

EFFECTS OF NUTRIENT ENRICHMENT ON WITHIN-STAND CYCLING IN A MANGROVE FOREST

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Abstract. Within-stand nutrient cycling is dependent on many factors, including primary productivity, nutrient-use efficiency, nutrient resorption, sclerophylly, decomposition, nutritional quality of plant tissue, and allocation to defense. The efficiency of these plant-mediated processes depends on nutrient availability in the environment and inherent functional properties of plants. However, little is known about how nutrient availability will affect these processes in forested wetlands in the tropics. In a factorial experiment we fertilized 48 dwarfed *Rhizophora mangle* (red mangrove) trees along tidal-elevation and water-depth gradients at Twin Cays, a range of intertidal, peat-based offshore mangrove islands in Belize, Central America. Initial results indicated that phosphorus (P) deficiency is a major factor limiting primary productivity. Phosphorus-fertilized trees had a significant decrease in P-use efficiency and P-resorption efficiency, but a significant increase in nitrogen (N)-use efficiency and N-resorption efficiency in their leaves compared with controls and N-fertilized trees. Sclerophylly decreased dramatically in P-fertilized trees, while the nutritional quality of the plant tissue increased. Phosphorus fertilization did not affect P leaching from green leaves. We found no fertilizer effect on the decomposition rates of leaf tissue, possibly due to higher phenolic concentrations in the P-fertilized trees compared with controls and N-fertilized trees. However, belowground decomposition of cotton strips increased in the substrate associated with P-fertilized trees. Environmental conditions related to position along a tidal gradient may be as important as nutrients in controlling belowground decomposition.

Key words: Belize, mangrove forests; decomposition, belowground; leaching; mangrove ecosystem; nutrient availability; nutrient cycling processes, plant mediated; nutrient ratios; nutrient-resorption efficiency; nutrient-use efficiency; P enrichment, effects on nutrient cycling; *Rhizophora mangle*; sclerophylly.

INTRODUCTION

Plants influence nutrient cycling in natural ecosystems through uptake, allocation, and loss of nutrients (Hobbie 1992). In both temperate and tropical latitudes, plant species adapted to low-nutrient habitats generally have well-developed nutrient-conservation mechanisms that acquire, use, and recycle nutrients efficiently (Jordan 1985, Aerts 1990). Studies on within-stand nutrient cycling have been conducted primarily in terrestrial, nitrogen (N)-limited ecosystems (cf. Shaver and Melillo 1984). Little is known about how nutrient availability affects plant-mediated nutrient-cycling processes in coastal wetlands that are N (Valiela and Teal 1979) or phosphorus (P) limited (Davis 1994, Feller 1995). In this paper, we focus on within-wetland nutrient-cycling processes in mangrove ecosystems. The primary goal of this study was to determine how nutrient availability affects within-stand nutrient-cycling processes for *Rhizophora mangle* L. (red mangrove) dominated

wetlands in the Neotropics with strongly P-deficient soils.

In low-nutrient environments, some plant species are more competitive because they possess mechanisms for nutrient conservation that acquire, use, retain, and recycle nutrients efficiently (Berendse et al. 1987, Aerts and Berendse 1988, Aerts 1990). Adaptations for nutrient conservation in low-fertility soils include evergreenness, sclerophylly, low photosynthetic capacity, long life-span for plant tissue, low levels of leaching from plant tissue, high investment in chemical and structural defense, low losses to herbivory, slow growth rates, high resorption efficiency of nutrients from senescing tissues, high nutrient-use efficiency, high nutrient-uptake efficiency, high root:shoot ratio, symbiotic mycorrhizal relationships, and low decomposability of litter (Loveless 1961, Beadle 1967, Janzen 1974, Grubb 1977, Bryant et al. 1983, Shaver and Melillo 1984, Medina and Cuevas 1989, Medina et al. 1990, Hobbie 1992, Aerts 1995).

As the availability of a limiting nutrient increases, the mechanisms used by plants to conserve that nutrient may become less efficient (Loveless 1961, Small 1972, Stachurski and Zimka 1975, Tilton 1977, Chabot and

Manuscript received 28 July 1997; revised 21 January 1998; accepted 17 March 1998; final version received 4 May 1998. For reprints of this Special Feature, see footnote 1, p. 2137.

Hicks 1982, Flanagan and Van Cleve 1983, Shaver and Melillo 1984, Vitousek 1984, Schlesinger et al. 1989, Escudero et al. 1992). A number of fertilization experiments have found that increased resource availability caused a decline in xeromorphy and in nutrient-use efficiency (e.g., Beadle 1967, Shaver and Melillo 1984, Lajtha and Klein 1988, Chapin and Shaver 1989, Lajtha and Whitford 1989, Feller 1995, 1996, Madeira et al. 1995, Wienand and Stock 1995). These changes in internal nutrient-cycling processes in response to external enrichment suggest that naturally low-nutrient habitats may have limited capacity as nutrient sinks. However, other studies have found that increased N and P had little effect on the efficiency of internal nutrient-conservation strategies in plants (e.g., Baddeley et al. 1994, Bowman 1994).

Species responses to alterations in nutrient availability influence within-ecosystem processes primarily through changes in the characteristics of plant tissues. Plant-mediated characteristics such as litter quality may affect within-stand nutrient cycling via their effects on rates of decomposition (Cromack and Monk 1975, Stark and Jordan 1978, Chabot and Hicks 1982, Day 1982, Melillo et al. 1982, Flanagan and Van Cleve 1983, Upadhyay and Singh 1985, French 1988, Hemminga and Buth 1991, Aber 1992, Enriquez et al. 1993, Gallardo and Merino 1993, Berendse 1994, Aerts 1995). Hence, low-nutrient, sclerophyllous litter, which contains high concentrations of recalcitrant carbon-based compounds, such as tannins and flavonoids, may decompose more slowly and with greater initial nutrient immobilization in comparison with high-nutrient, less "tough" litter (Aber and Melillo 1982, Melillo et al. 1982, Shaver and Melillo 1984, Horner et al. 1988).

