

FINAL REPORT

**The Significance of Nutrient Redistribution and Regeneration to the
Recovery of Mangrove Ecosystems of South Florida in
Response to Hurricane Andrew**

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PREFACE

The goal of this project was to evaluate the influence of light and nutrient resources relative to soil stressors as control of the patterns of mangrove forest development following hurricane disturbance in the Everglades National Park. The project supported dissertations Margueritte Koch at University of Miami (Chapters ONE and TWO) and Ronghua Chen of University of Southwestern Louisiana (Chapters THREE - SIX). Other products of this research project include manuscripts accepted or in submission to professional journals, and presentations at professional meetings and regional workshops. An additional product of this project is a M.S. thesis anticipated from Laura Lawton in December 1996, which was delayed due to an illness to Ms. Lawton requiring a one-year medical leave from university studies. The following are various products that were supported partially from this research project:

DISSERTATIONS

Koch, M. S. 1996. Resource availability and abiotic stress effects on *Rhizophora mangle* L. (ree mangrove) development in south Florida. Ph.D. Dissertation, University of Miami, Coral Gables, Florida. 134 p.

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ABSTRACTS AND PRESENTATIONS

Twilley, R.R., R. Chen, L. Lawton, V. Rivera-Monroy, J. Foret, S. Pelegri. 1995. Biogeochemistry of mangroves along the Shark River Slough, Florida. Estuarine Research Federation Biennial Meeting, Corpus Christi, November. p. 137.

Chen, R.H. and R.R. Twilley. 1995. The individual-based model for simulation of the development of mangrove forest. Bulletin of Ecological Society of America 76:45.

Twilley, R. R. The response of mangrove forest development along environmental gradients in the Shark River estuary. Florida Bay Workshop, July 1996.

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The research described in Chapters ONE and TWO in the southeast Everglades sites was supported by a Cooperative Agreement (CR-820667, Dr. S. Snedaker) with the US Environmental Protection Agency and UM. Partial funding for the modelling in Chapters FIVE and SIX was part of a Subcontract to USL from UM for an USEPA supported project on modelling the response of mangroves to global climate change (R.Twilley, PI of subcontract).

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EXECUTIVE SUMMARY

The disturbance caused by Hurricane Andrew caused major shifts in light and nutrient resource availability to mangrove communities. Leaf fall associated with wind induced gaps resulted in a significant pulse of light, organic matter and associated nutrients to the forest floor. Winds and associated tidal surge also caused resuspension and redistribution of sediments that altered nutrient resources along the path of the hurricane. These changes in nutrient pools and potential shifts in availability of light and nutrient resources are important to patterns and rates of forest regrowth. In addition, these forcings during hurricanes can also influence the distribution of stressors such as salinity and soil sulfide levels. The distribution of these stressors may confound the ability to predict patterns of mangrove regeneration based on the redistribution of nutrient resources due to the hurricane disturbance. Thus the focus on nutrient redistribution and utilization must take into account the interaction of nutrient resources and stressors on the development of mangrove forests. **The goal of this research program was to describe the impacts of Hurricane Andrew on the redistribution and regeneration of light and nutrient resources in mangrove wetlands, and how these ecological processes compare to patterns of nutrient resources and stressors in mangroves along the Shark River in Everglades National Park (ENP).**

Hurricane Andrew provided a large scale physical disturbance of mangrove forests that offers an excellent opportunity to study the relative influence of nutrient redistribution and regeneration on the successional patterns of mangrove ecosystem development. The resource-ratio hypothesis of Tilman (1988) suggests that community structure can be predicted based on the inequality of resource utilization by plants along environmental gradients. Yet in the presence of stressors, the role of resource utilization may be limited in determining community development. Hurricanes are natural experiments to test the ecological factors that influence the trajectories of community development. The path of Hurricane Andrew in nearly east to west direction across south Florida represents a transect through distinct geomorphological regions of south Florida. This allowed us to compare the response of an ecosystem, such as mangroves, to similar levels of disturbance in different environmental settings. Thus the relative influence on nutrient resources and stressors on growth and development of mangroves may be distilled from regional comparisons.

