition zones and the absence of sedimentation indicated that relatively few external nutrients reach the interior portions of the forest. Sedimentation rate along the shoreline averages  $0.88 \pm 0.33$  cm year<sup>-1</sup>, but little of this reaches the interior forest ( $0.09 \pm 0.03$  cm year<sup>-1</sup>) (McKee, unpublished data). The significantly higher growth rates for control trees in the fringe zone may be partly due to greater sedimentation and nutrient input compared to transition and dwarf zones. The consistent response to addition of N fertilizer along the tree-height gradient at MI 23 was in sharp contrast to the pattern of nutrient limitation detected in the mangrove forests at Twin Cays, Belize (Feller et al. 2003; McKee et al. 2002). In that forest, tree growth was N-limited in the fringe and P-limited in the interior dwarf stands, which were less than 50 m inland. McKee et al. (2002) hypothesized that the nutrient switching pattern observed in Belize reflected the interaction of external supply of nutrients with internal demand, which was influenced by other environmental stress factors that varied spatially. The tree-height gradient in Belize was characterized by spatial variation in flooding stresses as well as relative availability of N and P. Flooding-related stress may increase plant demand for P, whereas salinity stress may increase demand for N. Where availability of P

relative to N was lowest (in the dwarf zone), plants responded strongly to fertilization with P, but not with N (Feller et al. 2003). In Florida at MI 23, the trees responded significantly to addition of N (Fig. 1A–D). However, the response to N was greatest in the dwarf zone where salinity stress (and the requirement for N) was highest. In both cases, low relative availability of N (Florida) or P (Belize) coincided with the occurrence of other stresses which may have increased the requirement for the limiting nutrient. This effect may partly explain the switch from N to P limitation across Belizean island forests where flooding depth and duration increases with distance from the shoreline (Feller et al. 2003). Flooding and salinity stresses may also directly affect plant growth or ability to acquire limiting nutrients. For example, flooding may restrict root exploration of soil and/or decrease root surface area, which strongly influences acquisition of immobile ions such as phosphate (McKee 2001). Furthermore, the addition of N and P caused an increase in salinity (Table 2). Presumably, higher rates of transpiration caused accumulation of ions excluded from uptake in the transpiration stream, as described in Passioura et al. (1992).

As the availability of a limiting nutrient increases, do the mechanisms used by plants to recycle and conserve that nutrient become less efficient? Our results from MI 23 and Twin Cays for nutrient resorption efficiency and nutrient use efficiency for growth and photosynthetic electron transport indicate that increased availability of a limiting nutrient did change nutrient use and conservation patterns in mangrove forests. However, the patterns exhibited were complex. Our data suggest that responses depended not only on the nature of nutrient limitations but also on interspecific differences. In our second hypothesis, we predicted that under N-limiting conditions, N would be more tightly conserved via efficient internal nutrient cycling mechanisms than under N-enriched conditions. Contrary to these predictions, at MI 23 where growth was N-limited throughout the forest, increased N availability caused N resorption to increase in *A. germinans* in the dwarf zone but to decrease in *R. mangle* in the fringe. Addition of N also resulted in increased resorption of P in all three zones. These differences in nutrient conservation in response to fertilization may be related to interspecific physiological differences between *A. germinans* and *R. mangle* in their relative tolerance of environmental conditions (Ball 1996). In our study, adding N led not only to increased growth but also to enhanced nutrient conservation of both N and P by *A. germinans* in hypersaline conditions. The mangrove trees at MI 23 were proficient at resorbing N, the growth-limiting nutrient. Nutrient concentrations in senescent leaves suggest that under N-limiting conditions resorption of N by *R. mangle* and *A. germinans* is complete and reaches the maximal physiological levels proposed by Killingbeck (1996). In Belize, increased N availability had no effect on *R. mangle*'s ability to conserve N along an N to P limitation gradient, even in the fringe zone where growth was N-limited (Feller et al. 2003).

Although adding P had only a slight effect on growth rates at MI 23 during year 1, it caused a 13% increase in N resorption in P-fertilized dwarf trees. This result contrasts sharply with >60% increase in N resorption by P-fertilized trees in the dwarf zone at the Belize site.

Many factors, including salinity, may be influential in determining the local dominance and productivity of mangrove species (Smith 1992). At MI 23, salinity was 40–50% higher in the dwarf zone than in either the transition or fringe zones. Salt tolerance in *A. germinans* is energy and nutrient demanding because it involves salt excretion through leaf salt glands and synthesis of N-based compounds for osmoregulation (Popp 1984; Popp et al. 1988; Popp and Polania 1989). The physiological effects of salinity and interactions between salinity and N nutrition have also been documented for *Spartina alterniflora*, which employs similar mechanisms for salt tolerance. The tree-height and salinity gradients at MI 23 are somewhat analogous to *S. alterniflora*-dominated marshes in temperate latitudes. In those systems, as salinity increases, the amount of N required to sustain growth also increases (Bradley and Morris 1992). Sea salts also competitively inhibit uptake of  $\text{NH}_4$ , which diminishes *S. alterniflora*'s ability to osmoregulate (Bradley and Morris 1992). At MI 23, porewater salinity appears to contribute to the low stature and stunted growth of the dwarf trees in the interior of the forest, consistent with observations by Lin and Sternberg (1992). The results from our fertilization experiment at MI 23 suggest that growth limitation is due to interacting stressors, including salinity and nutrient availability.

Addition of the N fertilizer did not significantly alter the photosynthetic N use efficiency. Higher N concentrations in leaves (which were significantly enhanced by the N fertilizer) were associated with a decline in the efficiency with which N is used for photosynthesis, indicating allocation of N to other metabolic processes when N is no longer limiting. Fertilization with N significantly enhanced the utilization of P for photosynthesis. Thus, by relieving N limitation in leaf tissues, more P can be incorporated into the photosynthetic apparatus. At the level of individual leaves, addition of limiting nutrients appears to reduce the efficiency by which the limiting nutrient, in this case N, is used, while improving the utilization of other resources (e.g., P), which supports our second hypothesis.

Nitrogen limitation in MI 23 contrasts with a well-documented pattern of P-limitation in mangrove and other tidal and non-tidal wetlands elsewhere in Florida (Brown 1981; Caraco et al. 1990; Craft and Richardson 1997; Koch and Snedaker 1997; Chen and Twilley 1999; Daoust and Childers 1999; Chiang et al. 2000; Pant and Reddy 2001). We hypothesize that the mangrove forest at MI 23 is not P-limited because of direct or indirect physical or chemical impacts caused by impounding. Overall, our experiments in Belize and Florida show that essential nutrients were not uniformly distributed within or among mangrove ecosystems and provide experimental evidence



that not all ecological and physiological processes within an ecosystem were limited by the same nutrient.

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