EFFECTS OF NUTRIENT ENRICHMENT ON GROWTH AND HERBIVORY OF DWARF RED MANGROVE (*RHIZOPHORA MANGLE*)[1]

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Abstract. The objectives of this study were to determine responses by red mangrove (*Rhizophora mangle*) and its primary consumers to nutrient enrichment, to determine if nutrient limitation is responsible for the dwarf plant form of red mangrove, and to evaluate four competing hypotheses for the relation of nutrient status and invertebrate herbivory. In a factorial-designed experiment, I fertilized 48 dwarf trees along gradients of tidal elevation and water depth at Twin Cays, an intertidal mangrove island in Belize, Central America, and measured plant growth responses and herbivory for 2 yr. At the end of year-2, I compared biomass accumulation and analyzed plant tissue for chemical and structural composition. Dwarf red mangrove trees on this tidal island responded quickly and grew vigorously when treated with P and NPK fertilizers. Leaf number, leaf area, branching, shoot length, and aerial root production increased dramatically over 2 yr. N-fertilized trees grew very slowly and their responses were not different from Control trees. N-fertilized and Control trees changed little over 2 yr. Some responses to phosphorus-containing fertilizers vary by water depth and tidal elevation, but physicochemical factors do not explain the differences in growth responses. I conclude that phosphorus availability is a major factor limiting red mangrove growth at my study site in the interior of Twin Cays. Herbivory by two specialized, endophytic insect species (*Ecdytolopha* sp., which feeds in apical buds, and *Marmara* sp., which mines stem periderm) increased in P- and NPK-fertilized trees compared to N-fertilized and Control trees. Twice as many apical buds were damaged or destroyed and the frequency of mines increased by 6–8 fold. However, fertilization had no effect on feeding rates and standing damage by a leaf-feeding guild of generalist herbivores or on the frequency of shoots killed by stem borers. Herbivory by the two specialists was not related to C:N ratios, but it was inversely related to concentrations of phenolic compounds. Neither nutrient ratios nor concentrations of phenolics affected rates of herbivory by the generalist folivores. Although sclerophylly of red mangrove leaves decreased in P- and NPK-fertilized trees but not in N-fertilized and Control trees, there was no relationship between leaf toughness and herbivory by generalist folivores. These data suggest that sclerophylly in oligotrophic ecosystems may be an adaptive mechanism related to nutrient conservation, and that it is associated with red mangrove survival in phosphorus-deficient soil rather than an adaptation to herbivory.

Key words: dwarf red mangrove; fertilization experiment; generalist herbivores; herbivory; nutrient limitation; phosphorus limitation; plant growth responses; Rhizophora mangle; sclerophylly; specialist herbivore.

INTRODUCTION

The availability of mineral nutrients not only varies with the environment but also affects the productivity of plant species differentially depending on individual requirements and inherent potential growth rates (Grime 1977, Chapin et al. 1986, Lambers and Poorter 1992). Because of such complexities, nutrient limitation is best determined by fertilization experiments (Binkley and Vitousek 1991). In addition to resource limitations in the environment, loss of tissue to herbivores can significantly reduce plant productivity

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(Janzen 1974). Conversely, a plant's productivity may affect the survival, growth, and reproduction of its herbivores (Price 1991). The goals of this study were to determine the general patterns of responses by red mangrove (*Rhizophora mangle* L., Rhizophoraceae) and its primary consumers when conditions limiting optimal growth for the host plant are improved, and to determine the nature of nutrient limitation in a stand of slow-growing dwarf red mangrove trees.

Mangrove forests are generally considered oligotrophic ecosystems and the species that grow there are considered adapted to low-nutrient conditions (Hutchings and Saenger 1987, Lugo 1989); however, the study presented here is the first controlled experimental field test of this hypothesis. Lugo and Snedaker (1974) suggested that a nutrient deficiency may be responsible for the dwarf plant form of red mangrove, but this hy-

pothesis has not been tested. Plant species adapted to oligotrophic conditions are predicted to have a smaller proportional response to increased supplies of a limiting nutrient than wild plants associated with fertile soils or crop plants (Grime 1977, Chapin 1980, Chapin et al. 1986, Grubb 1989, Lambers and Poorter 1992). Chapin et al. (1987) suggested that slow growth, characteristic of perennial plants from infertile soils, is unlikely to be an adaptation to those conditions; rather, slow growth is probably a trade-off for traits such as nutrient storage and antiherbivore defense that maximize survival under these conditions. Some studies have shown that slow plant growth and low nutritive-quality plant tissue on infertile soils may also limit growth of herbivore populations (Janzen 1974, Scriber and Slansky 1984). Many slow-growing tree species from oligotrophic ecosystems have a characteristic physiognomy that includes low stature, evergreenness, and long-lived scleromorphic leaves (Grubb 1977, Miller and Stoner 1979). In the neotropics, this type of sclerophyllous vegetation prevails in montane forests, lowland rain forests (Camerik and Werger 1981, Grubb 1989, Medina et al. 1990), as well as mangrove forests (e.g., Tomlinson 1986). Experimental addition of fertilizers has shown that tropical montane trees in Jamaica and Venezuela are nitrogen-limited (Tanner et al. 1990, 1992). Lowland rain forests, such as the sclerophyllous bana forests in the Río Negro region in the northern Amazon basin are also very low in nutrients, especially nitrogen and phosphorus (Janzen 1974, Sobrado and Medina 1980, Medina et al. 1990). Based on nutrient inventories of soils and vegetation, Vitousek (1984) predicted that most wet lowland tropical forests are phosphorus limited.

Janzen (1974) suggested that tough, scleromorphic leaves, characteristic of plants growing in infertile habitats, may be an adaptive defense mechanism against herbivory. Higher herbivory on oak leaves during the spring when leaves are soft, rather than during late summer when leaves are hard, supports this hypothesis (Feeny 1970). In tropical lowland rain forests, sclerophylly (measured as leaf toughness) is the best predictor of higher rates of insect herbivory on mature leaves of twenty pioneer tree species relative to twenty persistent trees species (Coley 1983). In addition, chemical characteristics of plants indigenous to resource-limited habitats may also be adaptive defense mechanisms against generalist herbivores. Janzen (1974) suggested that plants growing in low-nutrient areas have high tannin concentrations as a defense against being eaten, because loss of a leaf to a herbivore should have a greater negative impact on the fitness of a plant growing on infertile soils than on fertile soils. The resource availability hypothesis states that plant species adapted to resource-limited habitats (e.g., infertile soil) have inherently slower relative growth rates, contain higher concentrations of carbon-based defensive compounds, and are less preferred as a food

source by herbivores than are species growing in more fertile habitats (Janzen 1974, McKey et al. 1978, Coley et al. 1985, Bazzaz et al. 1987). This hypothesis predicts that slow-growing plant species in resource-poor sites will suffer lower rates of herbivory compared to species adapted to resource-rich environments.

How do variations in the availability of nutrients within a habitat affect the chemical, structural, and growth characteristics and herbivory of an individual plant species adapted to an oligotrophic environment? Bazzaz et al. (1987) proposed a within-species interpretation of the resource availability hypothesis. They suggested that in resource-limited habitats within-species allocation of nutrients to growth has highest priority, and allocation to defense increases when resource-limiting conditions improve. This hypothesis predicts that at higher relative growth rates, concentration of defensive compounds will be greater than at lower relative growth rates; consequently, it predicts lower rates of herbivory in plants adapted to low nutrient conditions whose relative growth rates have increased in response to improved resource availability. An alternative view is provided by the carbon/nutrient balance hypothesis, which states that a woody plant's C:N ratio determines its nutritive quality and palatability to generalist herbivores and is an adaptive response to herbivory that evolved under constraints of availability of resources in the environment (Bryant et al. 1983). This hypothesis predicts that the C:N ratio of woody plant species should change in response to changes in nutrient availability and light; consequently, concentrations of carbon-based defensive compounds should rise in slow-growing, nutrient-stressed woody plants and decline in more rapidly growing, nutrient-enriched plants (Bryant 1987, Chapin et al. 1987, cf. Bazzaz et al. 1987). The carbon/nutrient balance hypothesis predicts lower rates of herbivory in nutrient-stressed plants (high C:N) and higher rates in fertilized plants (low C:N).

The plant-stress hypothesis offers another set of predictions relevant to herbivore responses to nutrient-limited plants (White 1974, 1978, 1984, Toumi et al. 1984, Mattson and Haack 1987). It states that insect herbivores preferentially attack stressed, including nutrient-stressed, plants because of the breakdown and mobilization of nitrogen-containing compounds. This hypothesis predicts that the amount of readily available nitrogen in stressed plant tissue increases, providing a better and more susceptible food source to herbivores. The result is increased herbivory and insect outbreaks on nutrient-stressed plants and decreased herbivory on plants relieved from stressed conditions.

The plant-vigor hypothesis is the antithesis of the plant-stress hypothesis (Price 1991). Unlike the other paradigms of plant–herbivore interactions that are based on observations of generalist herbivores, this hypothesis seeks to explain the feeding behavior of specialized, stenophagous herbivores. It states that vig-

orously growing plants or plant modules are more favorable to certain kinds of specialist herbivores than are stressed plants, and it predicts that some insect-feeding guilds, such as specialized endophytic gallers and shoot borers, preferentially attack the more vigorous plants, or plant modules, in a population.

Structure and growth of mangrove forests

Mangroves are facultative halophytes that form extensive forested wetlands along most of the world's tropical and subtropical coastlines (Lugo et al. 1989). These plants have characteristics of both pioneer and mature-phase species (Tomlinson 1986, Smith 1992). Mangrove seedlings and saplings have relatively high growth rates and are able to colonize forest gaps and newly created intertidal substrates. As trees, mangroves often form the overstory in old, undisturbed stands. Some mangroves, such as *Rhizophora* spp., are able to persist as suppressed juveniles in the shaded understory.

The physiognomy of mangrove ecosystems is extremely variable, ranging from dwarf forests in the interior of islands to towering forests along rivers (Lugo and Snedaker 1974). Primary productivity of mangrove forests ranges from very low values for scrub forests to very high values for fringing forests (Golley et al. 1962, Janzen 1974, Odum et al. 1982). The height of mangrove vegetation typically decreases with increasing salinity and decreasing nutrient availability, forming a characteristic tree-height gradient (Lugo 1989). Mangrove tree height usually decreases with distance from the water along low-energy coastlines, but it increases with distance along high-energy coastline (Lugo 1989). Large stands of stunted, dwarf trees are a common feature in the interior parts of mangrove forests in South Florida and in the Caribbean (Lugo and Snedaker 1974).

Dwarf red mangrove trees, in particular, have traits typical of plant species from diverse oligotrophic ecosystems, including slow growth, low stature, evergreenness, and sclerophylly. Differences in growth and forest stature may be due to residual effects of tidal and wave energy in a given zone as well as latitude, soil salinity, nutrient availability, and flooding frequency (MacNae 1968, Onuf et al. 1977, Cintrón et al. 1985, Lugo 1989, Jiménez and Sauter 1991). Differences in sclerophylly in mangroves have been attributed to a salinity gradient (Clough et al. 1982, Saenger 1982, Camilleri and Ribi 1983). Similar vegetation-height gradients in coastal salt marshes have been attributed to co-occurring multiple stresses, including nitrogen limitation, low redox potentials, and high sulfide content (Burdick et al. 1989). In mangrove forests, these abiotic soil factors that influence plant growth may also be modified over time by root systems of adult trees (Boto and Wellington 1984, McKee 1993a).

Herbivory in mangroves

Hypotheses explaining rates of herbivory have not been extensively tested in mangrove systems; however, Tomlinson (1986) suggested that plant–animal interactions are relatively unimportant in mangroves. Because of extremely high concentrations of tannins in mangrove tissue, some authors concluded that these plants are essentially inedible to most herbivores (Janzen 1974, Huffaker et al. 1984). Nonetheless, our recent studies in Belize indicate that the diversity and significance of the insect fauna associated with mangrove are greater than previously described (Rützler and Feller 1988, *in press a*).

Several correlative studies examined the relationship between levels of leaf herbivory and nutrient availability but yielded contradictory results (Onuf et al. 1977, Johnstone 1981, de Lacerda et al. 1986, Farnsworth and Ellison 1991). Onuf et al. (1977) compared two small mangrove islands near Ft. Pierce, Florida, that were physiognomically similar except that one was a rookery (high nutrient) while the other island was not (low nutrient). Input of bird guano at the high-nutrient site resulted in increased ammonium and phosphate in the interstitial water near prop roots. Onuf et al. (1977) found that rates of herbivory correlated with nutrient availability, plant growth, and leaf nitrogen content, with a greater loss of leaf material at the high-nutrient site compared to the low-nutrient site. Johnstone (1981) sampled leaves from 23 mangrove species in environmentally diverse swamps in Papua, New Guinea. He measured leaves to determine the amount eaten by insects, chloride content, and nitrogen content. He compared these parameters of plants from a low-nutrient site with those from a high-nutrient site that was fertilized with high nitrogen input from human and swine feces. Although Johnstone found that 5.8–15.7% of the leaf area in 12 genera of mangroves was consumed by herbivorous insects, none of the parameters he measured, including leaf nitrogen content and nutrient availability, correlated well with the rate of insect herbivory. de Lacerda et al. (1986) compared a low-nutrient, unpolluted mangrove site with a high-nutrient site enriched by sanitary and industrial effluent in Brazil. Herbivory and chemical characteristics of leaves for black mangrove (*Avicennia schaueriana* Stapf and Leechman ex Moldenke) and white mangrove (*Laguncularia racemosa* (L.) Graetn.f) were measured at both sites, but red mangrove was measured only at the unpolluted site. Ash, crude fiber, and water content were negatively correlated with herbivory; carbohydrates and total phenolics were positively correlated with herbivory; and total nitrogen showed no relationship with herbivory. Farnsworth and Ellison (1991) quantified herbivory in red mangrove and black mangrove (*A. germinans* (L.) Staern) in several coastal and island sites in Belize, including an island rookery. They found no evidence that herbivory by mangrove folivores was
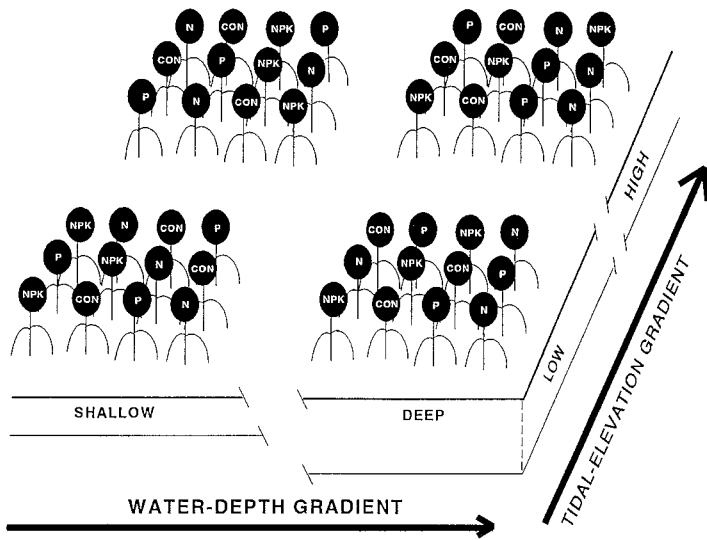
FIG. 1. Conceptual model of study site, showing the distribution of the fertilized dwarf red mangrove trees along naturally-occurring gradients in tidal elevation and water depth. The trees are growing in a permanently flooded pond that has a bottom topography that creates a shallow side and a deep side, across which the tides ebb and flood. Trees for experimental manipulation were haphazardly selected, 10 m apart, along transects across the tidal-elevation and water-depth gradients. The experimental design is a three-way factorial analysis of variance. Factors are Nutrients (NPK, P, N, Control), Tidal Elevation (low, high), and Water Depth (shallow, deep). $N = 48$ trees in experiment. Degrees of freedom: Nutrients = 3; Tidal Elevation = 1; Water Depth = 1; Nutrients × Tidal Elevation = 3; Nutrients × Water Depth = 3; Tidal Elevation × Water Depth = 1; Nutrients × Tidal Elevation × Water Depth = 3; Error = 32; Total = 47.

stimulated by nutrient enrichment. These results suggest an answer requires further, experimental examination of the role of nutrient limitation in levels of herbivory.