Nutrient, light, salinity, soil redox potentials, and other soil characteristics were determined across a range of mangrove forest heights across the South Florida peninsula encompassing large-stature trees (>10 m) on the west coast and dwarf forms (<1 m) in the southeast Everglades. Relationships were established between abiotic factors and *Rhizophora mangle* seedling growth rates in four height (cm) classes, 25-40, >40-55, >55-70, and >70-85. Light in open canopy gaps was an important determinant of seedling growth. Growth rates in gaps (0.32 ± 0.04 to 1.89 ± 0.18 mm d⁻¹) were two- to five-fold greater than adjacent closed canopy forests (0.14 ± 0.01 to 0.40 ± 0.07 mm d⁻¹). Among open canopy sites, labile soil phosphorus and soil redox potentials were significantly correlated to growth ($P < 0.05$; $r = 0.98$ and 0.89 , respectively). Interstitial salinity ranged from 0 to 27 ppt across sites, well below hypersaline conditions. Thus, under low salinity stress and high light availability, soil fertility is proposed to be the dominant factor controlling *R. mangle* seedling development to a sapling stage (>85 cm) in South Florida mangrove forests. In addition, soil anoxia is hypothesized to be an important stressor in lagoonal-bay estuaries and marsh-mangrove ecotones with minimal tidal exchange.

Patterns of biomass allocation and C-fixation rates in *Rhizophora mangle* seedlings were investigated in the Florida Everglades at sites with variable light and soil nutrients. Soil nutrient levels and light availability significantly influenced light-saturated C-fixation rates. Photosynthetic rates at light saturation decreased from 7.8 to 5.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with decreasing soil P. Low light under the canopy suppressed average daily photosynthetic rates 64% relative to an adjacent gap. Biomass allocation to photosynthetic tissue was also dependent on high light and soil

nutrients. Photosynthetic tissue comprised approximately 50% of the total above-ground biomass in open canopied, high nutrient sites, whereas under low soil P, only 12-13% of the total biomass was allocated to leaf tissues. A general trend was found across size classes in open and closed canopied sites: biomass partitioning to leaves increased with size class in the gap, while under the canopy, leaf biomass increased initially, but subsequently decreased with increasing size. The inability of *Rhizophora mangle* to allocate increasing biomass to photosynthetic tissues to compensate for low C-fixation rates under closed canopies, identifies this species as shade intolerant. Whole plant C-fixation rates were strongly correlated to seedling growth rates in southwest Everglades sites. These results indicate the importance of both C-production and foliar biomass partitioning for early mangrove development. However, further study is needed to reconcile limited growth in response to C-production in dwarf mangrove forests in the southeast Everglades.

The spatial gradients of soil nitrogen (N) and phosphorus (P) mineralization rates, extractable N and P pools, and P fractionation were examined in a mangrove land-margin ecosystem along the Shark River estuary in the Everglades National Park. The mean tree height of mangrove forests linearly declined with distance from the mouth near the Gulf of Mexico to the oligohaline regions of the estuary. Mangrove forests along the estuary represented a landscape gradient of soil N and P availabilities. Higher amounts of extractable ammonium were found in the marine site of the estuary near the Gulf of Mexico. Mean rates of net ammonification and relative ammonification per unit of total N based on 45 d incubation periods decreased exponentially with distance from the estuary mouth to inland sites. N mineralization was positively correlated with total P and available P, but negatively with N:P ratio. Total P and available P increased from the oligohaline to marine sites. There was no net P mineralization in the marine sites based on 45 d incubation periods. Residual P was the largest P fraction in all soils and decreased from 70% in the oligohaline site to 45% in the marine site along the estuary. The percentage of Ca-bound-P increased from 3.3% at the oligohaline site to 32.3% at marine sites. Ca-bound-P pool was larger than Fe-Al-bound P pool in the marine sites, while the reverse was found in the mesohaline and oligohaline sites. The landscape gradient of P in the study area indicates that the Gulf of Mexico is the major source of P in this mangrove land-margin ecosystem rather than direct terrigenous input from inland watershed.