Mangrove forests are frequently described as oligotrophic, coastal wetland ecosystems, with a specialized flora adapted to low-nutrient conditions (e.g., Hutchings and Saenger 1987, Lugo 1990). However, the stature and productivity of these tropical swamps vary dramatically. In the Caribbean, canopy height ranges from 30 m or more in riverine systems or bird rookeries to ≤ 1.5 m in vast stands of old-growth, dwarf trees behind the coastal fringe (Lugo and Snedaker 1974, Lugo 1997). These responses suggest that mangroves are clearly not restricted to oligotrophic environments. Mangrove species that flourish in low-nutrient environments have very efficient mechanisms for retaining and recycling nutrients (Boto 1982, Twilley et al. 1986). According to Alongi et al. (1992), biological and environmental factors that influence nutrient retention in mangrove forests include resorption of N prior to leaf fall, burial of detritus by crabs, efficient nutrient uptake, high investment in chemical defenses, variations in tidal inundation, sediment type, rainfall, climatic disturbances, and topography.

Rhizophora mangle is an evergreen tropical tree and one of the dominant mangrove species in coastal wetlands throughout most of the Caribbean (Tomlinson

1986). Experimental fertilization studies in Belize involving dwarfed *R. mangle* trees, estimated to be >50 yr old, growing in shallow ponds, have shown that primary production in these old-growth forests is severely P limited (Feller 1995). Within-stand cycling of nutrients in old-growth mangrove forests is higher than in successional mangrove stands, as well as other forested wetlands or upland rain forests (Lugo et al. 1990, Lugo 1997). However, little is known about how nutrient availability affects ecological processes related to nutrient retention and cycling in mangrove ecosystems.

Research goals

The objectives of this research were to compare within-plant and local, within-stand patterns of nutrient conservation and cycling by *R. mangle* in response to increased nutrient availability. In a fertilization experiment, we measured nutrient-use efficiencies, nutrient resorption, leachability of green leaves, leaf-litter decomposition, and belowground decomposition in a monospecific stand of dwarfed *R. mangle* trees growing on organic, peat-based soil in a carbonate setting. We attempted to answer the following questions: (1) How does increased nutrient availability affect nutrient-use efficiency and resorption in *R. mangle*? (2) How do changes in the nutritive, structural, and chemical qualities of *R. mangle* leaf tissue in response to increased nutrient availability affect rates of litter decomposition? (3) Does increased nutrient availability affect the susceptibility of green leaves to P loss via leaching? (4) How does increased nutrient availability in the peat substrate affect rates of belowground decomposition?

Results from this manipulative experiment serve as a simultaneous test for the following hypotheses:

Hypothesis 1: As the availability of a nutrient that limits primary production increases, the mechanisms used by plants to 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, Twilley 1988, Schlesinger et al. 1989, Escudero et al. 1992). From this hypothesis and the initial results from this fertilization experiment (Feller 1995), it follows that P enrichment will cause a decrease in dwarfed *R. mangle*'s ability to withdraw P from senescing leaves prior to abscission and a decrease in nutrient-use efficiency.

Hypothesis 2: Plant-mediated characteristics such as litter or substrate quality determine rates of decomposition; hence, higher-nutrient litter decomposes faster with less initial nutrient immobilization than lower-nutrient litter (Aber and Melillo 1982, Melillo et al. 1982, Shaver and Melillo 1984, Twilley 1988). This hypothesis predicts an increase in the rates of decomposition of *R. mangle* leaf litter from P-enriched trees.

Hypothesis 3: Belowground decomposition rates increase with increased availability of nutrients in the substrate (Flanagan and Van Cleve 1983). Based on

this hypothesis, P enrichment will cause an increase in belowground decomposition rates.

MATERIALS AND METHODS

Study site

This study was conducted at Twin Cays, a peat-based, 92-ha range of small mangrove islands located in the lagoon just inside the crest of the barrier reef of central Belize (16°50' N, 88°06' W), ~12 km from the mainland. Twin Cays does not receive terrigenous freshwater or sediment input that may increase nutrient levels in fringe, riverine, and nearshore mangrove forests. This range of mangrove islands developed ~7000 yr BP on Pleistocene limestone and has an underlying peat deposit ~7-m thick (Macintyre et al. 1995). It has been a mangrove community throughout its entire Holocene history. Since 1980, Twin Cays has been the primary study site for the Smithsonian Institution's National Museum of Natural History Field Station on nearby Carrie Bow Cay (Rützler and Feller 1988, 1996, *in press*). Several studies provide detailed descriptions of the vegetation, geomorphology, geochemistry, and hydrology of Twin Cays (e.g., Wright et al. 1991, McKee 1993, Feller 1995, Woodroffe 1995).

Experimental design

Trees were fertilized at 6-mo intervals with 300 g of a complete (NPK) fertilizer as $\text{NH}_4:\text{P}_2\text{O}_5:\text{K}_2\text{O}$ (10:15:15), an N fertilizer as NH_4 (45:0:0), or a P fertilizer as P_2O_5 (0:45:0). To fertilize, procedures similar to those described in Feller (1995) were used. Doses (150 g) of fertilizer were placed in each of two holes (7×30 cm) cored into the peat substrate on opposing sides of a tree, directly beneath the outermost margin of its canopy. Dialysis tubing was used to deliver the fertilizer. The same holes were used for each application to avoid excessive disturbance to the substrate and root systems. For control trees, holes were cored and sealed but no fertilizer was added. After the fertilizer was inserted into cored holes, each hole was sealed with a peat plug. Intervals of 10 m were left between trees for buffer zones as a precaution against possible lateral seepage of nutrients. This fertilization experiment was established in July 1989, using dwarfed *Rhizophora mangle* trees along intersecting gradients of tidal elevation and water depth in a permanently flooded 1-ha stand in the interior of Twin Cays (Feller 1995). The entire site is submerged except during unusually low-tide events when the shallow, high-tidal-elevation area drains down to the peat surface. The experimental design is a three-way ($4 \times 2 \times 2$) analysis of variance (ANOVA) that involves four levels of nutrient treatment and two levels each of tidal elevation and water depth. The design is a fixed-effects model with interactions. The fixed factors are nutrients (control, N, P, NPK), tidal elevation (low, high), and water depth (shallow, deep), with three replicates for a total of 48 trees.