Research goals

The objectives of this research were to compare the general patterns of plant growth in response to increased availability of N and P and to determine how these responses affected herbivory of red mangrove. In a manipulative fertilization experiment, I examined both plant and herbivore responses to nutrient enrichment of dwarf trees growing in a monospecific stand on organic, peat-based soil. Plant growth and herbivory of fertilized red mangrove were examined to answer the following questions: (1) Is mineral nutrient limitation responsible for the slow growth and characteristic physiognomy of dwarf red mangrove trees in the interior of a mangrove island? If so, which nutrient most determines the oligotrophic character of the mangrove soil? (2) How do nutritive, structural, and chemical qualities of red mangrove tissue change in response to increased nutrient availability? (3) How does increased nutrient availability affect herbivory in red mangrove? In addition, results of this manipulative experiment serve as a simultaneous test for the competing hypotheses: within-species resource availability (Bazzaz et al. 1987); the carbon/nutrient balance (Bryant et al. 1983); the plant-stress (White 1974, Mattson and Haack 1987); and the plant-vigor (Price 1991) in herbivory.

MATERIALS AND METHODS

Study site

The field component of this study was conducted at Twin Cays, a peat-based, 92-ha range of six intertidal mangrove islands located in the lagoon just inside the crest of the barrier reef of central Belize, ≈22 km

southeast of the coastal town of Dangriga. Because of its distance from the mainland, Twin Cays is isolated from the effects of freshwater and sediment inputs from coastal runoff that may increase nutrient levels in fringing, riverine, and nearshore mangrove forests. Peat cores, 7 m deep, and radiocarbon dates show that this range of mangrove islands developed ≈7000 yr ago atop a Pleistocene high (I. A. Macintyre, *unpublished data*). Twin Cays is the primary study site and experimental field laboratory for the Smithsonian Institution's National Museum of Natural History Field Station on nearby Carrie Bow Cay (Rützler and Feller 1988, *in press a, b*).

The tide in this region of the Caribbean is microtidal and mixed semidiurnal (Kjerfve 1982). Twin Cays has a measured 21-cm tidal range, and tidal exchange with the interior of the islands occurs through deep, narrow creeks and across broad, shallow ebb-flood channels (Wright et al. 1991). Tidal flow and velocity attenuate and apparently terminate as water moves up channels into the ponds and interior areas of Twin Cays.

Typical of many island mangrove systems in the Caribbean, red mangrove at Twin Cays forms a dense seaward fringe, 3–7 m tall. Black mangrove and white mangrove of lower stature usually occur behind this fringe at higher tidal elevations. The interior portions of its larger islands are forested in large stands of dwarf red mangrove trees <1.5 m tall.

Experimental design

During July 1989, trees for experimental manipulation were chosen from a stand of ≈5300 dwarf red mangrove trees, 120 × 100 m, located in a permanently flooded ponded area along the eastern margin of Hidden Lake in the interior of the easternmost island of Twin Cays. At this site, tidal elevation and water depth vary along two environmental gradients approximately perpendicular to each other (Fig. 1). Tides ebb and flood

the site through creeks connected to the Main Channel that bisects Twin Cays, so water along the tidal gradient is differentially exchanged and mixed during high and low tides. Four transects, 10 m apart, were laid out on the shallow side of the site, going from low tidal elevation to high tidal elevation. Four similar transects were laid out on the deep side of the site. The shallow area was ≈40 m from the deep area, and the low tidal elevation area was ≈30 m from the high tidal elevation area. To determine the vector for the transects along the tidal-elevation gradient, I tracked floating corks during ebb tide. Transects along the water-depth gradient were laid out perpendicular to the tidal elevation transects. Water depth, measured at mid-flood tide during the new moon, ranged from 11 to 22 cm on the shallow side and from 30 to 54 cm on the deep side. The experimental design was a three-way (4 × 2 × 2) factorial analysis of variance (ANOVA) that involved four levels of nutrient treatments and two levels each of tidal elevation and water depth. The design was a completely crossed, fixed-effects model with interactions. The fixed factors were Nutrients (NPK, P, N, and Control); Tidal Elevation (high and low); Water Depth (deep and shallow). For reference purposes, the study site was subdivided into four quadrants defined by the water-depth and tidal-elevation gradients: quadrant I, low tidal elevation × shallow water depth; quadrant II, low tidal elevation × deep water depth; quadrant III, high tidal elevation × shallow water depth; quadrant IV, high tidal elevation × deep water depth. Forty-eight trees, 12 per quadrant, of near uniform size, were selected as they occurred at ≈10-m intervals along the tidal-elevation and water-depth transects to accommodate nutrient enrichment in three replicates (4 Nutrient × 2 Tidal Elevation × 2 Water Depth × 3 replicates = 48 trees). The 10-m intervals were left between transects and trees for buffer zones as a precaution against possible lateral migration of nutrients.

The four levels of Nutrient in 300-g doses were NPK (10:15:15) as NH_4:P_2O_5:K_2O, P (0:45:0) as P_2O_5, N (45:0:0) as NH_4, and Control (no nutrient enrichment). Nitrogen as NH_4 was used in this experiment in both the NPK and N treatments because, like other wetland soils, the ammonium ion is the primary form of mineralized nitrogen in mangrove soils. Nitrate (NO_3) is reduced and lost quickly from anaerobic, flooded soils such as those that persist at Twin Cays (Patrick 1960, Patrick and Mikkelsen 1971, Gambrell and Patrick 1978). The Nutrient treatment level for each tree within each replicate was determined randomly. The NPK fertilizer was applied in two 150-g Jobe tree stakes per tree. Granular triple superphosphate (P_2O_5) and ammonium (NH_4) fertilizers were applied in two 150-g doses enclosed in dialysis tubing (Spectrapor Membrane Tubing, 40-mm diameter, 6000–8000 molecular weight cut off). To apply the fertilizers at the start of the experiment, I cored two holes, 7-cm diameter by 30-cm deep, into the peat substrate on opposing sides

of each tree, directly beneath the outermost margin of the canopy. After tree stakes or filled sections of dialysis tubing were inserted into cored holes, each hole was sealed with a peat plug taken from a nearby unvegetated patch and was covered with a concrete weight. For Control trees, holes were cored and sealed but no fertilizer was added. To minimize damage to roots and surrounding peat, the same holes were used for each fertilizer application, and trees were fertilized twice a year, in July and January, from July 1989 through July 1991. Trees were labeled with aluminum tags (Al Tags) and surveyor tape. Shoots were labeled with small pieces of aluminum tags. Leaves were marked with waterproof black ink marks on their abaxial surfaces. Direct observations of a separate set of similarly marked leaves were not different from unmarked leaves, suggesting that the ink does not damage leaves or discourage herbivores.

Measurements of plant responses

Baseline measurements were made at the onset of this experiment in July 1989, prior to the trees receiving their first nutrient treatment. Plant-growth responses to treatments were measured at 6-mo intervals, during the same periods when trees were refertilized, January and July, 1990–1991. Tree height was measured vertically from the substrate to the tallest part of a tree. Leaf production was based on the performance of five randomly selected, terminal unbranched shoots (first-order branches) per tree. Pilot data were collected to determine the appropriate sample size for number of leaves per tree by Sokal and Rohlf's (1981:263) iterative method. Leaf-length variances and coefficients of variation for 10 dwarf trees at Hidden Lake suggest that the appropriate sample size is 30–35 leaves per tree. Because the mean number of leaves per shoot on dwarf trees is between six and seven leaves, the sample size was five shoots.

To determine effects of the Nutrient treatment on leaf production, leaves on the five selected shoots were measured in situ during July 1989, July 1990, and July 1991. Leaf area (cm^2) was calculated as the mean leaf area per shoot. During July 1990 and 1991, leaf area was measured with a LI-COR 3000 Portable Leaf Area Meter (LI-COR, Lincoln, Nebraska, USA). Leaf-area values for July 1989 were calculated using a regression equation obtained from 300 measured leaf lengths and area-meter values for similar leaf lengths and length-to-width ratios. Leaf number was the mean number of leaves per shoot, based on the same five shoots per tree.

At the end of the experiment in July 1991, I harvested one shoot per tree to evaluate leaf-biomass production and to conduct leaf-tissue analyses. Leaf mass per unit area (g/cm^2) and area-meter values were used to calculate leafy biomass (g) per shoot (Witkowski and Lamont 1991).

To determine the effects of the Nutrient treatment on

wood production and branching, I measured the length of the original, unbranched shoots plus the number and length of all their lateral branches or subshoots that developed subsequent to the initial fertilization. Woody biomass per shoot was estimated based on measurements from the set of shoots harvested from experimental trees at the end of this experiment. Because wood density probably varies continually along the length of a shoot, the center 5-cm section of each shoot was selected as an objectively defined sampling unit for making comparisons. This section was cut from each harvested shoot with a scalpel. Midpoint diameters and fresh mass were measured and volumes were calculated. Shoot sections were weighed to constant dryness at 40°–60°C. Wood density was calculated using the formula $\rho = m/V$; where m is dry mass (g), and V is volume (cm^3) of the 5-cm section of a harvested shoot. Density calculations and volume of shoots and subshoots were used to estimate woody biomass per shoot.

The numbers of aerial roots and propagules produced per experimental tree were counted during each sampling period. Only new, ungrounded roots were counted. Consequently, aerial root production may be underestimated because fast-growing roots that grounded in <6 mo would not have been included in these counts. Propagules in all stages of development from flower bud to empty cotyledonary collar were included in the count. Aborted flowers or buds were not included.

To assess the response of canopy-leaf area to the Nutrient treatment, I measured the leaf area index (LAI) for each of the 48 fertilized trees. I used a plumb-bob method which has been used in previous mangrove forest studies (Cintrón and Novelli 1984, Brown and Ewel 1987). To avoid bias, I determined LAI as the mean number of contacts of leaves against a weighted plumb line, lowered five times at randomly selected points through the canopy of each tree from a height of 3 m and counted by an unbiased observer.

In lieu of growth rates expressed in terms of conventional growth analysis that are based on serial harvests of groups of entire plants (Evans 1972), I used demographic growth analysis to determine the effects of Nutrients on plant growth rates (McGraw and Garbutt 1990a, b). Growth rates were determined for individual plants based on serial, nondestructive counts and measurements of leaves and shoots. I calculated absolute growth rates per month for year-1 (July 1989 to July 1990) and year-2 (July 1990 to July 1991) for each experimental tree for shoot elongation ($cm \cdot mo^{-1} \cdot shoot^{-1}$), leaf number ($number \cdot mo^{-1} \cdot shoot^{-1}$), and leaf area ($cm^2 \cdot mo^{-1} \cdot shoot^{-1}$).

Leaf and stem analysis

Leaf samples for analysis were harvested in August 1991. Mature leaves from a penapical position on first-order branches were collected from each of the 48 trees, and leaf area (cm^2) and fresh mass (g) were measured.

Leaves were air dried in the field and later freeze-dried to constant weight. The difference between fresh mass and dry mass was used to determine leaf water content. Percentages of C and N were determined with a LECO Elemental Analyzer, Model 600, LECO Corporation, St. Joseph, Michigan, USA. Portions of the freeze-dried leaves were block-digested for macronutrient and micronutrient analyses using an inductively coupled plasma spectrophotometer (ICP) by Analytical Services, Wetland Biogeochemistry Institute, Louisiana State University. These values were used to calculate the nutrient ratios C:N, C:P, and N:P.

Portions of the freeze-dried leaf samples were used for phenolic assays by K. L. McKee, Wetland Biogeochemistry Institute, Louisiana State University. Ground tissue was extracted for 10 min in a 50% acetone solution. The extract was used to determine total phenolic content by the Folin-Denis method with tannic acid used as a standard. With quebracho tannin as a standard, condensed-tannin concentration was determined using the vanillin assay for catechin-based tannins and the BUOH/HCl assay for proanthocyanins (Mole and Waterman 1987).

A separate set of penapical leaves was harvested from each fertilized tree to determine fiber content and toughness. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) analyses (Van Soest 1963) were performed by the Forage Testing Laboratory, Northeast Regional Dairy Herd Association in Ithaca, New York, USA. Acid detergent fiber is equivalent to crude fiber and measures primarily lignin and cellulose; NDF analysis measures lignin, cellulose, and hemicellulose. Both values are thought to be negatively correlated with herbivory (Van Soest 1963).

To quantify sclerophylly, I measured leaf mass per unit area (g/cm^2), which is the inverse of specific-leaf area (SLA, cm^2/g). Leaf mass per unit area varies directly with the hardness or toughness of leaves (Sobrado and Medina 1980, Medina et al. 1990, Witkowski and Lamont 1991). For another index of leaf toughness, freshly collected leaves were measured using a "penetrometer" (custom built), based on a design by Feeny (1970). To compare the toughness of leaves in similar positions among the four Nutrient levels and to determine how toughness varies among leaves on a shoot, freshly collected leaves from the penapical leaf position and from the basal leaf position on a shoot (i.e., the oldest, nonsenescent leaves on a shoot) were placed in a portable cooler and measured within 5 hr of collecting. The penetrometer measures the force necessary to punch a blunt 5-mm-diameter rod through a leaf.

To evaluate nutritional differences in woody tissue resulting from fertilization of red mangrove trees, I measured nitrogen, carbon, and water content of shoots harvested from each experimental tree. Percentages of C and N were determined with a CHN Autoanalyzer by Analytical Services, USL.

Edaphic analysis

Because nutrient availability is often controlled by physicochemical factors, the study site was characterized for nutrient concentrations as well as salinity, pH, redox potential and sulfide concentrations (Mendelssohn and McKee 1987, McKee et al. 1988, Binkley and Vitousek 1991). During each field season, I measured pore-water salinity at 15-cm depth in the rhizosphere of each experimental tree. In July 1991, pore-water samples were collected from the substrate at each tree using a large plastic syringe fitted with a probe and flexible tubing. Samples were placed in acid-washed glass vials, filtered through a 0.45-μm filter, and fixed with sulfuric acid. These samples were subsequently analyzed for macronutrients and micronutrients with ICP spectrometry by Analytical Services, LSU. Nitrogen (as NH_4) was measured by Analytical Services, USL.

In June 1990 after 1 yr of nutrient treatment, redox potentials, sulfide levels, pH, and pore-water salinity were measured at each of the 12 NPK-fertilized and 12 Control trees, and also at four Soil Control areas located in four unvegetated plots, approximately 10 × 10 m, at my study site by K. L. McKee and I. A. Mendelssohn. Measurements were taken at two soil depths (1 cm and 15 cm) at each tree and Soil Control.

Herbivory measurements

At the start of the experiment in July 1989, the entire aboveground portion of each of the 48 trees was thoroughly examined for herbivores and damage in its buds, leaves, shoots, bole, and aerial roots. Damaged woody parts were left on the trees, because clipping dead branches off trees may introduce pathogens that spread into adjacent undamaged parts, and tagged for subsequent recognition. Dead shoots were split apically and inspected in situ to determine cause of death (wood borer or other) and species of wood borer. I attempted to remove all insects, crabs, and other macroscopic arthropods from the 48 trees so that each tree began the experiment with a near zero load of leaf and shoot herbivores as well as secondarily associated organisms. Thereafter, no organisms were removed from any of the 48 trees until after August 1991. Specimens collected in July 1989 and from adjacent trees during the course of this experiment were used for identification and vouchers. Vouchers are deposited in the Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

To evaluate the effects of fertilization on herbivory, I calculated rates of damage to leaves produced by the five shoots initially selected. These rates were calculated for 6-mo intervals, based on measurements of individual leaves, beginning when a leaf was in the apical position and again on the same leaf 6 mo later. Many of the leaves in the apical position were not yet at full size when they were drawn initially. If the deciduous stipules which subtended a recently unfolded leaf pair had fallen off, that leaf pair was considered to be in the apical position and was drawn at the beginning of a 6-mo interval and again 6 mo later. Pairs of new leaves exposed by an opening apical bud were not drawn if the stipules had not fallen. These exposed leaves were considered to be still in the bud. Rates of herbivory were calculated for four such intervals, from July 1989 through July 1991. Leaves were traced, including all holes and damaged areas, to avoid removing leaves from the experimental trees during the course of my study, as well as to determine rates of herbivory based on individual leaves. To make a leaf tracing, a leaf was first held steady by sandwiching it between hinged sheets of a clear Plexiglas drawing board, 20 × 25 cm; it was then traced onto a piece of 0.08-mm polyethylene sheeting fitted to the drawing board. Only leaf blades, not petioles, were drawn to avoid damage to the plants with the drawing board.