Mangrove forest structure, growth, soil nutrient resources and pore water stressors were examined along the longitudinal gradient of the Shark River estuary in the Everglades National Park. Patterns of forest structure were based on 34 yrs of growth since Hurricane Donna destroyed most of the mangrove resources in this region in 1960. Forest basal area increased from lower values at the upstream and intermediate locations of the estuary (19.61 and 20.72 m²/ha, respectively) to nearly double these values at two downstream locations (40.36 and 39.67 m²/ha) near the mouth of the estuary. Tree density with dbh >10 cm was 1900/ha in the downstream location, which indicated a more mature stand than in the upstream location where only 334 trees/ha were >10 cm dbh. *Laguncularia racemosa* had a higher importance value in the downstream location, whereas *Rhizophora mangle* dominated in the intermediate and upstream locations. Biomass increments were higher at the downstream sites (10.73 and 11.96 Mg·ha⁻¹·yr⁻¹) than at the lower stature forest in the upstream and intermediate sites (3.23 and 4.20 Mg·ha⁻¹·yr⁻¹). Pore water salinities in mangrove soil were < 35 g/kg at all three sampling seasons and sulfide concentrations were generally < 0.15 mmol/L. There was no spatial trend of total C and N contents per unit soil volume, nor in C:N ratios among the sites. However, total P, extractable P and extractable ammonium contents increased from the upstream sites to the sites at the mouth of the estuary. Soil properties in the downstream marine region of the Shark River estuary include high levels of nutrient resources and low concentrations of toxic stressors supporting a region of optimum growth of mangroves. A regression of mangrove basal area on concentrations of soil total P per unit volume suggest that the landscape gradient of mangrove forest development is

associated with soil P resources along this subtropical estuary.

The vertical distributions of organic matter, nitrogen and phosphorus in mangrove soils were investigated with a mechanistic and process-based model. The nutrient mangrove model (NUMAN) was developed from the SEMIDEC and CENTURY soil organic matter models and parameterized with data from four mangrove sites along the Shark River estuary. The soil characteristics in the four mangrove sites varied greatly in both concentrations and profiles of soil C, N and P. Organic matter, expressed as percentage of ash free dry weight, decreased from 82% in the upstream locations to 30% in the marine sites. Comparisons of the simulated and observed results demonstrated that the landscape gradient of soil characteristics can be adequately modeled by accounting for plant production, litter decomposition and export, and allochthonous input of inorganic materials. The results illustrated that the increase in organic matter content and decrease in soil bulk density from mangrove sites at the mouth of the estuary to those at upstream locations was controlled mainly by variation in allochthonous inputs of inorganic material and mangrove root production. Model simulations showed that the greatest change in organic matter, N, and P occurred in the soil surface, but changes were also evident at depths ranging from 1 cm to 5 cm at some of the sites. The rapid decomposition of labile organic matter was responsible for this decrease in organic matter. Simulated mineralization rates of nitrogen decreased quickly with depth, which corresponded with the decrease of labile organic matter. Fitting the simulation results of the model to observed nutrient profiles indicated that N and P dynamics are tightly linked to organic matter retention. In the future, NUMAN will be modified and linked to a mangrove forest gap model to simulate the feedback mechanisms of soil nutrient recycling, which controls development of the mangrove wetlands.

A computer model (MANGAL) derived from an individual-based gap model (FORMAN) and a soil organic matter model (NUMAN) was developed to investigate mangrove forest dynamics in relation to soil characteristics. Simulated forest structure was compared to that of three mangrove forests along the Shark River estuary, Florida, with a known disturbance history. Simulations of total and species-specific basal area of each mangrove site fit well with data from field surveys of the forests. Low nutrient availability in the intermediate site of the estuary limited the forest development. The measured size-class distribution of *Rhizophora mangle* showed higher frequencies for the smaller size classes, however, that of *Laguncularia racemosa* was bell-shaped. The model accurately tracked this pattern for each species. Mangrove succession was projected using the present stand condition of the downstream marine site in the estuary. Without disturbance, dominance of *L. racemosa* was eventually replaced by *R. mangle* or *Avicennia germinans*, depending on the recruitment rate of *A. germinans*. Simulated basal area of the three mangrove species along gradients of soil nutrient resource and salinity illustrated a change in competitive balance among the three species over time. *L. racemosa* dominated in fertile soils with low stress at early stages of recovery, but its abundance decreased while *A. germinans* increased in this region. The dominance of *R. mangle* was limited to regions with low nutrient availability and low salinity.