As indices of nutrient-use efficiency (NUE), we measured nutrient-resorption efficiency and biomass production per unit of nutrient (N and P) invested for each experimental tree. Resorption efficiency (RE) was calculated as the percentage of N and P (mass N or P per unit leaf area) recovered from senescing leaves prior to leaf fall as (e.g., Staaf 1982, Chapin and Kedrowski 1983, Chapin and Van Cleve 1989):

$$100 \times \left[\frac{[\text{N or P (mg} \cdot \text{cm}^{-2})]_{\text{greenleaves}} - [\text{N or P (mg} \cdot \text{cm}^{-2})]_{\text{senescentleaves}}}{[\text{N or P (mg} \cdot \text{cm}^{-2})]_{\text{greenleaves}}} \right] = \text{RE.}$$

Nitrogen-use efficiency (NUE_N) and P-use efficiency (NUE_P) were calculated as the inverse of their concentrations (g nutrient/g biomass) in senescent leaves (senescent leaf biomass per unit of nutrient) from each of the 48 fertilized *R. mangle* trees (Gerloff 1976, Chapin 1980, Vitousek 1982, Chapin and Van Cleve 1989). As proposed by Killingbeck (1996), nutrient concentrations in senescent leaves were also used as an index of "nutrient proficiency," or the level to which species can reduce nutrients in their senescing leaves. In July 1994 we collected mature green leaves from a penapical stem position and fully senescent yellow leaves on first-order branches, and measured leaf area (in square centimeters). In this mangrove wetland where the trees are growing in a permanently flooded area, leaf litter immediately falls into water where nutrients are lost via leaching. Consequently, yellow leaves in a basal position that could be removed from a stem with only slight pressure were assumed to represent the senescent leaf litter. Leaves were air-dried in the field and later dried to constant mass at 70°C in a convection drying oven. Leaf tissue was ground in a Wiley mill to pass through a 40-(0.38 mm-) mesh screen. Concentrations of C and N were determined with a Perkin-Elmer CHN Autoanalyzer at the Smithsonian Environmental Research Center (Edgewater, Maryland, USA). Portions of the leaf samples were block-digested in nitric acid (Williams et al. 1986) for macronutrient and micronutrient analyses using an inductively coupled plasma spectrophotometer (ICP) at Wetland Biogeochemistry Institute, Louisiana State University (LSU; Baton Rouge, Louisiana, USA). Lignin content (acid detergent fiber) was measured on another set of green and senescent leaves at the Forage Fiber Testing Laboratory, Ithaca, New York, USA. Nutrient and lignin concentration data (in milligrams per gram dry mass of leaf tissue) were used to calculate C:N, C:P, N:P, and lignin:N ratios.

We measured potential leaching losses for green leaves to account for leaching as a possible source of P loss from the fertilized trees. In February 1995 we collected 32 mature, green leaves from the penapical position on each of the 48 trees in the experiment. Leaves were selected with <0.1% leaf damage. These leaves were sealed in plastic bags and kept cool for

TABLE 1. Results of three-way ANOVAs performed on various measured nutrient data, based on senescent leaf tissue collected from fertilized *Rhizophora mangle* trees (Twin Cays, Belize). Sources of variation analyzed were fertilization treatment (control, N, P, NPK), tidal elevation (low, high), and water depth (shallow, deep).

Source of variation	N-resorption efficiency	P-resorption efficiency	C:N	C:P	N:P	Lignin:N	Nutrient-use efficiency (NUE)†	
							N	P
Nutrients (Nt)	16.935***	8.263***	18.198***	42.354***	39.655***	9.654***	52.062***	11.106***
Tidal elevation (TE)	0.824	38.120***	0.006	3.025	0.533	1.159	3.249	0.449
Water depth (WD)	0.011	3.286	0.393	1.200	2.877	0.005	1.127	0.001
Nt × TE	4.294*	7.278*	1.394	2.383	0.228	1.316	2.240	0.062
Nt × WD	0.169	0.840	0.208	3.371*	3.343*	0.298	3.313*	0.317
TE × WD	0.457	5.453*	0.001	6.328*	6.039*	0.737	5.619*	0.062
Nt × TE × WD	0.870	0.247	3.984*	0.130	0.587	2.682	0.065	3.581*

Notes: Proportional data are arcsine square-root transformed; values reported are *F* statistics. *N* = 12 trees per nutrient level; *N* = 24 trees per water-depth level; *N* = 24 trees per tidal-elevation level. * *P* ≤ 0.05; ** *P* ≤ 0.01; *** *P* ≤ 0.001.

† Grams biomass/grams nutrient.

three days before the leaching experiment could be done. Approximately 400 cm² of leaf material were wiped and sealed inside a 2.2-L (gallon-size) plastic bag. Leaf petioles were sealed with wax. We added 100 mL deionized water to each bag of leaves and immediately placed it on a rotating table for 15 min. This time interval was determined from a preliminary analysis of the leachate from *R. mangle* leaves over a 1.5-hr period. Based on conductivity data, >90% of the leaching occurs in the first 15 min. After 15 min, a 20 mL aliquot was removed from each bag. Prior to analysis with ICP, samples were kept frozen. For each of the 48 samples, the amount of P in a leachate was calculated from the ICP-determined concentration (in micrograms per liter) in an aliquot multiplied by the total volume of water used per bag (0.1 L), divided by the leaf area (in square centimeters) of a leaf sample.

We also determined decomposition rates for leaf litter from each of the 48 trees used in the experiment. We put 7–10 g of air-dried leaf litter in 1-mm² mesh Fiberglas litter bags. A subset of the litter was oven-dried for nutrient analyses and wet-dry biomass conversion. All biomass values were expressed on an oven-dried basis. Litter bags from all trees were incubated fully submerged in a common area near the middle of the experimental area where water depth was ~30 cm at flood tide, which did not drain completely at low tide. These bags were left in the field for 6 mo, February to August 1995. Decomposition rates were calculated for each litter bag from percentage mass remaining, using Olson's (1963) exponential decay model: $X/X_0 = e^{-kt}$, where X/X_0 = fraction remaining, t = elapsed time (in years), and k = the decay constant.