I measured the leaf tracings, using AUTOCAD Release 9 1982. Following the contour of leaf margins, I reconstructed complete leaf outlines on damaged leaves and measured the intact, whole leaf area for each leaf plus each individual damaged area on a leaf. The sum of the damaged areas was tabulated. Values for intact leaf area and damaged areas were used to calculate leaf area and percentage leaf area removed when a leaf was in the apical position and again on the same leaf 6 mo later. To determine the rate of herbivory per 6-mo interval, I calculated differences in percent leaf area removed between each sequential sampling times.

Herbivory in the apical bud by the red-mangrove bud moth, *Ecdytolopha* sp., (Olethreutidae) typically caused symmetrical damage to leaf pairs but sometimes also caused entire leaf pairs to abort or apical bud mortality. To compare levels of damage by this herbivore in response to the nutrient treatment, I recorded the number of aborted leaves and damaged buds on the experimental trees.

To determine if fertilization for 2 yr had any effect on the rate of feeding by primary stem borers, I inspected all shoots on the experimental trees for evidence of primary stem borers. At the end of the experiment, all dead shoots were clipped from the 48 manipulated trees at 3 cm from their branch gaps where they joined the next higher order branch and were dissected with a pocket knife. Species of wood borer were recorded, if known.

In Belize, red mangrove hosts four undescribed species of microlepidopterans (Gracilariidae, *Marmara* spp). One mines in leaves (*Marmara* sp. nov. 1), one in shoot periderm (*Marmara* sp. nov.2), one in propagule periderm (*Marmara* sp. nov. 3), and one in aerial root periderm (*Marmara* sp. nov. 4) (I. C. Feller, *personal observation*). To determine if these miners fed differentially in response to nutrient enrichment, the number of mines was counted on each of the 48 trees in July 1991, 2 yr after fertilization treatments began.

TABLE 1. Summary of three-way repeated-measures ANOVAs performed on tree height (cm), number of aerial roots per tree, leaf area per shoot (cm^2), number of leaves per shoot, shoot length (cm), and number of subshoots per shoot of fertilized red mangrove trees by Nutrients, Nt (NPK, P, N, Control); Tidal Elevation, TE (low, high); Water Depth, WD (shallow, deep). Analyses are based on measurements repeated in July of 1989, 1990, and 1991 (Time effect, T) for all variables except shoot length and number of subshoots per shoot, which are based on July 1990 and 1991 measurements. Tree height and leaf area are log-transformed; counts of aerial roots, leaves, and subshoots are square root transformed. Values are F-statistics. $N = 12$ trees per Nutrient level; $N = 24$ trees per Water-Depth level; $N = 24$ trees per Tidal-Elevation level.

Source of variation	Tree height (cm)	Number of aerial roots	Leaf area (cm^2)	Number of leaves	Shoot length	Number of subshoots
Nutrients (Nt)	2.244	23.780***	27.632***	50.652***	72.224***	30.248***
Tidal Elevation (TE)	6.870*	8.756**	15.770***	18.788***	14.224**	4.531*
Water Depth (WD)	3.359	14.677***	1.163	1.209	0.061	0.045
Nt × TE	0.897	3.280**	3.661*	5.882**	4.996**	1.748
Nt × WD	1.889	4.086*	0.337	0.782	0.782	0.300
TE × WD	9.675**	13.050**	0.312	0.367	0.252	0.372
Nt × TE × WD	0.096	0.463	3.828*	1.332	0.257	0.355
Time (T)	175.717***	43.512***	108.395***	118.489***	20.298***	3.418
T × Nt	30.441***	9.755***	23.633***	38.350***	5.258**	1.254
T × TE	5.901**	2.091	0.044	3.620*	0.064	0.003
T × WD	3.231*	1.317	0.167	0.303	0.240	0.210
T × Nt × TE	2.373*	1.281	0.599	1.397	0.161	0.021
T × Nt × WD	0.733	0.979	2.016	1.064	0.380	1.020
T × TE × WD	2.030	1.043	2.712	0.151	1.277	0.084
T × Nt × TE × WD	1.163	1.004	0.717	0.284	0.167	0.131

*$P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Statistical analysis

I used a repeated-measures ANOVA to look for possible differences over a 2-yr period in plant-growth and herbivory variables as a result of Nutrients, Tidal Elevation, Water Depth, and their interactions. I used an independent-measures ANOVA to look for differences in variables based on material harvested at the end of the experiment. When an ANOVA found a significant Nutrient treatment effect, I 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 (SYSTAT, Wilkinson 1991). The denominator of the F ratio is 32 in all cases.

To analyze for heteroscedasticity, probability plots of all variables and ANOVA residuals were examined. For heterogeneous variances, I transformed continuous data using logarithms and transformed noncontinuous data (counts) using the square root. For data sets containing many zero values, log transformations are based on ($x + 1$) and square-root transformations are based on ($x + 0.5$). Because herbivory rates were small and included zero values, they were log transformed as: $\ln(100 \times$ herbivory rate $+ 1)$. Proportions were transformed using arcsine-square root to correct for platykurtosis. With data sets containing a large number of zeros ($\geq 30\%$), I used nonparametric statistical tests (Kruskal-Wallis), because transformations cannot adjust such data for heteroscedasticity.

RESULTS

Plant-growth responses

Although responses varied by position along the tidal-elevation and water-depth gradients, nutrient enrich-ment resulted in significant differences in most plant-growth variables measured in this study (Table 1). For all measures, P and NPK fertilizers caused similar and significant increases in plant growth; whereas N fertilizer had no effect (Fig. 2). By the end of the second year of treatment (July 1991), tree height increased by 60 and 70% in P- and NPK-fertilized trees, respectively, but did not change significantly for the N-fertilized and Control trees (Fig. 2A). The number of new aerial roots produced by P- and NPK-fertilized trees increased by >30 fold but remained constant for N-fertilized and Control trees (Fig. 2B). Similarly, the number of leaves and the leaf area (cm^2) per shoot increased dramatically for trees fertilized with P and NPK, but showed no change for N-fertilized and Control trees (Figs. 2C and 2D). Branching, measured as the number of subshoots per shoot, also increased significantly on trees fertilized with P and NPK, but few if any subshoots were produced on N-fertilized and Control trees (Fig. 2E). Shoot length, including the original unbranched main shoot and all the new subshoots it produced during the 2-yr experimental period on P- and NPK-fertilized trees, was 4–5 times greater than on N-fertilized and Control trees (Fig. 2F).

For both years of this study, the demographic growth rates for the P- and NPK-fertilized trees, based on leaf area ($cm^2 \cdot mo^{-1} \cdot shoot^{-1}$) and number of leaves (number$\cdot mo^{-1} \cdot shoot^{-1}$) were significantly greater than rates for N-fertilized and Control trees (Fig. 3A, B). These rates of leafy growth for year-1 were significantly greater than for year-2. However, growth rates of woody tissue, based on shoot elongation ($cm \cdot mo^{-1} \cdot shoot^{-1}$) were significantly greater during year-2 than year-1 (Fig. 3C). In the second year, the shoot elon-
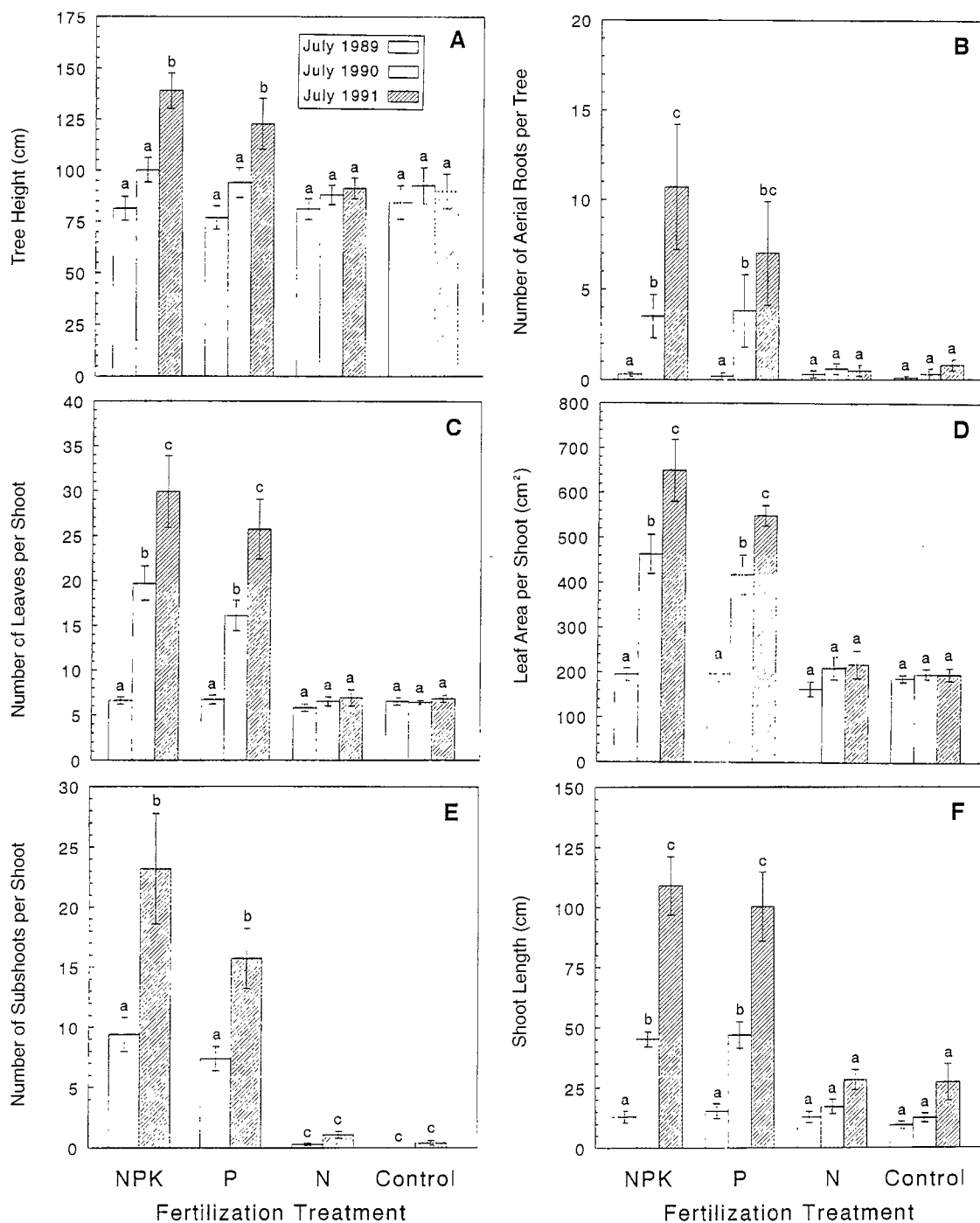
FIG. 2.   Growth responses (means ± 1 SE) for fertilized dwarf red mangrove trees by Nutrients (NPK, P, N, Control) over 2 yr of treatment. Data are for (A) tree height, (B) number of aerial roots, (C) number of leaves per shoot, (D) leaf area per shoot, (E) number of subshoots per shoot, and (F) shoot length. Within a graph, bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrast analyses within a three-way ANOVA. $N = 12$ trees per Nutrient level.

gation rates for NPK-fertilized trees were significantly greater than for P-fertilized trees. These growth rates in N-fertilized and Control trees were similar both years and were always significantly lower than growth rates for P- and NPK-fertilized trees.

The patterns for leaf and wood biomass production, based on dry mass (g) of leaves and shoots harvested at the end of year-2, parallel demographic measurements. Values for leafy biomass per shoot for trees fertilized with P and NPK were similar, but both treat-
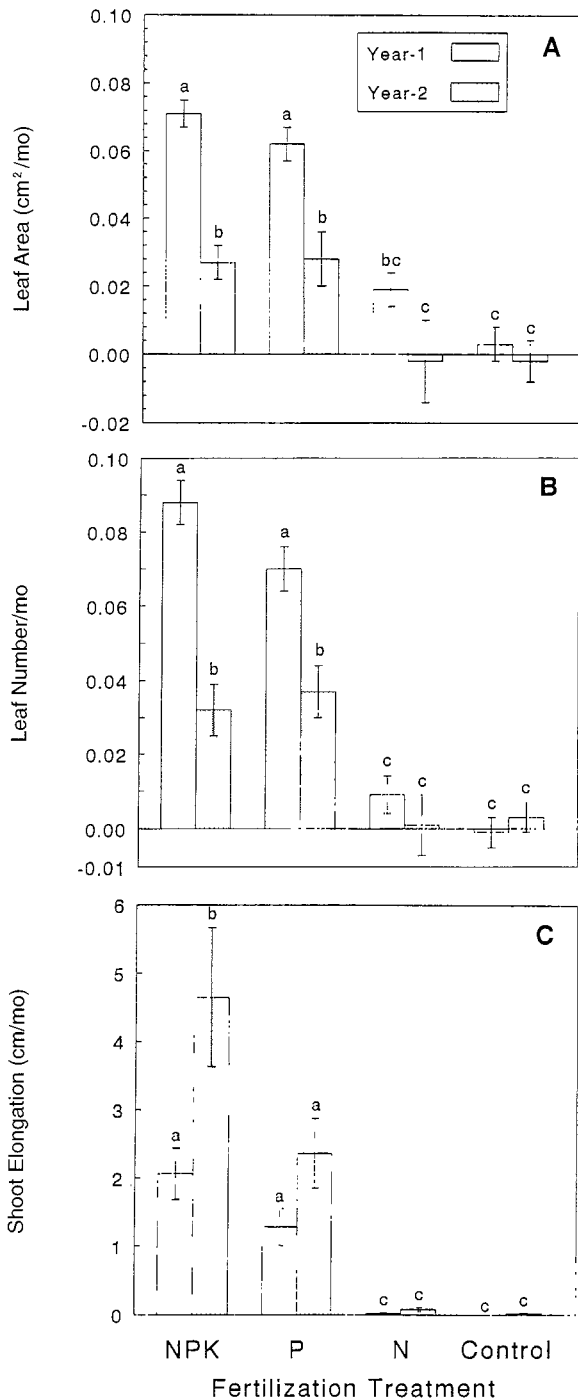
FIG. 3. Demographic growth rates (means ± 1 SE) for fertilized dwarf red mangrove trees for year-1 (July 1989–July 1990) and for year-2 (July 1990–July 1991) by Nutrients (NPK, P, N, Control). Growth rates are calculated on a per shoot basis for (A) leaf area (cm²/mo), (B) leaf number/mo, and (C) shoot elongation (cm/mo). Within a graph, bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrast analyses within a three-way ANOVA. $N = 12$ trees per Nutrient level.

ments were significantly greater than for N-fertilized and Control trees (Fig. 4A). Woody biomass per shoot for NPK-fertilized trees was significantly greater than for P-fertilized trees, but both were significantly greater than for N-fertilized or Control trees (Fig. 4B).