CHAPTER 1

RHIZOPHORA MANGLE L. SEEDLING DEVELOPMENT INTO THE SAPLING STAGE ACROSS RESOURCE AND STRESS GRADIENTS IN SUBTROPICAL FLORIDA

ABSTRACT

Nutrient, light, salinity, soil redox potentials, and other soil characteristics were determined across a range of mangrove forest heights across the South Florida peninsula encompassing large-stature trees (>10 m) on the west coast and dwarf forms (<1 m) in the southeast Everglades. Relationships were established between abiotic factors and *Rhizophora mangle* seedling growth rates in four height (cm) classes, 25-40, >40-55, >55-70, and >70-85. Light in open canopy gaps was an important determinant of seedling growth. Growth rates in gaps (0.32 ± 0.04 to 1.89 ± 0.18 mm d⁻¹) were two- to five-fold greater than adjacent closed canopy forests (0.14 ± 0.01 to 0.40 ± 0.07 mm d⁻¹). Among open canopy sites, labile soil phosphorus and soil redox potentials were significantly correlated to growth ($P < 0.05$; $r = 0.98$ and 0.89 , respectively). Interstitial salinity ranged from 0 to 27 ppt across sites, well below hypersaline conditions. Thus, under low salinity stress and high light availability, soil fertility is proposed to be the dominant factor controlling *R. mangle* seedling development to a sapling stage (>85 cm) in South Florida mangrove forests. In addition, soil anoxia is hypothesized to be an important stressor in lagoonal-bay estuaries and marsh-mangrove ecotones with minimal tidal exchange.

INTRODUCTION

Mangroves are considered one of the most productive ecosystems worldwide, providing a continuous source of organic carbon to tropical and subtropical coastal food webs (Heald 1969, Odum 1970, Carter et al. 1973, Twilley 1988). On a regional scale, productivity rates vary across mangrove physiographic and geomorphic types (Lugo and Snedaker 1974, Snedaker and Brown 1981, Twilley et al. 1986, Day et al. 1987). Riverine mangroves, which are analogs of freshwater forested wetlands, are characterized as nutrient rich because of an influx of terrigenous mineral sediments and an autochthonous nutrient source (Brown and Lugo 1982, Day et al. 1987, Lugo et al. 1988). Mangrove forests associated with carbonate sediments where allochthonous nutrients are restricted primarily to the coastal fringe are characterized as nutrient poor (Spackman et al. 1969, Thom 1984, Woodroffe 1992). Litterfall rates (g C m⁻² d⁻¹), as an indicator of net primary production, are highest among riverine sites (12.6) (Lugo and Snedaker 1974), moderate in coastal fringing mangroves (2.7) (Pool et al. 1975), and lowest in scrub or dwarf forests associated with carbonate sediments (0.28) (Pool et al. 1975). Litterfall rates decrease as complexity indices, such as canopy height and basal area, decline from riverine to dwarf mangrove types (Brown and Lugo 1982). This relationship suggests the importance of forest structure to net primary production.

Because of the ecological importance of organic carbon to coastal marine communities, a major focus of mangrove research has been on forest structure and productivity. Fewer studies have investigated forest development. The influence of biotic and abiotic factors in seedling establishment and early survivability has been investigated in an effort to understand mangrove zonation patterns (Rabinowitz 1978, Burns and Ogden 1985, Smith 1987ab, Ellison and Farnsworth 1993, Clarke and Allaway 1993, McKee 1995a). In the majority of these studies, seedling growth rates were rarely measured. The paucity of data on mangrove seedling growth across complex environmental gradients has limited our understanding of the factors controlling mangrove seedling survival to the sapling stage. Low sapling densities in closed canopy mangrove forests (Smith 1987a, Clark and Allaway 1993), as well as in open canopy dwarf forests in South Florida (personal observation), suggest a critical step in mangrove maturity occurs

between the seedling and sapling stages of development.

Mangrove seedling growth to the sapling stage may be limited by the availability of resources, primarily nutrients and light, and exposure to high soil salinity and persistent flooding. In fact, nutrients and light are the two dominant resources defining structural development and growth rates across wetland forest types (Lugo et al. 1976, Smith 1987b, Jimenez 1988, Ellison and Farnsworth 1993). Lugo et al. (1976) concluded, based on output from a simulation model, that mangrove succession rates and biomass maximums at steady state are primarily determined by external nutrient loads and nutrient use efficiency, particularly in photosynthesis.