As an index of belowground decomposition in this mangrove wetland, we measured the loss of tensile strength of cotton strips imbedded into the peat beneath each of the fertilized *R. mangle* trees, according to methods described in Maltby (1988). The weave and composition of these cotton strips are homogeneous. Initially, a vertical slit was sliced into the substrate directly under the canopy of each tree, 90° from the

fertilizer insertion point. As a control (t_0), a 12 × 30 cm cotton strip was inserted into the slit and immediately removed, rinsed in fresh water, and air-dried. A second, identical strip was inserted and left in place. After 5 wk (t_1), these strips were also removed, rinsed in fresh water, and air-dried. We measured the tensile strength of 2-cm-wide sections from each of the cotton strips at 2–4 cm, 6–8 cm, and 15–17 cm with a Mecmesin Advanced Force Gauge (AFG-1000N [Mecmesin Limited, West Sussex, UK]). The percentage cotton tensile-strength loss (%CTSL) was calculated for the t_1 strips relative to the control t_0 strips as:

$$\%CTSL = \frac{CTSL_{t_0} - CTSL_{t_1}}{CTSL_{t_0}} \times 100.$$

Statistical analysis

We used an independent-measures ANOVA to look for differences in variables based on material harvested in this experiment. When an ANOVA found a significant nutrient-treatment effect, we used a pairwise a priori orthogonal contrast matrix to locate differences among the four nutrient levels: NPK vs. P; NPK vs. N; NPK vs. control; P vs. N; P vs. control; N vs. control (Wilkinson 1990). To analyze for heteroscedasticity, probability plots of all variables and ANOVA residuals were examined. For heterogeneous variances, we transformed continuous data using logarithms and transformed noncontinuous data (counts) using the square root. Proportions were transformed using arcsine-square root to correct for platykurtosis.

RESULTS

Although responses varied by position along tidal-elevation and water-depth gradients, the nutrient treatment in this experiment had highly significant effects on patterns of nutrient use and cycling in *Rhizophora mangle* (Table 1). Plant responses to P and NPK fertilizers were alike for all the variables we measured. Similarly, responses to N fertilizer were not different from control trees. This pattern was similar to *R. man-*

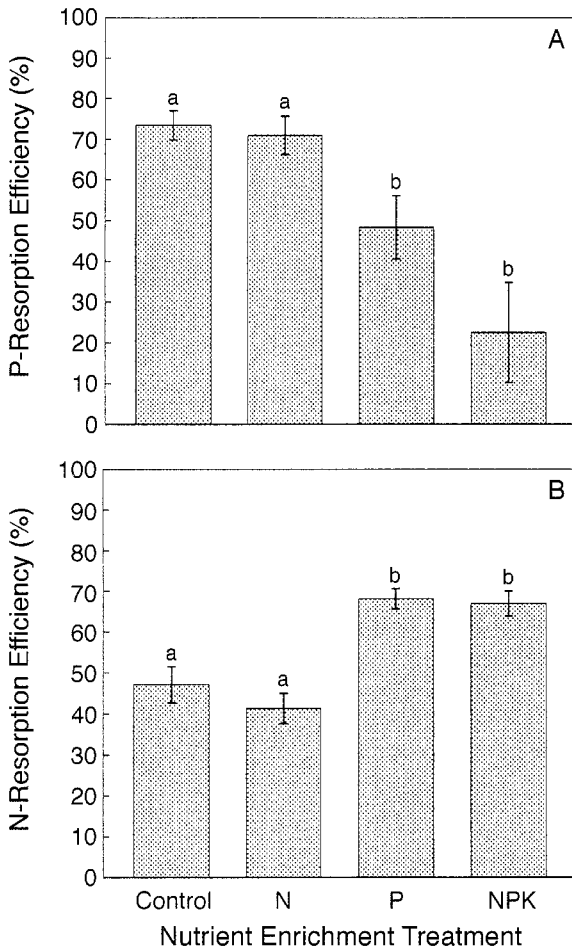


FIG. 1. (A) Phosphorus-resorption efficiency and (B) nitrogen-resorption efficiency in fertilized dwarfed *Rhizophora mangle* trees, by nutrients. Values are means \pm 1 SE. Bars with the same lowercase letter above are not significantly different at $P > 0.05$, using a three-way ANOVA and orthogonal contrast analyses. $N = 12$ trees per nutrient-enrichment level.

gle's growth responses to P rather than N, which showed that P deficiency is a major factor responsible for the slow growth and low stature of these dwarfed trees (Feller 1995).

Resorption efficiency, or the percentage of the maximum pool of P or N in mature leaves (i.e., leaf P or N mass per unit leaf area) resorbed by a plant during senescence prior to leaf fall, was strongly affected by nutrient treatment (Table 1). Phosphorus-resorption efficiency decreased significantly when P availability was increased with P and NPK fertilizers (Fig. 1). In contrast, N-resorption efficiency increased significantly in these P- and NPK-fertilized trees, suggesting a positive interactive effect of P availability on leaf N dynamics. Both N and P resorption efficiencies were similar in control and N-fertilized trees.

Neither tidal elevation nor water depth had an impact on N resorption. However, pooled across nutrient-treatment levels, trees in the higher portion of the tidal-elevation gradient had significantly lower P-resorption efficiencies than trees at lower tidal elevation (Table 1). The lowest values occurred at the higher tidal elevation where P and NPK fertilizers caused a $\sim 78\%$ decrease in P-resorption efficiency relative to controls, compared with a decrease of $\sim 35\%$ at the lower elevation.

Patterns of nutrient-use efficiency (NUE), expressed as senescent-leaf biomass per unit of nutrient, for both N and P in senescent leaves, were also significantly affected by the nutrient treatment in this experiment (Tables 1 and 2). Higher resorption of N in the P- and NPK-fertilized trees resulted in significantly higher NUE_N values compared to control or N-fertilized trees. There were also significant differences in NUE_P . In contrast with patterns of NUE_N , P and NPK fertilizers caused NUE_P to decrease greatly compared with the control and N-fertilized trees. Because of much higher levels of P resorption by control and N-fertilized trees, their NUE_P values were 3–4 times greater than in P- and NPK-fertilized trees.