All tree responses also varied significantly with position along the tidal-elevation gradient, and several variables also varied along the water-depth gradient (Table 1). After 2 yr, (by July 1991) tree height, number of aerial roots, leaf area, number of leaves, shoot length, and number of subshoots were all greater for trees in the lower portion of the tidal-elevation gradient, and the number of aerial roots was significantly greater in the deeper portion of the water-depth gradient (Tables 1 and 2). Furthermore, the July 1991 harvests showed that trees produced significantly more leafy biomass per shoot (12.73 ± 2.16 g, mean ± 1 SE) in the low tidal elevation than in the high tidal elevation (9.07 ± 0.90 g; $F = 10.738$, df = 1, $P \leq 0.01$), as
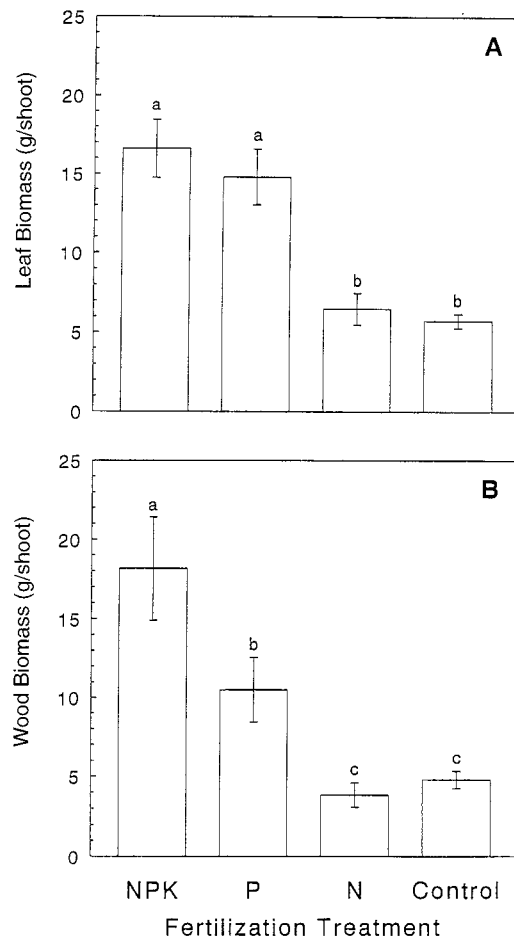

FIG. 4. Accumulation per shoot (means ± 1 SE) of (A) leaf biomass and (B) wood biomass in fertilized dwarf red mangrove trees following 2 yr of treatment by Nutrients (NPK, P, N, Control). Within a graph, bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrast analyses within a three-way ANOVA. $N = 12$ trees per Nutrient level.

TABLE 2. Growth performance of dwarf red mangrove trees for tree height (cm), number of aerial roots, leaf area (cm²), number of leaves, shoot length (cm), and number of subshoots by Tidal Elevation and Water Depth over 2 yr of treatment. Values are means ± 1 SE. N = 24 trees per Tidal-Elevation level; N = 24 trees per Water-Depth level.

	Growth parameters	Tidal elevation		Water depth	
		Low	High	Deep	Shallow
July 1989	Tree height (cm)	84.67 ± 4.44	77.25 ± 3.85	87.19 ± 4.73	74.73 ± 3.17
	No. aerial roots	0.25 ± 0.11	0.17 ± 0.08	0.33 ± 0.12	0.08 ± 0.06
	Leaf area (cm²)	210.74 ± 10.94	160.20 ± 8.36	177.76 ± 11.99	193.19 ± 9.81
	No. leaves	7.00 ± 0.31	5.78 ± 0.24	6.07 ± 0.34	6.72 ± 0.25
	Shoot length (cm)	12.77 ± 1.62	13.07 ± 1.81	12.28 ± 1.79	13.56 ± 1.64
	No. subshoots	0	0	0	0
July 1990	Tree height (cm)	101.53 ± 5.15	85.94 ± 3.33	97.84 ± 5.67	89.62 ± 3.04
	No. aerial roots	3.26 ± 1.09	0.92 ± 0.43	3.30 ± 1.12	0.88 ± 0.34
	Leaf area (cm²)	384.14 ± 41.77	259.52 ± 18.70	318.37 ± 40.30	325.29 ± 28.40
	No. leaves	14.65 ± 1.86	9.69 ± 0.90	11.66 ± 1.60	12.68 ± 1.49
	Shoot length (cm)	35.57 ± 4.48	24.29 ± 3.24	29.73 ± 4.62	30.13 ± 3.47
	No. subshoots	1.08 ± 0.24	0.63 ± 0.19	0.84 ± 0.22	0.88 ± 0.20
July 1991	Tree height (cm)	123.54 ± 8.66	97.96 ± 4.56	117.67 ± 8.66	103.83 ± 5.55
	No. aerial roots	6.25 ± 2.26	3.21 ± 0.95	6.92 ± 2.30	2.54 ± 0.71
	Leaf area (cm²)	494.34 ± 67.68	334.70 ± 35.80	412.17 ± 60.20	416.87 ± 52.84
	No. leaves	20.90 ± 3.50	13.74 ± 1.93	17.24 ± 2.91	17.40 ± 2.93
	Shoot length (cm)	77.45 ± 11.78	52.07 ± 8.88	63.16 ± 11.89	66.35 ± 9.48
	No. subshoots	2.60 ± 0.60	1.69 ± 0.47	2.18 ± 0.55	2.11 ± 0.55

well as significantly more wood biomass in the low tidal elevation (12.12 ± 2.16 g) than in the high tidal elevation (6.76 ± 0.95 g; F = 12.761, df = 1, $P \le$ 0.001) after 2 yr of treatment.

A Tidal Elevation × Water Depth interaction caused tree height and numbers of aerial roots to be greater for trees in the low tidal elevation plus deep water depth position (Quadrant II) than for trees in other parts of the study site (Fig. 5A, B). At the end of the second year of this study, there was a physiognomically obvious and significant Tidal Elevation × Nutrient interaction effect on tree "vigor," such that the number of leaves, leaf area, shoot length, as well as leafy and woody biomass produced by P- and NPK-fertilized trees in the low tidal-elevation position were significantly greater than P- and NPK-fertilized trees in the high tidal elevation portion of the site (Tables 1 and 3). In addition, a Water Depth × Nutrient interaction is manifested in significantly more aerial roots on P- and NPK-fertilized trees in the deep than shallow water in the study area.

Growth responses by red mangrove to NPK and P fertilizers dramatically altered the overall canopy structure, as measured by leaf area index (LAI), particularly at the lower of the two tidal elevations. P- and NPK-fertilized trees have significantly higher LAI values than N-fertilized trees and Control trees (Fig. 6). Because of a Nutrient × Tidal Elevation interaction, trees fertilized with P and NPK in the low tidal elevation have significantly higher LAI values than similarly treated trees in the high tidal elevation.

Reproduction

Dwarf red mangrove trees at Hidden Lake and other similar sites at Twin Cays seldom flower, and flowers that do form usually abort (I. C. Feller, *personal obser-*

vation). Occasionally, dwarf trees set fruit, but their propagules are typically small and misshapen. At the start of this experiment in July 1989, none of the 48 trees had any flowers, flower buds, or propagules. In July 1991, after 2 yr of nutrient enrichment, the NPK- and P-fertilized trees had 0.95 ± 0.32 (mean ± 1 SE) and 0.65 ± 0.23, respectively, flowers or propagules per shoot, compared to 0 ± 0 and 0.09 ± 0, respectively, for N-fertilized and Control trees. These data, based on the five shoots selected initially, indicate a significant increase in flowering in trees that received supplemental phosphorus (Kruskal-Wallis: χ^2 = 17.672, df = 3, P = 0.001). None of the 12 N-fertilized trees and only one of the 12 Control trees had flowers, buds, or propagules; whereas, eight of the 12 NPK-fertilized trees and seven of 12 P-fertilized trees were flowering and producing propagules.

Chemical composition of plant tissue

Nutrient-enrichment effects on macronutrient and micronutrient concentrations in red mangrove tissue varied by nutrient (Table 4). In leaves harvested from a penapical position on each tree, concentrations of carbon and leaf water content (mg/g dry mass) did not vary by treatment. Phosphorus concentrations were significantly higher in P- and NPK-fertilized trees than in N-fertilized or Control trees. Differences in foliar nitrogen concentrations among Nutrient levels were suggestive (P = 0.06), but were not significant (ANOVA, $P > 0.05$). These data suggest that nitrogen concentrations in leaves from the NPK-, P-, and N-fertilized trees may be higher than in Controls. Carbon and nitrogen concentrations in wood tissue did not vary among Nutrient levels, but the wood water content in P-fertilized trees was significantly greater than in N-fertilized and Control trees (Table 5). Potassium was
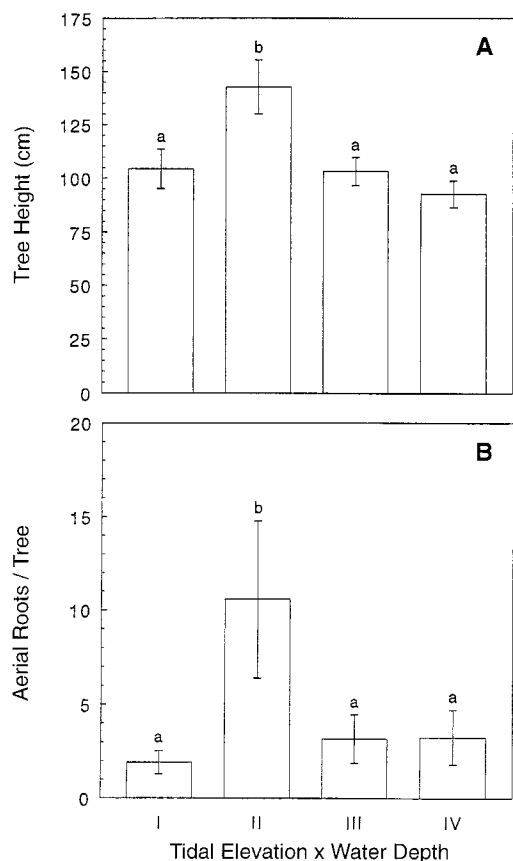
FIG. 5. Variations (means ± 1 SE) in (A) tree height and (B) number of aerial roots per tree along intersecting environmental gradients of tidal elevation and water depth for dwarf red mangrove trees following 2 yr of treatment. The x axis represents combinations of Tidal Elevation × Water Depth, which divide the study site into four quadrants: Quadrant I (low Tidal Elevation × shallow Water Depth); Quadrant II (low Tidal Elevation × deep Water Depth); Quadrant III (high Tidal Elevation × deep Water Depth); Quadrant IV (high Tidal Elevation × deep Water Depth) . Within a graph, bars with the same letter are not significantly different at P > 0.05 using orthogonal contrast analyses within a three-way ANOVA. N = 12 trees per Tidal Elevation level × Water Depth level.

also significantly lower in leaves from trees enriched with NPK and P. Except for slightly higher concentration in the NPK-treatment level than the Control, magnesium concentrations were similar among Nutrient levels. For zinc, P-fertilized trees had significantly higher concentrations than either N-fertilized or Control trees, but there were no other significant, experiment-wide differences. None of the other measured concentrations of elements varied with treatment. Neither Tidal Elevation, nor Water Depth, nor their interaction, had significant effects on the concentration of any of the measured elements.

The Nutrient treatment altered the availability of essential nutrients and changed the balance of these nutrients in red mangrove leaf tissue. Although the C:N

ratio in fresh leaves did not vary significantly (ANOVA, $P > 0.05$) among Nutrient levels (NPK, 34.61 ± 1.53; P, 36.73 ± 1.98; N, 36.91 ± 2.05; Control, 40.90 ± 1.42), there were significant shifts in C:P ($F = 22.268$, df = 3, $P \leq 0.001$) and N:P ($F = 14.680$, df = 3, $P \leq 0.001$) ratios because of increased phosphorus concentrations in P- and NPK-fertilized trees. The C:P ratios in NPK- (601.3 ± 40.2) and P-fertilized trees (703.1 ± 38.7) were not different (ANOVA, $P > 0.05$); however, they were significantly lower than in N-fertilized (1232.9 ± 74.1) and Control trees (1283.3 ± 194.7): (ANOVA, orthogonal contrast analyses, P vs. N, $F = 24.226$, df = 1, $P \leq 0.001$; P vs. Control, $F = 22.735$, df = 1, $P \leq 0.001$; NPK vs. N, $F = 42.823$, df = 1, $P \leq 0.001$; NPK vs. Control, $F = 40.772$, df = 1, $P \leq 0.001$). The N:P ratios in NPK- (17.53 ± 1.15, mean ± 1 SE) and P-fertilized trees (19.66 ± 1.47) were not different (ANOVA, $P > 0.05$), but both were significantly lower than in N-fertilized (34.55 ± 2.67) and Control trees (31.58 ± 4.64): (ANOVA, orthogonal contrast analyses, P vs. N, $F = 20.632$, df = 1, $P \leq 0.001$; P vs. Control, $F = 12.080$, df = 1, $P \leq 0.001$; NPK vs. N, $F = 31.957$, df = 1, $P \leq 0.001$; NPK vs. Control, $F = 20.735$, df = 1, $P \leq 0.001$).

Secondary compound responses of leaves

To determine if levels of carbon-based defensive compounds were affected by differences in Nutrient treatment levels, concentrations of condensed tannins and total phenolics were measured in penapical leaves from each of the 48 experimental trees. Concentrations of condensed tannins were significantly affected by the Nutrient treatment ($F = 9.970$, df = 3, $P \leq 0.001$). Concentrations were similar among P- and NPK-fertilized trees and both were significantly higher than N-fertilized and Control trees (Fig. 7A). Nitrogen-fertilized and Control trees had similar condensed tannin concentrations. Concentrations of total phenolics were also significantly affected by the Nutrient treatment ($F = 5.739$, df = 3, $P \leq 0.01$). Total phenolic concentrations in P- and NPK-fertilized trees were similar but only NPK-fertilized trees had significantly higher concentrations than N-fertilized and Control trees (Fig. 7B).

Sclerophylly, leaf toughness, and fiber content

Thick, scleromorphic leaves are characteristic of the dwarf red mangrove trees at Twin Cays (I. C. Feller, *personal observation*). Such xeromorphic traits may be affected by nutrient availability (Loveless 1961). After 2 yr, significant differences in leaf toughness developed due to the Nutrient treatment for leaves in a penapical position ($F = 15.174$, df = 3, $P \leq 0.001$), and for leaves in a basal position ($F = 39.218$, df = 3, $P \leq 0.001$) on a stem. Leaf toughness on P- and NPK-fertilized trees decreased by 34–38% on penapical leaves and by 45–50% on basal leaves, relative to leaves in

TABLE 3. Growth responses for fertilized dwarf red mangrove trees as affected by Nutrients (NPK, P, N, Control), Tidal Elevation (low, high), and Water Depth (shallow, deep) following 2 yr of treatment. Values are means ± 1 SE. Within a row, means with same superscript letters are not significantly different at $P > 0.05$ using a three-way ANOVA and orthogonal contrast analyses. $N = 12$ trees per Nutrient level; $N = 24$ trees per Tidal Elevation level; $N = 24$ trees per Water Depth level.

	Growth parameters							
	NPK	P	N	Control	NPK	P	N	Control
	Low tidal elevation				High tidal elevation			
No. aerial roots	12.0[a] ± 7.0	11.0[a] ± 5.0	1.0[b] ± 1.0	1.0[b] ± 1.0	9.0[a] ± 2.0	3.0[b] ± 1.0	0.0[b] ± 0.0	1.0[b] ± 0.0
No. leaves	36.9[a] ± 6.2	33.0[a] ± 5.0	7.3[c] ± 1.2	6.4[c] ± 0.7	22.8[b] ± 4.5	18.5[b] ± 2.4	6.6[c] ± 1.5	7.1[c] ± 0.6
Leaf area	803.61[a] ± 105.01	762.95[a] ± 61.64	215.46[c] ± 40.23	195.34[c] ± 29.15	495.81[b] ± 1.84	425.19[b] ± 67.21	221.15[c] ± 55.02	196.66[c] ± 11.47
Shoot length	118.09[a] ± 10.76	129.41[a] ± 22.27	23.68[c] ± 4.24	38.62[bc] ± 13.19	99.80[a] ± 2.39	59.90[b] ± 7.94	32.81[c] ± 7.13	15.76[c] ± 5.40
Leaf biomass	20.00[a] ± 2.55	18.99[a] ± 1.77	6.36[c] ± 1.18	5.57[c] ± 0.83	13.19[b] ± 1.64	10.59[b] ± 1.54	6.59[c] ± 1.60	5.90[c] ± 0.33
Wood biomass	23.79[a] ± 5.11	14.38[b] ± 3.24	5.21[c] ± 1.16	5.08[c] ± 0.58	12.50[b] ± 1.99	6.60[c] ± 0.81	3.48[c] ± 1.19	4.48[c] ± 0.90
	Shallow water depth				Deep water depth			
No. aerial roots	6.0[a] ± 2.0	3.0[a] ± 1.0	0.0[c] ± 0.0	1.0[c] ± 0.0	15.0[b] ± 6.0	11.0[b] ± 5.0	1.0[c] ± 0.0	1.0[c] ± 1.0

the same positions on Control trees (Fig. 8A). Penapical and basal leaves on N-fertilized trees were similar to Control trees. Neither Tidal Elevation nor Water Depth affected penapical or basal leaf toughness (ANOVA, $P > 0.05$).