In South Florida, lightning strike and hurricane disturbances facilitate light and nutrient availability to seedling recruits. Tropical storm surges have been reported to deposit ≥ 10 cm of sediment onto the forest floor (Craighead and Gilbert 1962, Smith et al. 1994). High winds increase the production of detritus from leaf, branch, and tree fall (Smith et al. 1994 and personal observations), opening extensive canopy gaps that supply light energy for seedling development (Jimenez and Lugo 1985, Smith et al. 1994). Medium-size light gaps are generated through lightning strikes (Craighead and Gilbert 1962), whereas individual tree falls produce small gaps (Ellison and Farnsworth 1993). Each of these disturbances provides new resource niches that can promote seedling development.

Even under optimal nutrient and light conditions, however, abiotic stress may limit mangrove seedling growth (Lugo et al. 1976). Two dominant stressors characteristic of coastal wetland ecosystems are soil salinity and persistent soil flooding. Soil salinity imposes a high metabolic cost to compensate for salt exclusion and excretion processes (Ball 1988). Exposure to high soil salinity can directly affect photosynthesis as well as indirectly limit carbon fixation by restricting stomatal opening (Ball 1988). Cintron et al. (1978) found a negative correlation between soil salinity and mangrove development in arid regions of Puerto Rico. Persistent soil flooding also inhibits plant development by restricting root oxygen availability. This lack of root oxygen minimizes aerobic root respiration and metabolic energy available for growth (McKee and Mendelssohn 1987). Crab burrowing adjacent to roots has been shown to moderate soil flooding effects (Smith et al. 1991). However, crabs are usually absent in coastal lagoons with limited or no tidal exchange. Thus, soil salinity, aeration, and resource availability may all be important determinants of mangrove seedling development to the sapling stage.

To investigate abiotic factors influencing mangrove development in South Florida, the following research questions were posed: (i) Do nutrient, light, salinity, soil redox potentials, and other soil characteristics differ among mangrove forest structural types including the large-stature mangrove forests on Florida's west coast, short-stature mangroves at the marsh-mangrove ecotone, and dwarf forests in the southeast Everglades? (ii) Does resource availability and/or abiotic stress restrict rates of seedling development into the sapling stage? (iii) What is the importance of a resource pulse caused by Hurricane Andrew (August 1992) to seedling growth rates? To address these questions, size-specific growth rates, leaf production, and soil characteristics were measured in open and closed canopy sites and relationships established between abiotic factors and *Rhizophora mangle* development.

Study Sites

This study examines *R. mangle* populations along the west coast of South Florida in Everglades National Park (ENP) and sites in the southeast Everglades (Fig. 1.1). These two regions represent riverine and dwarf forests, respectively, with distinct nutrient input and tidal regimes (Lugo and Snedaker 1974). West coast sites receive mineral inputs from riverine-tidal estuaries (Craighead and Gilbert 1962, Spackman et al. 1969) with tidal ranges of 1 to 1.5 m along the coast. The southeast Everglades sites are characterized by carbonate marl soils (Tabb et al. 1967, Spackman et al. 1969) in association with lagoonal estuaries and minimal (< 1 m) tidal activity.

Five west coast sites were selected in ENP: 1) Broad River (BR), a hurricane-disturbed

open canopy site; 2) Little Shark River (LSR-O), an open canopy gap site (diameter ~25 m); 3) Little Shark River (LSR-C), a closed canopy site; 4) Upper Shark River (USR-O), an open canopy gap site (diameter ~7 m); and 5) Upper Shark River (USR-C), a closed canopy site (Fig. 1.1). No definitive causative mechanisms could be provided for LSR and USR gaps; however, tree fall and lightning strikes are two major causes of mangrove canopy gaps in South Florida (Craighead and Gilbert 1962). Two additional sites were selected in the southeast Everglades: 6) a southeast Everglades marine (SEEM) dwarf mangrove open canopy site; and 7) a southeast Everglades freshwater (SEEF) dwarf mangrove open canopy site (Fig. 1.1).