Nutrient availability greatly affected the C:N, C:P, N:P, and lignin:N ratios in leaf litter produced by the

TABLE 2. Characteristics of senescent leaf tissue, including biomass, mass ratios based on carbon (C), nitrogen (N), phosphorus (P), and lignin concentrations, and nutrient-use efficiency (NUE) from fertilized dwarfed *Rhizophora mangle* trees.

Parameter	Nutrient treatments			
	Control	N	NPK	P
Biomass (g/m ²)	330.4 ^a \pm 5.3	330.3 ^a \pm 5.8	259.7 ^b \pm 7.8	268.9 ^b \pm 8.4
C:N (mg/g dry mass)	99.1 ^a \pm 7.3	74.8 ^a \pm 6.3	128.5 ^b \pm 9.4	136.4 ^b \pm 3.7
C:P (mg/g dry mass)	6088 ^a \pm 421	5539 ^a \pm 547	1751 ^b \pm 355	1637 ^b \pm 366
N:P (mg/g dry mass)	64.3 ^a \pm 6.4	78.9 ^a \pm 9.8	12.7 ^b \pm 2.1	12.1 ^b \pm 2.8
Lignin : N (mg/g dry mass)	40.7 ^a \pm 3.2	29.7 ^a \pm 4.2	52.1 ^b \pm 5	53.5 ^b \pm 1.6
NUE_N (g biomass/mg N)	0.23 ^a \pm 0.02	0.18 ^b \pm 0.02	0.27 ^c \pm 0.02	0.28 ^c \pm 0.01
NUE_P (g biomass/mg P)	14.1 ^a \pm 0.92	13.0 ^a \pm 1.19	3.4 ^b \pm 0.77	3.8 ^b \pm 0.74

Notes: Values are means \pm 1 SE. Within a row, means with the same superscript lowercase letter are not significantly different at $P > 0.05$, using a three-way ANOVA and orthogonal contrast analyses. $N = 12$ trees per nutrient enrichment level.

TABLE 3. Results of ANOVAs with regression of the decay constant (k) against litter-quality parameters for dwarfed *Rhizophora mangle*.

Litter-quality parameter	F	P	r^2
C:N ratio	6.895	<0.01	0.138
N resorption efficiency	4.660	<0.05	0.102
NUE _P (g biomass/g P)†	5.002	<0.05	0.104

Note: $N = 48$ trees.

† NUE_P = nutrient-use efficiency of phosphorus.

trees that received P and NPK fertilizers (Table 2). In addition, leaf mass per unit area declined by 18–21% in the P- and NPK-treated trees. These variables are generally considered to vary inversely with the palatability and decomposability of plant tissue. Nutrient ratios were calculated from concentrations of C, N, and P in green and senescent leaf tissue from each of the 48 experimental trees. Although the concentrations of C and N and the C:N ratios in green leaves varied little among the treatment levels (Feller 1995), nutrient levels had a significant effect on the C:N ratio of leaf litter. The C concentrations in leaf litter did not vary significantly by nutrient (ANOVA, $P > 0.05$). However, N recovery from senescing leaves increased by 42–45% in P- and NPK-fertilized trees. Thus, leaf litter from those trees had less N by mass, and higher C:N ratios than the N-fertilized and control trees (Table 2). The C:P ratios in leaf litter also varied significantly among the nutrient levels. The C:P ratios in control and N-fertilized trees were almost 4 times greater than in P- and NPK-fertilized trees. Because of the effect of P-containing fertilizers on P recovery from senescing leaves, the differences in C:P ratios in the leaf litter of control vs. P- and NPK-fertilized trees were twice the differences in C:P ratios reported for green leaves (Feller 1995). Water depth also had a significant effect on these ratios. Leaf litter from trees on the shallow side of the site had lower C:P values, with the lowest values occurring in litter from the P- and NPK-fertilized trees. N:P ratios in leaf litter were also significantly different among the nutrient levels (Table 1). Leaf litter from P- and NPK-fertilized trees had significantly lower N:P ratios than litter from control and N-fertilized trees. In control trees these N:P ratios were not significantly different from N-fertilized trees but were >5 times as great as in P- and NPK-fertilized trees. The highest N:P ratios occurred in the deep side of the site at low tidal elevation. Lignin:N ratios were calculated from concentrations of acid detergent fiber (ADF) and N in *R. mangle* leaf litter. Although lignin concentrations in green and senescent leaves and lignin:N ratios for green leaves did not vary among nutrient-treatment levels (ANOVA, $P > 0.05$; Feller 1995), they did vary significantly in leaf litter (Table 1). Because of differential N resorption among nutrient-treatment levels, leaf litter from P- and NPK-fertilized

trees had significantly higher lignin:N ratios than litter from control or N-fertilized trees (Table 2).

Concentrations of P in the leachate from green-leaf samples from each of the 48 experimental trees were compared with inductively coupled plasma spectrophotometry. However, nutrient treatment did not affect the leaching losses of P from fertilized dwarfed *R. mangle* leaves (ANOVA, $P > 0.05$). Other experimental factors, i.e., tidal elevation and water depth, did not affect leaching losses of P from *R. mangle* leaves.

We found no significant differences in the decay constant (k), or in the half-life for leaf litter among the experimental factors, i.e., tidal elevation, or water depth (ANOVA, $P > 0.05$). Decay constants varied from 0.8 to 1.8, with 1.21 ± 0.01 as the mean (± 1 SE) k value for all 48 trees in the experiment. The half-life of the leaf litter ranged from 140 d to 343 d, with 218.6 ± 7.4 d as the mean (± 1 SE). Regression analyses were done to examine the relationships between k values and initial litter-quality parameters, (i.e., C:N, C:P, lignin:N, N:P, N and P resorption efficiencies, NUE_N, and NUE_P). Based on analysis of variance, only C:N ratios, N resorption efficiency, and NUE_P were significantly related to the decay constant (Table 3). However, these factors explained relatively little of the variance in rates of litter decomposition in this study.