Sclerophylly, which varies directly with leaf mass per unit area (g/cm^2), was significantly affected by the Nutrient treatment ($F = 9.077$, df $= 3$, $P \le 0.001$; Fig. 8B). Values for leaf mass per unit area of leaves in a penapical position on P- and NPK-fertilized trees were similar, but both were significantly lower than on N-

fertilized and Control trees. Neither Tidal Elevation nor Water Depth affected leaf mass per unit area of leaves (ANOVA, $P > 0.05$).

After 2 yr of treatment, there were no significant differences in the acid detergent (ADF) and neutral detergent fiber (NDF) content of penapical leaves, expressed by leaf biomass (mg/g) or by leaf area (mg/cm^2) among Nutrient treatment levels (ANOVA, $P > 0.05$). In addition, neither Tidal Elevation nor Water Depth affected ADF and NDF content of leaves (ANOVA, $P > 0.05$).

Edaphic characteristics of the study site

Measurements of pore-water salinity at the 48 trees, taken at 15-cm depth, averaged from near seawater (33 g/kg) to slightly hypersaline with very little variation across the site during each sampling time: January 1990, 36.9 ± 0.3 g/kg; July 1990, 38.8 ± 0.3 g/kg; January 1991, 34.9 ± 0.2 g/kg; July 1991, 37.3 ± 0.3 g/kg. Pore-water salinity was slightly but significantly higher during the summers in July than during the winters in January (ANOVA, $F = 125.383$, df $= 1$, $P \le 0.000$). Trees in the low-tidal elevation portions of the site had pore-water salinities that were slightly but significantly higher than trees in the high-tidal elevation portion (ANOVA, $F = 20.506$, df $= 1$, $P \le 0.001$). Except for July 1991 when salinity was uniform across the site, pore-water salinity in the low tidal elevation portion of the site was 1–3 g/kg higher than in the high tidal elevation. Average low-tidal elevation salinity values for winter and summer, respectively, were 36.7 ± 0.3 g/kg and 38.6 ± 0.5 g/kg, compared to 35.1 ± 0.2 g/kg to 37.5 ± 0.3 g/kg for the high tidal elevation. There were no significant differences in pore-water salinity in the rhizosphere of the experimental trees based
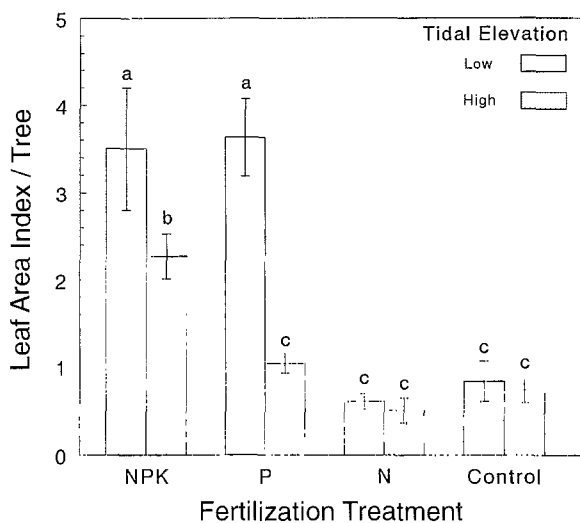

FIG. 6. Leaf area index (LAI; means ± 1 SE) of fertilized dwarf red mangrove trees by Nutrients (NPK, P, N, Control) and Tidal Elevation (low, high) following 2 yr of treatment. Bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrasts within a three-way ANOVA. $N = 6$ trees per Nutrient level × Tidal Elevation level.

TABLE 4. Nutrient concentrations (mg/g) in fresh leaves of fertilized red mangrove trees after 2 yr by Nutrients (NPK, P, N, Control). Values are means ± 1 SE. Within a row, means with the same superscript are not significantly different at $P > 0.05$ using orthogonal contrasts within the three-way ANOVA. $N = 12$ trees per Nutrient level.

	Nutrient-treatment levels			
Nutrient	NPK	P	N	Control
C	422.10[a] ± 3.40	418.20[a] ± 4.50	413.00[a] ± 4.60	411.20[a] ± 3.40
N	12.50[a] ± 0.60	11.30[ab] ± 0.60	11.60[ab] ± 0.70	10.20[b] ± 0.40
Leaf-water content	614.78[a] ± 6.83	612.44[a] ± 12.66	609.34[a] ± 9.77	633.00[a] ± 12.10
P	0.738[a] ± 0.054	0.616[a] ± 0.042	0.346[b] ± 0.019	0.363[b] ± 0.031
K	4.839[a] ± 0.612	5.181[a] ± 0.662	10.050[b] ± 0.846	9.605[b] ± 1.114
Ca	12.543[a] ± 1.115	13.698[a] ± 1.044	15.525[a] ± 1.156	14.717[a] ± 1.316
Mg	4.406[a] ± 0.231	4.767[a] ± 0.446	5.923[a] ± 0.499	5.606[a] ± 0.569
Na	12.694[a] ± 1.681	12.720[a] ± 1.029	13.692[a] ± 1.444	14.000[a] ± 1.849
Fe	0.073[a] ± 0.031	0.039[a] ± 0.006	0.036[a] ± 0.010	0.030[a] ± 0.003
As	0.043[a] ± 0.007	0.045[a] ± 0.007	0.052[a] ± 0.009	0.034[a] ± 0.006
Cu	0.055[a] ± 0.029	0.026[a] ± 0.006	0.015[a] ± 0.002	0.014[a] ± 0.002
Zn	0.023[ab] ± 0.006	0.035[a] ± 0.016	0.012[b] ± 0.002	0.011[b] ± 0.002
Mn	0.004[a] ± 0.001	0.004[a] ± 0.001	0.005[a] ± 0.001	0.005[a] ± 0.001

on Nutrient treatment levels at any time during this study (ANOVA, $P > 0.05$).

To determine if nutrient enrichment affected the oxidation-reduction processes in the soil at the study site, the 12 NPK-fertilized and 12 Control trees, along with four unvegetated patches as Soil Control, were used to compare soil redox potentials (Eh), sulfide concentrations, and pH. Characterization of the soil oxidation status based on this subset of the experiment was done because of time and expense limitations, and because the 24 trees in the NPK and Control treatment levels represented the full range of growth responses in the experiment and were spaced randomly across the entire study site. Comparison of soil Eh values for NPK-fertilized and Control trees at 1 cm and 15 cm indicates that soil was moderately reduced at both depths; however, there were no significant differences between these two treatments at each soil depth (Fig. 9A). For each soil depth, soil at NPK-fertilized and Control trees was significantly less reduced than in nearby unvegetated, Soil-Control areas which were strongly reduced. Sulfide concentrations (mmol/L) in the pore water at 15 cm differed significantly among NPK-fertilized trees, Control trees, and Soil Controls (Fig. 9B). Sulfide concentrations at NPK-fertilized and Control trees were not significantly different, but both were significantly lower than for the unvegetated Soil-Control areas. There were no significant differences in pH among Control and NPK-fertilized trees and Soil Controls

(ANOVA, $P > 0.05$), and there were no significant differences at 1 cm and at 15 cm (ANOVA, $P > 0.05$). Values for pH across the study site were uniformly near neutral (6.6 ± 0.0, $N = 30$).

At the end of year-2, pore water extracted from a 15-cm soil depth beneath each of the 48 trees was analyzed for essential nutrients to determine how the Nutrient treatment affected their concentrations (Table 6). As expected, the most dramatic changes occurred in the concentrations of phosphorus and nitrogen (as NH_4) associated with trees fertilized with those nutrients. Relative to Control trees, soil-phosphorus concentrations at P-fertilized trees increased by 18- to 27-fold and, at NPK-fertilized trees they increased by six- to nine-fold. Phosphorus levels at the N-fertilized and Control trees were very low, ranging in concentration from 0.153 to 0.877 mg/L. There were some slight, but significant, variations in the concentrations of potassium, calcium, and zinc across the study site. Potassium concentration in pore water at NPK-fertilized trees was not significantly different from Control trees but was different from P- and N-fertilized trees. Concentrations of iron, magnesium, and manganese were similar across the study site.

Herbivory: folivore responses

Effects of the Nutrient treatment on herbivory varied by specific herbivore and specific plant tissue. Rates of herbivory on red mangrove leaves, based on leaf

TABLE 5. Concentrations (mg/g) of carbon (C), nitrogen (N), wood-water content, and C:N ratio in shoot wood harvested from fertilized dwarf red mangrove trees after 2 yr by Nutrients (NPK, P, N, Control). Values are means ± 1 SE. Within a row, means with the same superscript letters are not significantly different at $P > 0.05$ using orthogonal contrasts within the three-way ANOVA of log-transformed data. $N = 12$ trees per Nutrient level.

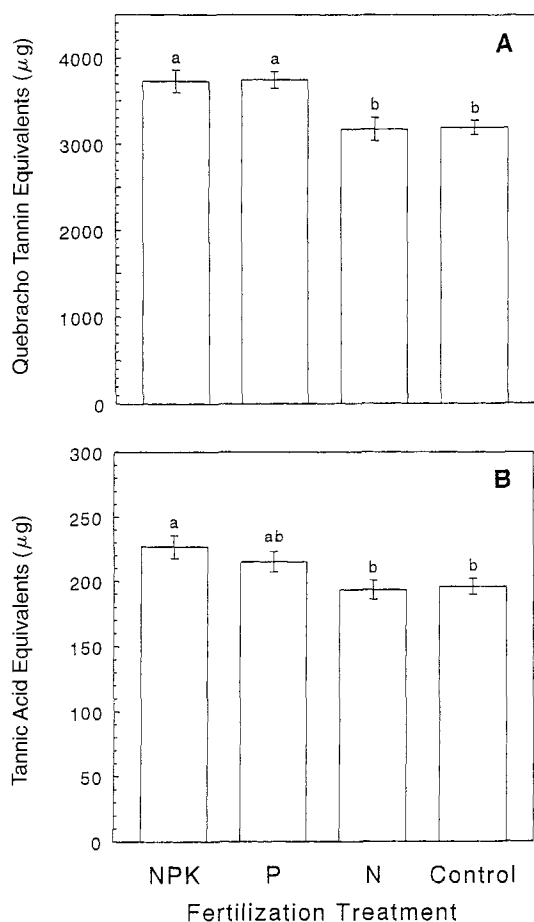|	Nutrient-treatment levels			
Nutrients	NPK	P	N	Control
C	363.08[a] ± 6.20	352.85[a] ± 4.69	352.31[a] ± 5.66	352.55[a] ± 5.64
N	3.56[a] ± 0.53	4.44[a] ± 0.43	4.66[a] ± 0.59	3.59[a] ± 0.31
Wood-water content	534.32[a] ± 11.33	563.37[b] ± 10.45	532.64[a] ± 6.73	528.72[a] ± 8.05
C:N	126.91[a] ± 19.86	87.02[a] ± 8.11	85.67[a] ± 8.21	104.60[a] ± 7.61

FIG. 7. (A) Condensed tannin and (B) total phenolic concentration in penapical leaf tissue in fertilized dwarf red mangrove trees by Nutrients (NPK, P, N, Control) following 2 yr of treatment. Values are means ± 1 SE. Within a graph, bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrast analyses within a three-way ANOVA. $N = 12$ trees per Nutrient level.

Large differences in bud damage caused by *Ecdytolopha* sp. developed among the Nutrient treatment levels following 2 yr of treatment. At the start of this experiment, 2 to 7% of the apical buds on the 48 trees were damaged by *Ecdytolopha* sp., and there was no significant difference among trees receiving the four Nutrient levels ($\chi^2 = 2.572$, df = 3, $P = 0.462$; Table 7). At the end of the experiment, there was a significant difference in the frequency of *Ecdytolopha*-damaged apical buds among Nutrient levels ($\chi^2 = 9.719$, df = 3, $P = 0.020$). On P- and NPK-fertilized trees, 28% and 19%, respectively, of the buds were damaged or missing; whereas, on N-fertilized and Control trees, only 10% and 9% respectively, were damaged or missing. There were no differences in the frequency of *Ecdytolopha* sp. damage by Water Depth or Tidal Ele-
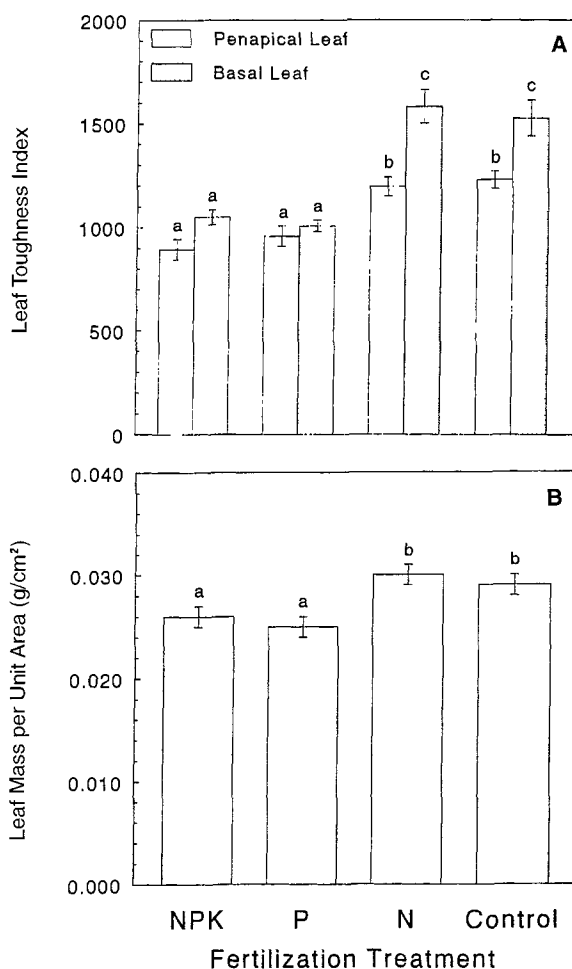

FIG. 8. (A) Leaf toughness index, or the force required to break a 5-mm diameter rod through a leaf, for penapical and basal leaves; and (B) Leaf mass per unit area (g/cm²) of penapical leaves from fertilized dwarf red mangrove trees by Nutrients (NPK, P, N, Control) following 2 yr of treatment. Values are means ± 1 SE. Bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrast analyses within a three-way ANOVA. $N = 12$ trees per Nutrient level.
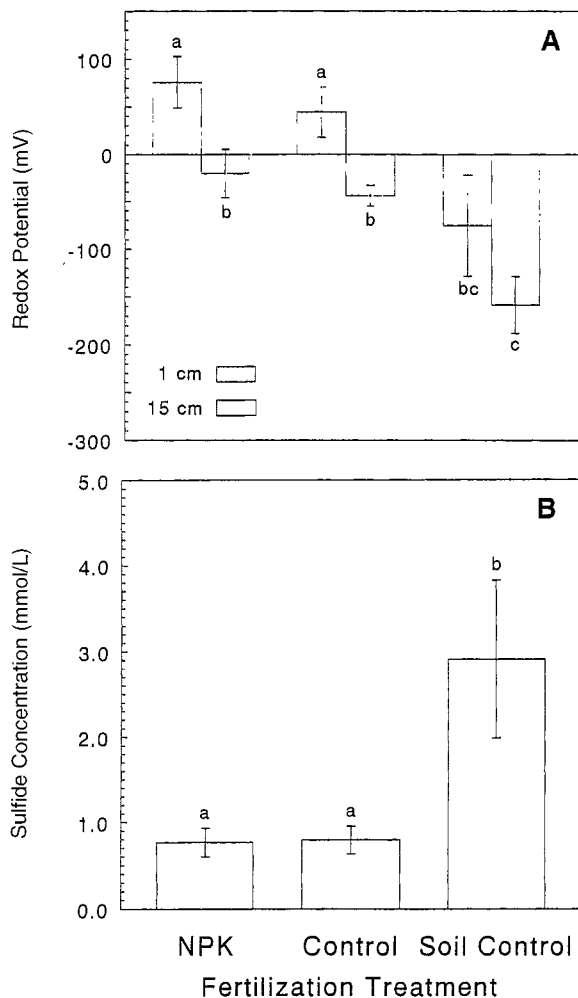
damage accumulated over four 6-mo intervals that began with the apical leaf pair on a shoot, were similar among Nutrient levels (ANOVA, $P > 0.05$). These rates of herbivory were low and variable, and they produced no consistent pattern (Fig. 10A, B). There were no significant rate changes over 2 yr and no indication of seasonal variation in rates of herbivory whether calculated as the percentage of leaf area damaged per 6-mo interval or as total leaf area (cm²) damaged per 6-mo interval. Although rates of herbivory did not vary among Nutrient levels, they differed significantly by Water Depth and Tidal Elevation. During the last 6-mo interval, the rate of herbivory on trees was significantly greater in the deep (6.4 ± 2.2%), rather than shallow (0.9 ± 0.2%), Water Depth ($F = 4.887$, df = 1, $P = 0.007$) and, it was significantly greater in the low (4.5 ± 2.0%), rather than high (2.8 ± 1.2%), Tidal Elevation ($F = 3.295$, df = 1, $P = 0.035$).