METHODS

Rhizophora mangle growth

In this study, *R. mangle* was used as the test species because of its ubiquitous distribution across the South Florida peninsula present in both tall stature (~15 m) and dwarf (~1 m) forests. Growth rates in four height (cm) classes (25-40, >40-55, >55-70, and >70-85) were measured to determine the recruitment rates of seedlings into the sapling stage (>85 cm). Eight *R. mangle* individuals within each size class were randomly selected and tagged. Height was measured on 15-18 August 1994 in ENP and 21 September 1994 in the southeast Everglades. These dates represent the initial conditions or t_0 . The terminal or main shoot of each individual was located, and the tag was secured with a plastic cable tie around the shoot above the last branch. If a branch was not present, a permanent mark was made on the upper node below the last pair of leaf scars, and all measurements were taken above this mark. Total leaf number, number of leaf scars, main stem length above the mark or last branch, and total plant height were recorded. Stem length (S_0) was measured with calipers to 0.1 mm. Seedling branching was also recorded, and presence of a branch as a terminal shoot was noted. After 151 days (t_{151}), all seedlings were re-measured (S_{151}), and new branches were recorded. No seedlings in the 25-40 cm size class were found in the fresh water site (SEEF-O), therefore the smallest size class was omitted at this site. Stem elongation rate or E in mm d^{-1} was calculated as:

$$E = \Delta S / \Delta t = (S_{151} - S_0) / (t_{151} - t_0) \quad [1.1]$$

Net leaf production was determined from leaf fall and new leaf production. Leaf fall (L_{fall}) was calculated from the number of leaf scars at t_{151} minus leaf scars at t_0 . Net leaf production (L_{prod}) over the 151 day sampling period was calculated based on the following formula:

$$L_{prod} = (L_{t151} + L_{fall}) - L_{t0} \quad [1.2]$$

Soil sampling

Soil cores

Soil cores ($n = 2$) were extracted from BR, LSR, USR, SEEM, and SEEF sites using plastic cores (5.2 cm diameter, 40 cm height) on 10-11 December 1994. Determination of within-site soil nutrient spatial variability was not within the scope of the present study. Therefore, soil cores taken from LSR and USR sites were sampled between closed and adjacent open canopy gaps, with the assumption that total soil nutrients are similar within sites. Soil cores were extruded and sectioned into 0 to 10 and 10 to 30 cm sections, and wet weights were determined within 24 hrs of sampling. Wet soil sections were mixed, and subsamples were taken to ascertain dry weights and bulk densities. Wet soil (0.2 g dry wt) was added to centrifuge tubes (50 ml) and P was extracted sequentially according to a modified soil P fractionation scheme (Hieltjes and Lijklema 1980). This fractionation scheme is based on chemical extractants separating soil P into the following inorganic (P_i) and organic forms (P_o): (i) exchangeable labile P_i (1 M NaCl

extractable); (ii) labile microbial Pi (NaHCO_3 extractable); (iii) Fe- and Al-bound Pi (0.1 M NaOH); (iv) Ca-bound Pi (0.5 M HCl extractable); (v) alkali-extractable organic Po; and (vi) residual organic Po ($\text{K}_2\text{S}_2\text{O}_8$ digestion). Both labile forms of P are considered directly available for biotic uptake, while a complex set of biogeochemical processes, including shifts in pH equilibria and soil oxic-anoxic conditions, influence the bioavailability of NaOH- and HCl-extractable P (Mortimer 1941, Otsuki and Wetzel 1972). Residual organic P is frequently composed of highly refractory compounds and is assumed to be biologically unavailable.

Fractionations followed the protocol of Koch and Reddy (1992) with two modifications. First, a bicarbonate extraction step was included: 20 ml of 0.5 N NaHCO_3 were added to the residual soil following the exchangeable Pi extraction step. Secondly, a substitution of 1 M NaCl for 1 M KCl as the exchangeable extractant was made because of the potential range in salinity among sites. To determine soil pH, a 1:1 soil:water ratio (10 g wet weight) slurry was allowed to equilibrate for 2 hr, after which the pH was recorded using a standardized combination pH electrode. Dry soil used to calculate bulk density was ground, and two subsamples were analyzed for TN and TC on a LECO-600 C:H:N elemental analyzer.

Interstitial nutrients, salinity, and redox potentials

Pore water was sampled in four replicate plots at BR, LSR-O, LSR-C, USR-O, USR-C, SEEM, and SEEF sites during May 1995. Pore water was extracted using a syringe and three-way valve attached to a plastic tube (0.65 cm diameter) with small diameter (~0.5 mm) holes drilled 0-5 cm from the closed-off tip. A 20-30 ml sample was drawn from 40 cm, immediately filtered (0.45 μ), and kept on ice before being frozen or immediately analyzed (24 hr) for nutrients. Salinity was measured in the field from a filtered subsample on a pre-calibrated field refractometer. Soluble reactive P (SRP), NH_4^+ , and $\text{NO}_3^- + \text{NO}_2^-$ were determined on an autoanalyzer using standard methods (USEPA 1979). All samples were corrected for autoanalyzer refractive index associated with variable salinities (Froelich and Pilson 1978).