Although responses varied by position along the tidal-elevation and water-depth gradients, nutrient enrichment did have a significant impact on belowground decomposition (Fig. 2). The percentage cotton tensile-strength loss (%CTSL) after 5 wk was significantly greater for cotton strips imbedded into soil adjacent to P- and NPK-fertilized trees than for those adjacent to control and N-fertilized trees. Pooled across nutrient-

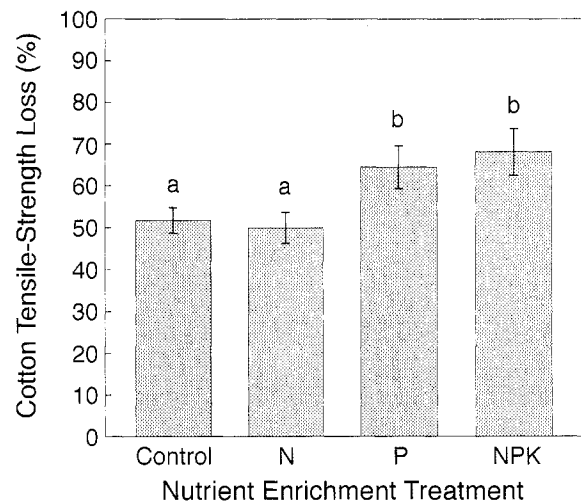


FIG. 2. Tensile-strength loss of cotton strips embedded in the substrate adjacent to fertilized dwarfed *Rhizophora mangle* trees, by nutrients. Values are means ± 1 SE. Bars with the same lowercase letter above are not significantly different at $P > 0.05$ using orthogonal contrast analyses within a three-way ANOVA. $N = 12$ trees per nutrient-enrichment level.

treatment levels, there were significantly higher %CTSL values (ANOVA, $F = 8.045$, $df = 1$, $P < 0.05$) in the high-tidal-elevation portion ($64.7 \pm 2.9\%$) of the site at Twin Cays compared with the low tidal elevation ($52.9 \pm 3.6\%$). Similarly, there were significantly higher values (ANOVA, $F = 4.622$, $df = 1$, $P < 0.05$) in the shallow-water-depth portion ($62.9 \pm 3.7\%$) of the site than in the deep-water-depth portion ($54.3 \pm 3.1\%$). The %CTSL rates on the deep side at low tidal elevation were uniformly low, ranging from 42% to 45% regardless of nutrient level. In the other parts of the site, there were significant differences among nutrient levels, with consistently higher %CTSL rates associated with the P- and NPK-treatment levels. Overall, the highest rates occurred in the shallow, high-tidal-elevation portion of the site.

DISCUSSION

Results from this long-term fertilization experiment conducted in a dwarfed *Rhizophora mangle* forest in Belize established that P availability had a dramatic impact on within-stand nutrient cycling in this wetland. This pattern is consistent with initial results that showed that P deficiency was a major factor responsible for the slow growth and low stature of old-growth dwarfed *R. mangle* forests that dominate the landscape in the interior of mangrove islands off the coast of Belize (Feller 1995, 1996). Our control plants were extremely proficient at resorbing P, returning >70% to the plant prior to leaf fall and leaving a concentration of ~0.1 mg/g dry mass P in senesced leaves. These values suggest that under P-limiting conditions resorption of P by *R. mangle* is complete and reaches the maximal physiological levels proposed by Killingbeck (1996). However, P resorption decreased by 20–50% when we fertilized to increase the availability of soil P. Similarly, biomass per unit of P (nutrient-use efficiency for phosphorus, NUE_P) declined significantly with increased availability of P. Our experiment also showed that differences in P loss from senescing leaves depends on resorption rather than differential leaching of this element. These data support our 1st hypothesis that states that as the availability of a nutrient that limits primary production increases, the mechanisms used by plants to conserve the limiting nutrient become less efficient (Loveless 1961, Small 1972, Stachurski and Zimka 1975, Tilton 1977, Chabot and Hicks 1982). In nutrient-limited mangrove wetlands where most of the leaf litter is exported by tidal flushing, internal nutrient conservation via efficient nutrient resorption and use is clearly advantageous. Our experiment demonstrated that resorption processes are linked to nutrient availability, which is consistent with Steyer (1988) who found that resorption efficiency in mangrove forests decreased along a natural gradient of increasing soil fertility. Similar results have been obtained for other ecosystems (e.g., Miller et al. 1976, Turner 1977, Boerner 1984, Shaver and Melillo 1984, Vitousek 1984,

Kost and Boerner 1985, Dierberg et al. 1986, Schlesinger et al. 1989, Escudero et al. 1992, DeLucia and Schlesinger 1995). However, several other studies have found little or no relationship between nutrient availability and resorption efficiency (e.g., Ostman and Weaver 1982, Staaf 1982, Chapin and Kedrowski 1983, Killingbeck and Costigan 1988, Lajtha and Klein 1988, Aerts and De Caluwe 1989, Chapin and Shaver 1989, Chapin and Moilanen 1991, Del Arco et al. 1991, Millard and Proe 1991, Millard 1993, Baddeley et al. 1994, Bowman 1994, Minoletti and Boerner 1994).

Our results also showed that, for *R. mangle*, biomass per unit of P (NUE_P) varied directly with P resorption so that both declined dramatically with increased P availability. In contrast, Aerts et al. (1999) found that in temperate bogs and fens soil nutrient availability had little effect on nutrient resorption and that nutrient concentrations in mature leaves had a greater impact on nutrient-use efficiency than did resorption efficiency. Our results also conflict with Escudero et al. (1992), who suggested that increased leaf longevity, rather than resorption, is a more effective adaptation for increasing the efficiency of nutrient use. In *R. mangle*, nutrient availability had no detectable effect on leaf longevity during 2 yr of treatment (Feller 1995).