FIG. 9. (A) Redox potentials and (B) sulfide concentrations (means ± 1 SE) of the pore water associated with 12 NPK-fertilized trees, 12 Control trees, and 4 Soil Control areas, or unvegetated patches within the study site at Twin Cays. Redox potentials are for 1 cm and 15 cm soil depths; sulfide concentrations are for 15 cm soil depth. Within a graph, bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrast within a three-way ANOVA.

vation ($P > 0.05$). Although its active feeding is limited to apical buds, *Ecdytolopha* sp. can cause several forms of damage including abortion of one or more embryonic leaf pairs prior to their emergence from the apical bud, deformed or misshapened leaves, premature abscission of symmetrically damaged leaves after leaf expansion, or bud death. This damage is also recognizable by several different symptoms which include blackened, embryonic leaves and stipules around the bud, empty leaf nodes above the basal leaf pair, and missing apical buds. If an apical bud is killed, the shoot frequently cannot produce new leaves or subshoots (I. C. Feller, *personal observation*). The higher percentage of damaged or missing apical buds in the NPK- and P-fertilized trees also represents a much higher level of lost leaf-production potential than in the N-fertilized and Control trees.

From July 1989 to July 1991, there was a significant increase in number of aborted leaves among Nutrient levels ($F = 6.418$, df $= 3$, $P < 0.001$; Table 7). P- and NPK-fertilized trees had significantly more aborted leaves than either N-fertilized or Control trees after 2 yr. However, because NPK- and P-fertilized trees had many more leaves than the N-fertilized and Control trees, there was no significant change in the proportion of aborted leaves per shoot among Nutrient levels (ANOVA, $P > 0.05$). Although leaf abortion may be caused by other factors such as wind or birds or by other species of herbivores, my observations at Twin Cays suggest that *Ecdytolopha* sp. is the primary cause of premature abscission.

Herbivory: xylovore responses

In Belize, the periderm of young red mangrove shoots is mined by larvae of *Marmara* sp. nov. A larval mine typically spans a 5 to 10 cm section in the distal portion of a stem. It frequently crosses nodes between the leaf gaps, but does not cause leaf abortion (I. C. Feller, *personal observation*). There were large differences in the frequency of this *Marmara* sp. among the Nutrient levels. It occurred in similar density in 100% of the P- and NPK-fertilized trees (NPK: 0.87 ± 0.24,

TABLE 6. Mean concentrations of nutrients in pore water extracted from a 15-cm depth beneath fertilized red mangrove trees after 2 yr by Nutrients (NPK, P, N, Control). Units for NH_4 values are μmol/L; units of other nutrients are mg/L. Values are means ± 1 SE. Within a row, means with the same superscript are not significantly different at $P > 0.05$ using orthogonal contrasts within the three-way ANOVA. $N = 12$ trees per Nutrient level.

| Pore-water nutrients	Nutrient-treatment levels			
	NPK	P	N	Control
NH_4	7.46[a] ± 2.1980	2.52 ± 1.5680	66.45[c] ± 29.0640	1.09[b] ± 0.3822
P	2.0833[a] ± 1.0319	6.1541[b] ± 2.1421	0.3410[c] ± 0.0636	0.2307[c] ± 0.0180
K	460.6[a] ± 9.3	426.8[bc] ± 10.7	425.3[b] ± 9.9	445.8[ac] ± 5.3
Ca	443.3[a] ± 7.6	425.6[a] ± 8.5	406.2[b] ± 12.2	439.9[a] ± 4.0
Mg	1756.2[a] ± 38.0	1661.2[a] ± 41.8	1610.0[a] ± 51.1	1714.1[a] ± 27.4
Fe	0.2329[a] ± 0.0045	0.2301[a] ± 0.0028	0.2255[a] ± 0.0025	0.2129[a] ± 0.0208
Mn	0.0210[a] ± 0.0022	0.0235[a] ± 0.0028	0.0198[a] ± 0.0019	0.0197[a] ± 0.0019
Zn	0.0908[a] ± 0.0108	0.1681[b] ± 0.0169	0.1270[a] ± 0.0134	0.1120[a] ± 0.0185
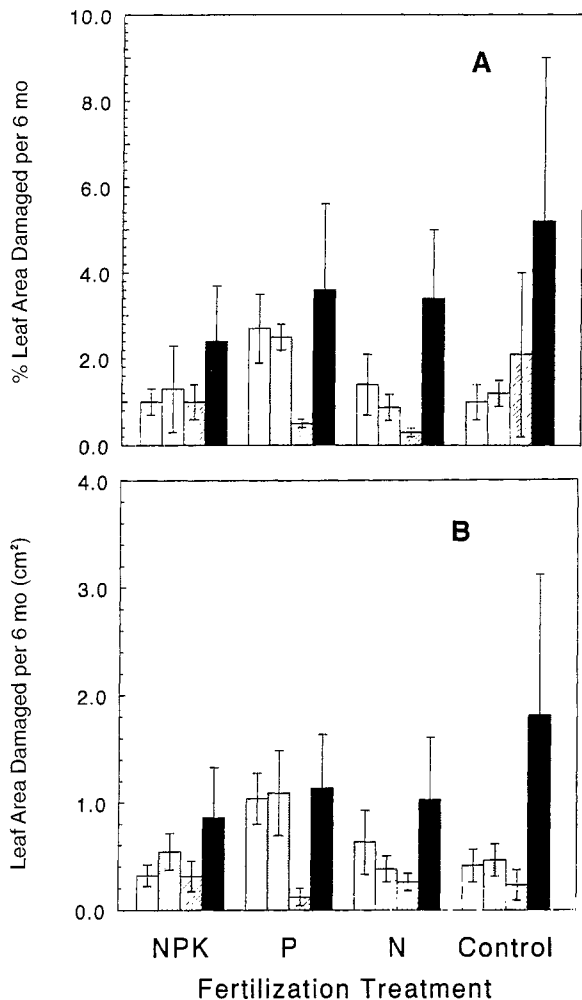
FIG. 10. Rates of herbivory (means ± 1 SE) by leaf-feeders, expressed as (A) percent leaf area damaged per 6 mo and (B) leaf area (cm²) damaged per 6 mo for fertilized dwarf red mangrove trees by Nutrients (NPK, P, N, Control) over 2 yr of treatment. Rates of herbivory are calculated from measurements over four 6-mo intervals between July 1989 and July 1991. Open bar represents July 1989 to Jan 1990; shaded bar, Jan 1990 to July 1990; hatched bar, July 1990 to Jan 1991; solid bar, Jan 1991 to July 1991. Within a graph, bars with the same letter are not significantly different at $P > 0.05$ using orthogonal contrast analyses within a three-way ANOVA. $N = 12$ trees per Nutrient level.

$N = 12$; P: 0.65 ± 0.15, $N = 12$). They did not occur at all in N-fertilized ($N = 12$) and Control trees ($N = 12$). Based on the five shoots originally selected per tree, P- and NPK-fertilized trees had ≈1 *Marmara* sp. larval mine per shoot.

In July 1991, all shoots that died on the 48 trees since July 1989 were harvested to determine if nutrient enrichment affected herbivory by stem-boring insects. Approximately 19% of the harvested dead shoots had been killed by stem-borers; however, there was no significant difference in the number of stem borers among Nutrient, Tidal-Elevation, or Water-Depth levels

(ANOVA, $P > 0.05$). Although unrelated to stem-borer damage, there was a significant Water-Depth effect (ANOVA, $F = 0.921$, df $= 1$, $P < 0.05$) and a significant Nutrient × Water Depth interaction on shoot death (ANOVA, $F = 3.848$, df $= 3$, $P < 0.05$). More dead shoots occurred on trees in deeper, rather than shallower water, and P- and NPK-fertilized trees in deeper water had significantly more dead shoots than similar treatment levels elsewhere in the site.

DISCUSSION

Plant-growth responses to nutrient enrichment

This study was designed to determine if nitrogen or phosphorus limitation was responsible for the dwarf plant form of red mangrove at Twin Cays and to document variation in response of trees along intersecting gradients of tidal elevation and water depth. The consistent growth responses of these dwarf red mangrove trees to P and NPK but not to N fertilization indicate that phosphorus is the major nutrient limiting growth of this species in the peat-based soils under mangrove forests in the interior of Twin Cays (Fig. 2). In a mangrove forest in northern Australia, *Rhizophora* spp. trees in the low intertidal responded to N fertilization while trees in the high intertidal responded to P fertilization (Boto and Wellington 1983). These authors suggested that the lower, tidally-influenced sediment exchange at the higher elevation was the major reason for phosphorus limitation in this area. Biomass and soil nutrient inventories suggest that phosphorus deficiency is the major factor limiting plant growth in wet tropical lowland forests (Vitousek 1984, Medina and Cuevas 1989, Medina et al. 1990). My study provides experimental evidence that is consistent with these observations. In addition to the experimental evidence, concentrations of nitrogen relative to phosphorus in the environment and in plant tissue are indicative of a phosphorus-limited system (Tables 4 and 6). The N:P ratios in leaf tissue of Control and N-fertilized trees in this experiment are >30, suggesting that these plants are phosphorus limited (Van den Driessche 1974, Ingestad 1979, Malmer 1988). After 2 yr of fertilization, mean N:P ratios are <20 in leaf tissue of P- and NPK-fertilized trees, which is near the range at which optimal growth occurs (Van den Driessche 1974, Ingestad 1979, Aerts et al. 1992). Analysis of the pore water from the soil surrounding the root systems of the Control and N-fertilized trees indicate that background phosphorus levels are extremely low. The high N:P ratios in pore water from the Control trees at my study site, as well as from other dwarf red mangrove stands in the interior of Twin Cays, also predict that phosphorus, rather than nitrogen, is limiting in these areas (McKee 1993a). In contrast, low N:P ratios in the low intertidal *Rhizophora* fringe forests around the periphery of Twin Cays suggest that these areas are more likely nitrogen limited

(McKee 1993a). In Australia, Boto and Wellington (1984) also found a similar contrasting pattern for N:P ratios at low and high tidal elevations that suggested nitrogen limitation at low tidal elevation and phosphorus limitation at high tidal elevation. These observations were confirmed by a fertilization experiment (Boto and Wellington 1983). Phosphorus in the peat soils of offshore mangrove islands, such as Twin Cays, is resupplied primarily through decomposition of organic material and by tidal delivery in seawater. Tidal delivery is limited to the Hidden Lake site and other interior ponded areas in Twin Cays because of channel roughness, mangrove-root friction, and channel storage that cause a reduced tidal flow and velocity as water moves up narrow creeks and across broad, shallow ebb-flood channels (Wright et al. 1991). Similar to Boto and Wellington's (1983) conclusion, decreased tidal exchange may contribute to the low availability of phosphorus in these interior areas.

The wide lagoon between Twin Cays and the Belizean mainland buffers this system from the influence of a terrigenous input of phosphorus and other nutrients in coastal runoff. In this high carbonate environment, $CaCO_3$ causes phosphate to precipitate out of the water, further reducing the availability of phosphorus (Binkley and Vitousek 1991, Littler and Littler 1990). In another fertilization experiment at Twin Cays, Littler and Littler (1990) found that phosphorus deficiency also limited the growth of psammophytic macroalgal communities. Phosphorus limitation in other marine systems has been documented experimentally, as well inferentially from N:P ratios (Atkinson and Smith 1983), for hypersaline coastal lagoons (Smith and Atkinson 1984), for eelgrass in a large temperate estuary (Murray et al. 1992), and for tropical seagrasses (Short 1987, Short et al. 1985, 1990, Fourqurean et al. 1992).

There were no significant differences in leaf and wood C:N ratios and wood nitrogen concentrations among the Nutrient levels (Table 5); however, the results for foliar nitrogen concentrations are equivocal. These marginally non-significant results suggest that NPK, P, and N fertilizers may have caused an increase in nitrogen uptake. Although foliar nitrogen may increase following fertilization with both phosphorus and nitrogen, growth responses in the N-fertilized trees were similar to Control trees. This trend supports the conclusion that phosphorus is the most limiting nutrient at Hidden Lake. Because of nitrogen-transformation processes that characterize mangrove and other wetland soils (Patrick and Mikkelsen 1971, Gambrell and Patrick 1978, Boto and Wellington 1984), the ammonium ion, rather than nitrate, is the primary form of mineralized nitrogen available to the red mangrove trees in the permanently-flooded, anaerobic soil that occurs at my study site on Twin Cays (McKee 1993a; R. R. Twilley, *personal communication*). Besides mineralized nitrogen from the decomposition of organic material, nitrogen fixation occurs locally in mangrove and

coral reef systems by cyanobacteria, such as those that grow abundantly in intertidal and supralittoral zones and that live as endobionts in sponges (e.g., Potts and Whitton 1977, Potts 1979, Rützler 1988, 1990). Vitousek (1984) suggested that the abundance of nitrogen-fixing plants in the tropics may be responsible for the high availability of nitrogen relative to phosphorus.

Although the differences were not significant, there was a consistent trend in most of the growth measurements of slightly higher values for trees fertilized with NPK than with P alone. There were slight increases in foliar nitrogen concentrations in the NPK-fertilized trees, suggesting that this effect is due to an improved balance between nitrogen and phosphorus provided by the complete fertilizer but not P alone. However, there were also significant decreases in concentrations of potassium in leaf tissue following both P and NPK fertilization with concomitant increases in potassium nutrient-use efficiency and a doubling of C:K ratios relative to N-fertilized and Control trees. These results suggest that potassium may be the next most limiting nutrient for red mangrove growth at Hidden Lake, and it may be in short supply in mangrove soil when uptake demands increase. Although potassium concentration is usually high in seawater, competitive uptake between sodium and potassium increases with increasing salinity (Ball et al. 1982, Clough et al. 1982). Tilman (1984) points out that when a limiting resource is added to a community, the increased biomass production may lead to increased demands on other resources. Based on fertilization studies of *Larrea tridentata*, Lajtha and Klein (1988) suggest that plants respond to nutrient ratios, and that an increase in the availability of one nutrient decreases the relative availability of other nutrients. Prolonged enrichment with phosphorus that leads to increased photosynthesis and net assimilation rates in red mangrove may cause increased potassium demands and lead to subsequent sensitivity to potassium availability. In old fields in Minnesota, Tilman (1984) found that although nitrogen was the most important limiting nutrient, magnesium was the next most limiting nutrient and it became limiting when nitrogen was added. In areas of high deposition of atmospheric nitrogen such as in wet heathlands and sphagnum bogs in northern Europe, a rapid shift from nitrogen limitation to phosphorus limitation has been detected and attributed to atmospheric pollution (Aerts and Berendse 1988, Aerts et al. 1992).