Soil redox potentials were measured at BR, LSR-O, LSR-C, USR-O, SEEM and SEEF sites in May 1995. Platinum electrodes were used to measure soil Eh at four depths (surface, 5, 15, and 30 cm). Platinum electrodes were previously calibrated using a quinhydrone solution in pH 4.0 and 7.0 with a calomel reference probe (mV readings at 25°C were 218 and 40.8 in pH 4.0 and 7.0, respectively). Eh was calculated by adding the calomel reference potential of 244 mV to the mV readings from the field. Five replicate probes were used for each depth measurement.

Statistical analyses

Descriptive statistics (mean and standard errors), ANOVA, Tukey's honestly significant difference (THSD) multiple mean comparison tests, t-tests, correlations, and non-parametric Kruskal-Wallis (KW), and Mann-Whitney-Wilcoxon tests were performed using STATISTICA 4.1 (StatSoft, Inc. 1994, Tulsa, OK USA). Stem elongation rates within each size class followed normal distributions. Therefore, mean comparisons of growth rates among sites were conducted using parametric tests, ANOVA and THSD. Leaf production rates were analyzed with non-parametric tests (KW) because multiple modality was present in some size classes. The mean separation technique for non-parametric tests used normal distributions according to Dowdy and Wearden (1991). All significant differences are at the $P < 0.05$ level unless otherwise stated. Means are reported in the text with standard errors.

RESULTS

Resource and stress gradients

Soils

Total N (TN) levels did not differ significantly among sites in the 10-30 cm profile, but

tended to decrease from west to east coast sites at 0-10 cm (Fig. 1.2a). Highest total P (TP) values ($>400 \mu\text{g cm}^{-3}$) were found at BR on the west coast, compared to an order-of-magnitude lower TP ($< 25 \mu\text{g cm}^{-3}$) in the southeast Everglades (Fig. 1.2b). Intermediate values for TP were characteristic of the upper reaches of the Shark River (USR) close to the marsh-mangrove ecotone (Fig. 1.1, 1.2b). Ratios of N:P showed an inverse relationship to TP and increased to >100 in southeast Everglades sites (Fig. 1.2c).

Total P is a gross indicator of soil P availability, whereas a breakdown of P into labile and non-labile pools provides additional information on conditions under which P would be available for biotic acquisition. Labile P_i (exchangeable + bicarbonate extractable) decreased from west coast to southeast Everglades sites, consistent with trends observed for TP (Table 1.1). BR and LSR also had ten times higher Ca-bound P (HCl- P_i) than USR, SEEM, and SEEF sites (Table 1.1). The Fe- and Al-bound P (NaOH P_i) was a minor component of the inorganic P pool in BR and LSR, whereas similar percentages for both forms were found in USR, SEEM, and SEEF sites. High organic P levels at USR relative to TP are evidenced by the low $\text{P}_i:\text{P}_o$ ratios (13%) at this site compared to BR (55%), SEEM (41%), SEEF (42%), and LSR (31%) sites. Residual P_o comprised a majority of the total organic P pool at all sites (Table 1.1).

Soil pH at all five sites was close to or slightly above neutrality (Table 1.1). Lower pH and bulk densities at the LSR and USR sites are characteristic of highly organic soils. Upper Shark River soils had 37% TC, a percentage that was higher than the range for all other sites 12-21% (Table 1.1). Carbonate marl soils in SEEM and SEEF sites, as well as inorganic marine sediments associated with BR, are reflected in high bulk densities at these sites (0.33 to 0.62 g cm^{-3} , Table 1.1). Low bulk densities, high water content, high TC, and high N:P ratios in the upper soil profile at the freshwater site (SEEF, Table 1.1 and Fig. 1.2) probably reflect the presence of benthic algal mats (~ 3 cm, personal observation), which are ubiquitous across Everglades low-salinity marshes.