In our study, the availability of P clearly also had a strong influence on within-plant N dynamics in *R. mangle* (Fig. 1). Nitrogen-resorption efficiency increased by >20% in response to increased P availability. Although the concentration of N remaining in senesced leaves indicated "complete" or "maximal" N-resorption proficiency for our control trees relative to data available for other species (Killingbeck 1996), our fertilization experiment showed that, under P-limiting conditions, N resorption is not complete in *R. mangle*. As a consequence of increased levels of N resorption, biomass per unit of N (NUE_N) increased significantly with increased availability of P. In contrast, Shaver and Melillo (1984) found that nutrient interactions had little or no effect on resorption efficiency. We have not found this pattern of responses reported previously in the literature. Although the mechanisms are unknown, these data suggest that in this low-nutrient ecosystem P deficiency is limiting not only growth but also other plant processes, and that N resorption is incomplete in *R. mangle* under P-limiting conditions. Similar performances by the P- and NPK-treated trees indicate that this response is not simply due to a shift from P to N limitation when they are provided with excess P.

Concentrations (in milligrams per gram dry mass) of N and P in senescing leaves for our control trees fall within the range of values from other mangrove studies (Table 4). From this summary, *Rhizophora* spp. consistently had more complete nutrient resorption for N than did *Avicennia* spp. (e.g., black mangrove). However, few studies have measured P concentrations in senesced leaves.

From published and unpublished studies that have

TABLE 4. Concentration levels (mg/g dry mass) of nitrogen (N) and phosphorus (P) in senesced leaves of mangrove species in different types of mangrove wetlands.

Species	Forest type	Location	Nutrient-concentration level (mg/g dry mass)		Source
			N	P	
<i>Rhizophora mangle</i>	Dwarf/scrub	Belize	5.1	0.1	this study
	Fringe		3.2	...	
<i>R. mangle</i>	Dwarf/scrub	Florida, USA	5.0	...	McKee and Feller (1995)
<i>Avicennia germinans</i>			14.0	...	
<i>R. mangle</i>	Mixed basin	Florida, USA	4.7	...	K. L. McKee, (<i>unpublished data</i>)
<i>A. germinans</i>			9.7	...	
<i>Laguncularia racemosa</i>			6.4	...	
<i>R. mangle</i>	Fringe	Florida, USA	3.7	...	Steyer (1988)
	Overwash		3.4	...	
	Mixed basin		4.8	...	
	Monospecific basin		6.1	...	
<i>A. germinans</i>	Fringe		5.1	...	
	Mixed basin		6.5	...	
	Monospecific basin		6.6	...	
<i>R. mangle</i>	Mixed basin	Florida, USA	6.1	...	Twilley et al. (1986)
	Fringe		6.5	...	
<i>A. germinans</i>	Mixed basin		10.3	...	
	Fringe		11.2	...	
<i>R. mangle</i>	Fringe	Florida, USA	4.0	...	Fell et al. (1974)
<i>R. mangle</i>	Fringe	Florida, USA	5.0	...	Heald (1971)
<i>A. marina</i>	Fringe	Australia	12.3	0.9	Clough and Attiwill (1974)
<i>R. apiculata</i>	Riverine	Australia	4.8	...	Bunt (1982)
<i>R. stylosa</i>			3.4	...	
<i>R. lamarckii</i>			3.5	...	
<i>A. marina</i>			8.3	...	
<i>R. stylosa</i>			4.0	...	
<i>R. stylosa</i>	Fringe	Australia	5.0	...	Poovachiranon et al. (1986)
<i>Ceriops tagal</i>	Fringe	Australia	2.0	...	Giddins et al. (1986)
<i>A. marina</i>	Fringe	Australia	8.5	...	Robertson (1988)
<i>C. tagal</i>			4.3	...	
<i>R. mucronata</i>		Kenya	2.9	...	Slim et al. (1996)
<i>C. tagal</i>			2.7	...	
<i>R. apiculata</i>	Fringe	India	6.8	0.6	Wafar et al. (1997)
<i>R. mucronata</i>			6.2	1.2	
<i>Sonneratia alba</i>			7.3	0.6	
<i>A. officinalis</i>			8.1	0.6	
<i>R. apiculata</i>			5.4	...	
<i>R. apiculata</i>	Riverine	Malaysia	5.4	...	Ong et al. (1982)

determined nutrient concentrations in mangrove leaf litter, values for *Rhizophora* spp. in diverse wetland types varied from 3.2 to 6.8 mg/g dry mass N (Table 4). All the values reported fall in the range indicative of "complete resorption" (Killingbeck 1996), which suggests that these species are extremely nutrient conservative. In contrast, several N concentrations reported for *Avicennia* spp. are >10.0 mg/g dry mass, which is the range Killingbeck (1996) described as "incomplete resorption." These studies suggest that *Rhizophora* spp. vs. *Avicennia* spp. differ strongly in their tissue nutrient status and that *Avicennia* spp. are less able to conserve nutrients via internal nutrient cycling. This trait may provide *R. mangle* with a com-

petitive advantage over other species of mangroves when nutrients are limiting. Although numerous biotic and abiotic factors contribute to the distinctive zonation patterns that characterize mangrove forests (Rabinowitz 1974, Smith 1987, McKee 1993, 1995a, b), competition among species based on their ability to use and conserve nutrients may influence community-level vegetation dynamics observed in these wetlands (Chen and Twilley 1998). Because of differences in abilities to compete for nutrients, shifts in species dominance have been documented for wet heathlands experiencing nutrient enrichment from external sources (e.g., Berendse and Aerts 1984, Aerts and Berendse 1988, Aerts et al. 1990).

Phosphorus availability also had dramatic effects on the nutritive, structural, and chemical quality of *R. mangle* leaf litter. Parameters implicated as indices of the substrate quality and decomposability of litter include sclerophylly, N and phenolic concentrations, and C:N, N:P, C:P, and lignin:N ratios (e.g., Cromack and Monk 1975, Aber and Melillo 1982, Chabot and Hicks 1982, Day 1982, Melillo et al. 1982, Flanagan and Van Cleve 1983, Pastor et al. 1984, Aerts and De Caluwe 1989, Taylor et al. 1989, Gallardo and Merino 1993, Berendse 1994). The relationship between P availability and the resorption efficiencies of both N and P appear to be responsible for the large differences that we observed in nutrient ratios. Concentrations of C and lignin were similar among the nutrient-treatment levels while concentrations of N and P in leaf litter decreased and increased, respectively, for trees fertilized with P or NPK. As a result, C:N and lignin:N ratios were significantly higher and N:P and C:P ratios were lower in those trees. A previous study found that sclerophylly (measured as leaf toughness) decreased and phenolic concentrations in *R. mangle* leaves increased in response to P enrichment (Feller 1995, 1996).