Two years of fertilization of these dwarf trees in a factorial experiment with N and P singly and in combination as a complete fertilizer (NPK) resulted in large differences in primary and secondary growth between trees receiving phosphorus- and nonphosphorus-containing fertilizers (Figs. 3 and 4). In addition, increased frequency of flowering and propagule formation caused by P and NPK fertilizers compared to unfertilized controls and N fertilizer is evidence that phosphorus is

limiting in this system. Over the 2 yr of this study, the physiognomy of the trees fertilized with P and NPK changed from small bonsai-like plants to vigorously growing saplings; however, the stature of N-fertilized and Control trees changed little in 2 yr. Both P and NPK fertilizers, but not N, caused large increases in productivity measured as leaf number, leaf area, and leafy biomass as well as leaf area index. Similarly, wood production, measured as shoot length, number of subshoots, and woody biomass, increased in response to P and NPK, but not N fertilizer. Monthly growth increases, nondestructively measured as demographic growth rates of module performances, were always higher on P- or NPK-fertilized trees than on N-fertilized or Control trees.

Because mangroves can inhabit nutrient-poor sites and grow very slowly in these areas, they have been regarded as low-nutrient-adapted plants (Huffaker et al. 1984). In support of this observation, triangular ordination analysis by Hutchings and Saenger (1987) indicates that mangroves generally show Grime's (1977) stress-tolerant strategy. Dwarf red mangrove trees at Hidden Lake had a large and rapid growth response to increased supplies of phosphorus in P and NPK fertilizers. Although the vertical growth of the canopies of P- and NPK-fertilized trees was a modest ≈0.5 m in 2 yr, linear growth by branch reiteration of new subshoots was extensive. The mean linear increase per shoot, including length of the original shoot and its subshoots, after 1 yr of fertilization was 0.47 m and 0.45 m and after 2 yr was 1.00 m and 1.09 m for P- and NPK-fertilized trees, respectively. Based on the number of shoots per tree in July 1989 (P: 23.8 ± 6.3; NPK: 28.3 ± 9.2) and the mean increases in shoot and subshoot length over the 2 yr study period, estimates for whole-tree linear increases after year-1 range from 10.8 m to 12.6 m and after year-2 range from 23.0 m to 30.5 m for P- and NPK-fertilized trees, respectively. Given this large and rapid response to increase nutrient availability, which is inconsistent with the stress-tolerant strategy (Grime 1977), it seems unreasonable to categorize red mangrove exclusively as a low-nutrient adapted plant.

The stature of the dwarf trees in quadrant II (lower tidal elevation × deep water depth) of the Hidden Lake site was greater than in other parts of the site (Fig. 5). Furthermore, most plant-growth responses to P and NPK fertilizers in the lower tidal elevation were generally more vigorous than in the higher tidal elevation. These differences are probably due to higher tidal import of nutrients to the lower elevation half of the site. Although the differences in tidal elevation and water depth vary by <0.25 m across my study site, trees in the lower, rather than the higher, portion of the site receive more tidal flushing.

At the end of year-1, redox potentials and sulfide levels were similar at the NPK-fertilized and Control trees (Fig. 9). Except for the unvegetated Soil Controls which had significantly lower redox potentials and higher sulfide concentrations than either the NPK-fertilized or Control trees, there were no significant differences across the experimental site regardless of tidal elevation or water depth. These edaphic factors are important determinants in zonation and structural development in mangrove and other wetland systems (Boto and Wellington 1984, Howes et al. 1986, McKee et al. 1988, Mendelssohn and McKee 1988, Burdick et al. 1989, McKee 1993a); however, they cannot explain the differences in growth within my study site at Hidden Lake. According to previous studies, nutrient availability and uptake may be mediated by edaphic factors related to sediment oxidation status, such as redox potential and sulfide concentration, and that these factors are influenced, in turn, by plant production (Boto and Wellington 1984, Howes et al. 1986, McKee 1993b). Lack of change in the oxidation status of the NPK-fertilized trees in my experiment may be explained by the timing of primary and secondary growth relative to sampling times. At the end of year-1, when redox potentials and sulfide concentrations were measured, growth response in the fertilized trees was primarily due to increased leaf number and leaf area. Woody growth including shoot elongation, new subshoots, and aerial roots during year-2 was much greater than during year-1. If belowground woody growth responded similarly, measurements may have been made before the plants could respond sufficiently to fertilizer treatments to affect the soil oxidation status. Increased root biomass during year-2 may have subsequently led to a more oxidized rhizosphere along with higher redox potentials and lower sulfide levels.

Lugo (1989) proposed that, within a given latitude, factors affecting mangrove productivity are determined by the combined influences of hydrologic energy, tidal exchange, salinity, and soil fertility. In south Florida, the dwarf growth form of red mangrove has also been attributed to low influx of nutrients from outside the system via tidal exchange (Lugo and Snedaker 1974, Pool et al. 1977, Odum et al. 1982). Decreasing tree height in mangrove forests has also been correlated with increasing soil salinity in Florida, the Caribbean, and Australia (Cintrón et al. 1978, Lugo et al. 1981, Boto and Wellington 1984). In temperate salt marshes, analogous growth forms are caused by edaphic factors such as high salinity, low redox potentials, and high sulfide levels in anaerobic, waterlogged soils where tidal flushing is impeded by a streamside berm (Morris 1984, Mendelssohn and McKee 1988, Burdick et al. 1989, Bradley and Morris 1990, 1991, 1992). Under these conditions, nitrogen uptake is inhibited and nitrogen limitation is secondarily induced (Mendelssohn 1979, Bradley and Morris 1990, 1991, 1992, Koch et al. 1990). However, at Hidden Lake, pore-water salinity is usually slightly higher at low tidal elevation than at high tidal elevation, while most plant growth responses were greater in the low tidal elevation portion of the

study area. Boto and Wellington (1983) reported an increased growth response by *Rhizophora* spp. to nitrogen enrichment in a salinity environment similar to conditions at Hidden Lake. In adjacent tropical marine ecosystems, nitrogen is usually considered the primary limiting nutrient (Ryther and Dunstan 1971, Howarth 1988); however, recent studies have shown that phosphorus is the growth-limiting nutrient in some carbonate-rich tropical marine macroalgal communities (Lapointe 1985, 1987, Littler et al. 1988, Littler and Littler 1990, Lapointe et al. 1992) and in hypersaline coastal lagoons (Smith and Atkinson 1984).

Plant structural responses to nutrient enrichment

Although there was little spatial or temporal variation in pore-water salinity, the degree of sclerophylly exhibited by dwarf red mangrove trees at Hidden Lake decreased substantially in response to fertilization in P- and NPK-fertilized trees (Fig. 8). Decreased leaf mass per unit area in response to P and NPK fertilization indicate that leaves on these trees are less sclerophyllous than leaves on N-fertilized or Control trees. In addition, P and NPK fertilizers caused leaves to become ≈30% less tough than leaves from N-fertilized and Control trees. These differences in leaf toughness are not explained by either estimate of leaf fiber content (ADF, NDF). These data, along with the growth responses and changes in nutrient balance in trees supplied with P and NPK fertilizers, demonstrate that sclerophylly in the dwarf red mangrove trees at Hidden Lake is likely related to phosphorus deficiency. Although these results are consistent with findings in other ecosystems (Loveless 1961, Beadle 1967, Small 1972, Specht and Moll 1983, Vitousek et al. 1988, Medina et al. 1990), they deviate from current hypotheses regarding sclerophylly in mangroves (Saenger 1982, Hutchings and Saenger 1987, Lugo et al. 1989). Nutrient deficiency rather than salinity and physiological drought appears to be the proximate cause of well-developed scleromorphic leaves of dwarf red mangrove at Hidden Lake.

Studies that have contrasted xeric species with species from nutrient-poor habitats suggest that the anatomical and physiological attributes associated with xeromorphy may have arisen via convergent or parallel evolution in response to a complex of environmental stresses (Givnish 1978, 1979, Connor and Doley 1981, Lamont and Kelly 1988, Stock 1988, Witkowski and Lamont 1991). Mangrove ecosystems are affected by multiple stresses acting simultaneously and perhaps interactively to determine the forest structure. Not only is there spatial variability of soil factors such as nutrient availability, salinity, and soil oxidation status, these factors have variable impact on the fertility of mangrove soil depending on demands and tolerances of individual mangrove species (McKee 1993b). The increased growth and decreased sclerophylly exhibited

by the dwarf red mangrove trees growing on peat at Hidden Lake in response to fertilization demonstrate that this species is phenotypically plastic rather than restricted in its growth potential like plant species adapted to low-resource availability (Grime 1977, Chapin et al. 1986).

My fertilization study demonstrates that phosphorus limitation is the proximate cause of reduced stature, slow growth, and high degree of sclerophylly of dwarf red mangrove trees at Hidden Lake. However, naturally occurring phosphorus and nitrogen availability in this mangrove system may be altered by high calcium carbonate concentration, hypersalinity, and edaphic factors related to anaerobic conditions in water-logged soils, such as low redox potentials and high sulfide content, that interfere with nutrient uptake (Clough et al. 1982, Ball et al. 1982, Morris 1984, Howes et al. 1986, Mendelssohn and McKee 1988, Burdick et al. 1989, Lugo et al. 1989, Bradley and Morris 1990, 1991, 1992).

Herbivore responses to nutrient enrichment

Rates of folivory, calculated as percent leaf area removed per 6-mo interval, show that fertilization of dwarf red mangrove trees with NPK, P, and N had little effect on consumption rates by herbivores that eat expanded leaves (Fig. 10). This leaf-feeding guild is composed primarily of moth larvae, including *Megalopyge dyeri* Hopp (Megalopygidae), *Marmara* sp. (Gracilariidae), *Automeris* sp. (Saturniidae), *Oiketicus kirbii* Guilding (Psychidae), the mangrove tree crab, *Aratus pisonii* (Sesarminae), and a large cricket (Orthoptera: Gryllidae), each of which has a distinctive feeding pattern. Except for the leaf-mining *Marmara* sp. which feeds only on red mangrove, these herbivores are generalists and have been observed feeding on all the local mangrove species (I. C. Feller, *personal observation*). In addition, several undetermined species of insect herbivores with various types of feeding patterns contributed to leaf damage on the experimental trees; consequently, rates of herbivory on expanded leaves are based on cumulative damage of all types to a leaf surface, including holes, mines, scrapes, and necrotic areas, rather than percent damage by each species of folivore. During this study, average rates of leaf folivory at Hidden Lake ranged from 1 to 4% leaf area damaged per 6-mo interval, and were not significantly different among Nutrient treatment levels. These rates are similar to the range of values for mature leaf-feeders reported for red mangrove in high and low nutrient sites in Florida by Onuf et al. (1977). Studies which surveyed static damage levels to mature *Rhizophora* spp. leaves rather than rates of damage are somewhat more variable, i.e., Papua New Guinea (3.5–8.6%; Johnstone 1981), Brazil (5.5–6.2%, de Lacerda et al. 1986), North Queensland, Australia (2.6–7.6%, Robertson and Duke 1987), and Belize (4.3–25.3%, Farns-

TABLE 7. Damage by *Ecdytolopha* sp. to dwarf red mangrove trees initial and after 2 yr of experimental manipulation by Nutrients (NPK, P, N, Control). Damage is estimated by the proportion of shoots with damaged or missing apical buds, the number of aborted leaves per shoot, and the proportion of aborted leaves per shoot. Values are means ± 1 SE, based on five shoots per tree. Within a column, means with the same superscript are not significantly different at $P > 0.05$ using a three-way ANOVA. Because of a high incidence of zeros, proportions of shoots with damaged or missing apical buds were analyzed using a Fisher's Exact Probability Test. $N = 12$ trees per Nutrient level.

Nutrient-treatment level	Proportion of shoots with damaged or missing apical buds		Number of aborted leaves per shoot		Proportion of aborted leaves per shoot	
	July 1989	July 1991	July 1989	July 1991	July 1989	July 1991
NPK	0.03[a] ± 0.00	0.28[a] ± 0.06	0.67[a] ± 0.11	3.02[a] ± 0.37	0.09[a] ± 0.02	0.09[a] ± 0.01
P	0.07[a] ± 0.01	0.19[a] ± 0.05	0.88[a] ± 0.12	2.86[a] ± 0.46	0.12[a] ± 0.02	0.11[a] ± 0.02
N	0.07[a] ± 0.01	0.10[b] ± 0.04	0.68[a] ± 0.11	1.08[b] ± 0.15	0.11[a] ± 0.02	0.16[a] ± 0.03
Control	0.02[a] ± 0.00	0.09[b] ± 0.04	0.77[a] ± 0.13	0.87[b] ± 0.11	0.10[a] ± 0.02	0.12[a] ± 0.01

worth and Ellison 1991). Rates of folivory from my study are for intervals that began when young leaves were in the apicalmost stem position; consequently, older leaves may accumulate additional damage that approximates levels reported in these other studies. Based on an average leaf longevity of 18 mo for red mangrove leaves at Twin Cays (R. R. Twilley, *unpublished data*), damage to older leaves on the trees at Hidden Lake may increase by two- to three-fold. Although some plant species suffer higher herbivory on their young leaves (e.g., Coley 1983), Farnsworth and Ellison (1991) report a significant increase in herbivory as red-mangrove leaves age. *Megalopyge dyeri*, one of the major herbivores at Twin Cays, belongs to a family of moths whose larvae preferentially feed on older leaves (M. Epstein, *personal communication*). Consequently, rates of herbivory may increase on older leaves on the red mangrove trees at Hidden Lake.

Although fertilization failed to have a significant effect on rates of leaf damage at the Hidden Lake site, water depth and tidal elevation did affect these rates during the last 6-mo interval of this study. Higher rates of folivory on trees in the deeper water side (6.4%) than in shallower water side (0.9%) and on trees at the lower tidal elevation (4.5%) than at higher tidal elevation (2.8%) are not explained by any of the leaf characteristics measured in this study. In contrast, Farnsworth and Ellison (1991) report significantly higher levels of herbivory at highest high water (higher tidal elevation) rather than at lowest low water (lower tidal elevation) at other sites on Twin Cays. In my study, the higher rates of folivory in deep, rather than shallow water and low, rather than high, tidal elevation may be attributable to the presence of the mangrove tree crab, *A. pisonii*. In July 1991, ≈10% of the leaves measured in the deeper, lower tidal-elevation quadrant of the study site had crab damage, but none of the leaves measured from any of the other quadrants had crab damage. Because trees in the deeper, lower tidal-elevation quadrant (Quadrant II) are significantly larger with a higher density of shoots than in other parts of the site, they may be preferred by *A. pisonii* (Warner 1967, Beever et al. 1979). Also, a stand of red mangrove fringe adjoins this quadrant so that crabs could

have reinvaded it more readily after the initial removal than they reinvaded other parts of the site that merged instead into red- and black-mangrove thickets. At Twin Cays, *A. pisonii* is seen frequently in the red mangrove fringe but not in the sparsely branched dwarf trees at Hidden Lake and in other similar stands (I. C. Feller, *personal observation*). These results and interpretations are consistent with Beever et al. (1979), who found increased population densities of *A. pisonii* in dense foliage associated with fringing red mangrove.

Although folivory of expanded leaves showed no response to NPK and P treatment levels, *Ecdytolopha* sp., a specialized, endophytic lepidopteran herbivore on apical buds of red mangrove did respond (Table 7). The proportion of damaged, or missing, apical buds caused by *Ecdytolopha* sp. increased by two- to three-fold, compared to Control trees, following 2 yr of treatment with P and NPK fertilizers. Damage by *Ecdytolopha* sp. occurred in 19% and 28%, and completely killed 9% and 12%, of the apical buds produced on P- and NPK-fertilized trees, respectively. Only 2% of the apical buds on both N-fertilized and Control trees were completely killed by *Ecdytolopha* sp. Because of dominance in the apical meristem and lack of viability of axillary meristems in red mangrove (Gill and Tomlinson 1969), destruction of an apical bud frequently prevented continued growth and leaf production by its shoot. After the standing crop of leaves had senesced, destruction of the apical bud lead to death of the shoot. Loss of yield or stature is an important measure of the effects of herbivory (Southwood 1978, Krischik and Denno 1983, Louda 1984), yet collateral components of herbivory such as the removal of growth and leaf-production potential are rarely included in studies of herbivory in mangrove systems (but see Onuf et al. 1977, Robertson and Duke 1987). The results of *Ecdytolopha* sp. damage to the fertilized trees at Hidden Lake are similar to those by Onuf et al. (1977), who reported significantly higher levels of lost leaf-production potential from red mangrove on a naturally fertilized, high-nutrient red-mangrove island (21.1%) compared with a low-nutrient island (7.8%).

Onuf et al. (1977) found a significantly greater number of aborted leaves due to the activities of *Ecdyto-*

TABLE 8. Effect of Nutrients (NPK, P, N, Control) on density of stem miners (*Marmara* sp. nov.) and stem borers in dwarf red mangrove trees following 2 yr of treatment. Values are means ± 1 SE. Counts of *Marmara* sp. are based on five shoots per tree. Counts of stem borers are based on total number per tree. Within a column, means with the same superscript letter are not significantly different at $P > 0.05$ using a Fisher's Exact Probability Test. $N = 12$ trees per Nutrient level.

Nutrient-treatment level	*Marmara* sp.	Stem borers
NPK	4.58 ± 1.21[a]	0.33 ± 0.14[a]
P	3.25 ± 0.75[a]	1.25 ± 1.03[a]
N	0[b]	0.33 ± 0.37[a]
Control	0[b]	0.33 ± 0.20[a]

lopha sp. At Hidden Lake, there was a significant increase in the frequency of aborted leaves attributed to *Ecdytolopha* sp. on P- and NPK-fertilized trees, but, because of their increased number of leaves, the proportion of leaves lost out of their total potential leaf production was not different after 2 yr of treatment and was not different from Control and N-fertilized trees. Estimates for the proportion of leaves per shoot missing due to leaf abortion show that July 1989 values are very similar to July 1991 values for all Nutrient treatment levels. These results indicate that leaf abortions caused by *Ecdytolopha* sp. increased in proportion to red mangrove's response to P and NPK fertilization, but that fertilization did not result in higher relative amounts of damage to individual trees.

In my study, the amount of red mangrove leaf tissue lost because of bud damage and death in response to feeding by *Ecdytolopha* sp. was three to four times the amount consumed directly by all other folivores. This result is similar to the findings of Onuf et al. (1977).

Increased phosphorus availability to the plants also caused large increases in the frequency of stem-mining *Marmara* sp. nov., another specialized, endophytic herbivore that mines the periderm of young red-mangrove shoots (Table 8). Larvae of this *Marmara* sp. occur at a density of almost one per shoot in trees fertilized with P and NPK, but did not occur at all on any of the Control or N-fertilized trees over the 2 yr of this study. At Twin Cays and other nearby mangrove islands, this miner is relatively common in shoots of fast-growing red mangrove plants such as saplings (I. C. Feller, *personal observation*), but I have not found evidence of its feeding in unfertilized, slow-growing dwarf or fringe trees. The distal portions of shoots of unfertilized dwarf and fringe trees, which may be several years old, have congested internodes and are covered with a hard, nonliving suberized periderm or "bark." Similar portions of shoots of fast-growing plants such as saplings and NPK- and P-fertilized trees are first-year growth, but they have elongated internodes and a thin, living periderm that is commonly mined by this *Marmara* sp. (I. C. Feller, *personal observation*). In addition to direct

damage, leaf miners can cause early leaf abscission and consequent losses of primary productivity (Faeth et al. 1981, Chabot and Hicks 1982, Kahn and Cornell 1983, Pritchard and James 1984, Risley and Crossley 1988, Collinge and Louda 1989, Stiling et al. 1991); however, I did not detect an accelerated rate of leaf fall due to stem-mining by *Marmara* sp. in my study at Hidden Lake. A larval mine typically spans ≈5–10 cm in the distal portion of a young shoot and frequently crosses a node between opposing leaf gaps, but it does not appear to cause leaf abortion (I. C. Feller, *personal observation*). Although primary stem borers can have collateral effects on primary productivity by diverting resources for wound-wood production, pruning shoots, or creating openings in the bark used by pathogens and secondary wood feeders, I have not observed such secondary effects associated with *Marmara* sp. stem mines. Thus, this *Marmara* sp. may have a nearly "commensal" relationship with red mangrove.

These data on herbivory along with simultaneous measures of red mangrove defensive and nutritional characteristics can be used to evaluate predictions of four current hypotheses regarding plant–herbivore interactions. My folivory data do not support the hypothesis that sclerophylly is an adaptive defense against generalist herbivory (Feeny 1970, Janzen 1974, Rausher 1981, Coley 1983, Lowman and Box 1983, Ohmart et al. 1985, Grubb 1986). There were no significant differences in the rates or levels of damage by generalist herbivores on expanded red mangrove leaves despite large decreases in leaf toughness following 2 yr of treatment with phosphorus-containing fertilizers. My results are more consistent with the oligotrophic-xeromorphism hypothesis, that sclerophylly is an adaptation for survival in phosphorus-poor soil (Loveless 1961, Beadle 1967).

My results are partially consistent with the within-species resource availability hypothesis (Bazzaz et al. 1987). This hypothesis states that allocation of resources to carbon-based chemical defenses increases in individual plants with higher relative growth rates. However, my data do not support the prediction of this hypothesis that increased concentrations of these chemical defenses should lead to lower, rather than higher or static, levels of herbivory. Concentration of total phenolics and condensed tannins in red mangrove leaves increased with increased phosphorus availability; but, low rates of folivory by a guild of generalist feeders of expanded leaves remained static while herbivory by two specialists, *Ecdytolopha* sp. and *Marmara* sp., increased dramatically. These results suggest that inherent defensive properties of red mangrove are very effective at keeping generalist folivores in check, but that populations of specialized, endophytic herbivores increase in response to increased nutrient availability and are unaffected or even favored by plant tissue with higher tannin concentrations. Alternatively, the external feeding folivores may be controlled by

other factors, such as predation, that were not measured in this study. Although tannins are important mediators of herbivore impact on many plant species (e.g., Feeny 1970, McKey et al. 1978, Lowman and Box 1983, Coley 1986, Smallwood and Peters 1986, Schultz 1988, Raubenheimer 1992), a number of other studies show that tannins do not affect, or even stimulate, feeding by some herbivores (e.g., Fox and Macauley 1977, Berenbaum 1980, Macauley and Fox 1980, Bernays 1981, Rausher 1981, Bernays and Woodhead 1982, Coley 1983, Cooke et al. 1984, Ohmart et al. 1985, Manuwoto and Scriber 1986, Faeth 1990).

Because there were no significant changes in C:N ratios among Nutrient treatment levels, my data do not directly test the carbon/nutrient balance hypothesis, which predicts higher rates of herbivory due to lower C:N and decreased allocation to carbon-based chemical defenses in response to increased nitrogen availability (Bryant et al. 1983). At Hidden Lake, increased availability of phosphorus to the NPK- and P-fertilized red mangrove trees fertilized for 2 yr not only increased allocation to phenolic compounds, but also increased levels of herbivory by specialists. Onuf et al. (1977) also found much higher levels of herbivory by *Ecdytolopha* sp., a specialist herbivore in apical buds of red mangrove, in the high-nutrient site than the low-nutrient site; however, they found no significant differences in the N concentration in apical buds from these two sites. Although they did not measure herbivory, Denslow et al. (1987) found similar increases in phenolic production as well as growth in tropical shrub species (*Miconia* spp., Melastomataceae and *Piper* spp., Piperaceae) in response to P fertilization. My results for specialist herbivores on red mangrove contrast with studies conducted on generalist vertebrate herbivores in boreal ecosystems. Those studies found that herbivory increased as C:N ratios and concentrations of phenolic compounds in plant tissue decreased in response to higher nutrient availability, as predicted by the carbon/nutrient balance hypothesis (Bryant et al. 1983, 1987, Larsson et al. 1986, Bryant 1987, Reichardt et al. 1991).

Depending on the system, nitrogen concentration in plant tissue is positively correlated with herbivory and herbivore survival (e.g., Feeny 1970, White 1974, 1978, Onuf 1978, Mattson 1980, Auerbach and Strong 1981, Rausher 1981, Myers and Post 1981, Vince et al. 1981, Denno 1983, Landsberg and Wylie 1983, Scriber and Slansky 1984, Denno et al. 1985, 1987, Bryant et al. 1987, Cates et al. 1987, Auerbach and Simberloff 1988, Athey and Connor 1989, Landsberg 1990, Baylis and Pierce 1991, Loader and Damman 1991, Ohmart and Edwards 1991), or, there is no relationship between nitrogen or protein concentration and the performance of herbivores (e.g., Faeth et al. 1981, Johnstone 1981, Lincoln 1985, Myers 1985, Ohmart et al. 1985, de Lacerda et al. 1986, Faeth 1990, Silvanima and Strong 1991). In my study, foliar nitro-

gen concentrations may have increased slightly, but wood nitrogen concentrations and the C:N ratio of red mangrove leaf and stem tissue were not affected by nitrogen (NH_4) or phosphorus fertilization. As a result, nitrogen parameters from this study are not indicative of the nutritive quality of the plant tissue and the level of constitutive carbon-based chemical defenses.

The results presented here contradict the plant-stress hypothesis (White 1974, 1978, 1984, Toumi et al. 1984, Mattson and Haack 1987). This hypothesis predicts increased herbivory on stressed, including nutrient-stressed, plants than on plants relieved from stressed conditions. Ratios of N-to-P in soil and plant tissue along with increased growth in response to NPK and P fertilizers demonstrate that the red mangrove trees at Hidden Lake are growing under nutrient-stressed conditions caused by a limited supply of phosphorus. Soil and tissue measurements also indicate high availability of N relative to P. Lower levels of herbivory by *Ecdytolopha* sp. and *Marmara* sp. on the phosphorus-stressed Control trees than on the P- and NPK-fertilized trees are opposite to the predictions of the plant-stress hypothesis. Results from this experiment suggest that populations of some specialized herbivores increase in response to improved nutritional quality provided by phosphorus fertilization. Herbivory is sometimes higher in low nutritive quality food (Slansky and Feeny 1977, Moran and Hamilton 1980, Price et al. 1980, Weis and Berenbaum 1989). However, higher levels of herbivory here, and in other studies, were associated with enhanced nutritional quality of plants growing in benign rather than nutrient-stressed environments (Onuf et al. 1977, Onuf 1978, Neuvonen and Haukioja 1984, Landsberg 1990, Price 1991).

The overall patterns of herbivory in my fertilization study support the plant-vigor hypothesis which predicts that specialized endophytophagous insect herbivores preferentially attack the more vigorous plants in a population (Price 1991). Populations and greater feeding damage by *Ecdytolopha* sp. and *Marmara* sp., two such specialized endophytic herbivores, were higher on the vigorously growing P- and NPK-fertilized trees.

CONCLUSION

Experimental evidence from this study suggests that phosphorus deficiency is a major proximate cause of the slow growth and low stature of dwarf red mangrove trees growing on the peat-based soil at Hidden Lake in the interior of Twin Cays. Although growth responses to fertilization and N:P ratios in plant tissue and in the soil indicate that these trees are phosphorus limited, this impediment to growth may be secondarily induced, or exacerbated, by physicochemical factors associated with saline, anaerobic water-logged soil, such as high salinity, low redox potentials, and high sulfide concentrations that inhibit uptake in addition to shortages in phosphorus supply rates. Growth increased dramatically in response to the addition of phosphorus

but not nitrogen. Several indices of plant performance demonstrate improved growing conditions for phosphorus-fertilized trees. Phosphorus in the peat-based soils of mangrove islands such as Twin Cays is limited to that supplied through decomposition or tidal import. In this high carbonate environment, $CaCO_3$ causes phosphates to precipitate out of the water, further reducing the availability of phosphorus (Binkley and Vitousek 1991, Littler and Littler 1990). In fringing, riverine, and nearshore mangrove forests, there may be increased supply of phosphorus from tidal import, runoff, and mineralization. In these systems, mangrove growth may be more sensitive to limitations of other nutrients such as nitrogen. Mangroves associated with different types of substrates should be evaluated to determine the effects of nutrient inputs on these systems. Because nutrient limitation is relative to soil type and plant species, similar manipulative experiments involving other mangrove species in other locations are needed to develop a broader understanding of the impact of nutrient input on mangrove forests and adjacent ecosystems.

The level of sclerophylly associated with dwarf red mangrove leaves diminished on trees with increased availability of phosphorus. These results suggest that increasingly tough, hard leaves of red mangrove may be a nutrient-conservation mechanism rather than an adaptation for physiological drought, salt accumulation, osmoregulation, or herbivore defense. Other nutrient-conservation mechanisms, such as leaf longevity, retranslocation of nutrients, and decomposition rates may also be affected by the change in resource availability provided by phosphorus enrichment. The addition of phosphorus caused a rapid and dramatic change in the xeromorphic physiognomy of dwarf red mangrove trees; even after the first year of treatment, phosphorus-fertilized trees resembled vigorously growing saplings.

The ammonium addition in this experiment had no effect on plant growth, wood nitrogen concentration, C:N ratio, leaf water content, fiber content, or rates of herbivory. Two possible explanations exist for this lack of response to increased N: (1) the study site had high availability of N relative to P, and P, rather than N, is limiting in this system; (2) physicochemical properties of these flooded, anaerobic soil, such as low redox potentials and high sulfide concentrations, and slightly hypersaline pore-water, inhibited NH_4 uptake so that this experiment did not succeed in increasing N availability for the plants. The former explanation is more likely because concentrations of NH_4, the primary form of nitrogen available to plants in waterlogged soil, increased dramatically in the NPK- and N-fertilized trees following 2 yr of treatment. Furthermore, slightly higher, although non-significant, concentrations of foliar nitrogen in NPK-, P-, and N-treatment levels suggest increased nitrogen uptake by the fertilized plants. In temperate salt marshes with physicochemical environ-

ments that are similar to those found at Hidden Lake, studies have shown that nitrogen limitation in these systems is the result of altered N uptake kinetics due to low redox potentials, high sulfide concentrations, and salinity (Morris 1984, Bradley and Morris 1990). However, fertilization studies in these nitrogen-limited systems have also demonstrated that additions of N caused increased concentrations of N in plant tissue, as well as increased growth, in the grass *Spartina alterniflora* growing in similar conditions (e.g., Valiela and Teal 1974, Linthurst and Seneca 1981). Additionally, Boto and Wellington (1983) showed increased growth and concentrations of leaf N in *Rhizophora* spp. in northern Australia at sites fertilized with NH_4 that had similar pore-water salinity and more reducing conditions than the Hidden Lake site. Soil and tissue analyses at Hidden Lake indicate high background availability of nitrogen relative to phosphorus in this environment.

Phosphorus-containing fertilizers caused an increase in phenolic compounds that previous studies suggested decreases the nutritive quality of plant tissue. Contrary to this expectation, insect herbivory was greater on plants with the highest concentration of phenolic compounds. Further, my results show that increased phosphorus availability leads to increased performance by specialist endophytic herbivores on red mangrove but had no effect on generalist foliage feeders. Phosphorus concentration and N:P ratios may be better assays of the nutritive quality and palatability of red mangrove tissue than are measures of leaf toughness, fiber content, nitrogen concentration, leaf water content, and condensed tannin and total phenolic concentrations.

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ILKA C. FELLER

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