Despite these substantial changes in litter quality in response to P enrichment as measured by these various parameters, rates of decomposition of leaf litter were similar among nutrient-treatment levels. Although regression analyses found significant correlations between litter decomposition rates and C:N ratios, N resorption efficiency, and NUE_p , all variables combined explained only ~20% of the variation in decomposition rates in the litter from the fertilized trees. Consequently, these results did not support our 2nd hypothesis that states that plant-mediated characteristics such as litter or substrate quality determine rates of decomposition (Aber and Melillo 1982, Melillo et al. 1982, Shaver and Melillo 1984). In our experiment, high-nutrient, less-tough litter from P- and NPK-fertilized trees did not decompose faster in situ than low-nutrient, tough litter from control trees. Instead, our study suggests that environmental factors within this mangrove wetland may be more important than the nutritive, structural, and chemical quality of *R. mangle* litter in controlling rates of decomposition. Alternatively, the small mesh size (1 mm²) of our litter bags may have excluded some critical macroconsumers and detritivores in this ecosystem. Decomposition of leaf litter in mangroves has been studied in a number of locations (e.g., Heald 1971, Fell et al. 1974, Van der Valk and Attiwell 1984, Twilley et al. 1986, Robertson 1988). The mean half-life for the leaf litter in this study is ~219 d, which is similar to the values reported for *R. mangle* litter in intertidal regions (Twilley et al. 1986, Robertson 1988). Our litter bags were incubated in a continuously flooded location near the middle of the dwarfed stand of *R. mangle* trees where this study was conducted. In other studies, mangrove leaf litter has been found to decompose faster in the subtidal than in the intertidal (Heald

1971, Robertson 1988, Robertson et al. 1992). Differences in decomposition rates between what we observed and these previous ones may stem from environmental differences between dwarf forests and fringe or basin forests where these other studies were conducted. The dwarf-mangrove wetlands along coastal Belize, such as the one where our study was conducted, are continuously flooded and tidally flushed with little or no accumulation of leaf litter. Large macroinvertebrates, such as sesarmid crabs, which are known to be important consumers of leaf litter in intertidal mangrove forests (e.g., Robertson 1986, Robertson and Daniel 1989), are absent from these flooded areas (I. C. Feller, *personal observations*). Dwarf mangrove stands in Belize are extremely open, with a leaf area index <0.5 (Feller 1995). During low tides at midday, water temperatures >40°C have been recorded for these areas (I. C. Feller, *unpublished data*). Such high temperatures may limit microbial growth and retard decay rates (Robertson et al. 1992). Although in situ rates did not vary, increased productivity in response to increased P availability obviously leads to larger amounts of more P-enriched *R. mangle* litter being produced (Feller 1995). This litter will eventually decompose and add to the nutrient inventory of the water that floods this system. In such P-limited mangrove forests, enrichment with P will lead to increased production—and possibly increased export to adjacent marine ecosystems—of litter with a higher P and lower N content. Our results suggest that because of changes in the efficiency of nutrient-conservation mechanisms for both N and P, enrichment with P may alter nutrient dynamics in mangrove forests.

Although we found no differences in leaf-litter decomposition among treatment levels, P enrichment did account for substantial increases in rates of belowground decomposition, measured by higher losses in cotton tensile strength in standardized cellulose strips imbedded into the substrate. These results support our 3rd hypothesis, which states that belowground decomposition rates increase with increased availability of nutrients in the substrate (Flanagan and Van Cleve 1983). These data suggest that the microbial community responsible for belowground mineralization processes may also be P limited. However, position along the tidal-elevation gradient also had a significant impact on belowground decomposition, with ~18% higher CTSL (cotton tensile-strength loss) values in the high, compared with the low, intertidal. These data indicate that aeration of the peat substrate by exposure to the air in upper parts of the intertidal and during very low lunar or spring tides may be as important as nutrient availability for controlling these processes.

In summary, in a P-limited mangrove wetland in Belize, increased P availability had a major impact on within-stand nutrient cycling in dwarfed *R. mangle* trees. Our results have significant implications for understanding how nutrient gradients along coastal areas

will impact nutrient cycles in mangrove ecosystems. This experiment has shown that the levels of recovery of N and P from senescing leaves were clearly affected by nutrient availability. Increased availability of P caused a decrease in P resorption and an increase in N resorption. These results indicate that resorption of N and P are related, but that fundamental differences occur in these processes in senescing leaves. Phosphorus fertilization may provide P necessary for the high-energy compounds required for loading more organic nitrogen compounds into the phloem during senescence. Differences in resorption efficiencies of N and P were directly related to differences in nutrient-use efficiencies and to nutrient ratios in leaf litter. However, the extent of the impact of P enrichment on these plant-mediated processes was controlled, in large part, by where the trees grew along naturally occurring gradients in tidal elevation and water depth. Despite significant differences in nutritive, structural, and chemical qualities of *R. mangle* leaf tissue in response to P enrichment, environmental factors exerted more control over rates of decomposition than did nutrient availability. Increased P had a significant effect on below-ground decomposition, but rates varied depending on water depth and tidal elevation. Further analyses are required to obtain a clearer picture of the microbial processes in the peat substrate.

ACKNOWLEDGMENTS

We thank the government of Belize for permission to work at our study sites and Klaus Rützler for support and permission to work at the Smithsonian Institution Marine Field Station at Carrie Bow Cay. We also thank Michael Carpenter, Erik Chick, Lisa Hartman, Kirstin Hauser, Margot Lystra, David Magayna, Gail Bradley Miller, Jeannine Wayson, and Sue Wells for assistance in the field and with analyses. Comments by Robert Twilley, Ernesto Medina, and an anonymous reviewer greatly improved this manuscript. Financial support was provided by research grants from the Caribbean Coral Reef Ecosystems Program (CCRE) and from the Environmental Science Program, Smithsonian Institution. This paper is CCRE Contribution Number 541.

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