Porewater

Porewater NH_4^+ pools were an order-of-magnitude higher in the southeast Everglades compared to sites along the west coast (Table 1.2). High NH_4^+ concentrations at SEEM and SEEF sites are consistent with the range (100-150 μM) found at these sites during a seasonal study in 1994 (Koch in prep.). They are also similar to upper ranges found in northern Everglades oligotrophic (low P) marshes (100 μM) (Koch et al. 1994). In contrast to high NH_4^+ concentrations, SRP levels were at the limit of detection (0.1 μM) in SEEM and SEEF sites (Table 1.2). Porewater SRP values were 10-fold greater in west coast sites compared to the southeast Everglades (Table 1.2). Porewater SRP ranges from 0.1 to 0.2 μM in northern Everglades marshes (Koch et al. 1994), which are equivalent to those found in SEEM and SEEF sites. In southeast Everglades sites, $\text{NO}_3^- + \text{NO}_2^-$ comprise only a small proportion of the total inorganic N pool (1-5%), whereas on the west coast, 13 to 50% of the total inorganic N is speciated into $\text{NO}_3^- + \text{NO}_2^-$ (Table 1.2). Nitrogen speciation may be influenced by soil reducing conditions. Soil redox potentials (Eh) were significantly higher in ENP than SEEM and SEEF sites (Table 1.2). Although inorganic nutrient pools and soil Eh can be transient over time, the data presented show the dissimilarity of interstitial nutrients and Eh between west coast and southeast Everglades sites.

Salinity also varies over time, depending on tidal height, precipitation, and evapotranspiration rates. However, interstitial salinity is relatively more constant than surface water salinity, and values reported for southeast Everglades soils (0-2 ppt, Table 1.2) are consistent with low bi-monthly salinities found at these sites in 1994 over a one-year period (Koch in prep.). Interstitial salinities recorded in ENP sites in May (Table 1.2) are similar to averaged porewater values reported in August and May 1995 at BR, LSR, and USR sites (18, 28, and 15 ppt, respectively) (Twilley et al. 1995). High precipitation during the dry season in 1994-1995

may have reduced salinity maximums. Moreover, interannual measurements in which drought years are included would be needed to identify salinity stress events in ENP and the southeast Everglades. Salinity values reported here are assumed to be low-to-average for ENP and southeast Everglades during non-drought years; however, these values reflect salinity ranges under which plant growth rates were determined in this study.

Contrasting closed and open canopy sites, salinities were slightly higher in the LSR-C than LSR-O site. However, both values are well below hypersaline conditions (Table 1.2). Porewater salinity and nutrient levels were not significantly different between USR-C and USR-O sites. Porewater SRP concentrations did not differ significantly between open and closed sites at LSR. Inorganic N was significantly higher in LSR-O than LSR-C site. Higher NH_4^+ concentrations at -40 cm are consistent with lower soil redox potentials in LSR-O (40 mV) compared to LSR-C (170) site at -30 cm (Table 1.2). Although porewater nutrient and salinity variations were found between open and closed canopy sites in LSR and USR sites, overall porewater chemistry within sites is more similar than among-site differences. The major factor defining open versus closed canopy sites is light availability. Light levels in LSR-C and USR-C averaged approximately 200 and 300 $\mu\text{M m}^{-2} \text{s}^{-1}$ compared to 1200 and 1300 $\mu\text{M m}^{-2} \text{s}^{-1}$ in adjacent gaps, respectively. These differences result in canopy light extinctions of 85 and 74% PAR in LSR-C and USR-C sites, respectively.

***Rhizophora mangle* growth rates**

Canopy gaps stimulated *R. mangle* seedling growth rates up to five-fold in the LSR-O and two-fold in the USR-O sites compared to adjacent closed canopies (Fig. 1.3). Stem elongation rates significantly ($P < 0.01$) increased with greater PAR in LSR-O size classes 1, 3, and 4 and size classes 1, 2, and 4 ($P < 0.08$) in the USR-O site. Stem elongation rates tended to increase in canopy gaps relative to closed canopies in all size classes, although differences were not significant in LSR size class 2 and USR size class 3 (Fig. 1.3). Under closed canopies, growth rates were similar between lower and upper Shark River sites in seedling size classes 1 and 2. In the upper two size classes under the canopy and in all size classes in gaps, LSR had significantly greater stem elongation rates than USR (Fig. 1.3). Higher seedling growth rates in the LSR gap and under the canopy relative to growth rates at USR, lends evidence to the supposition that factors in addition to light may be regulating seedling growth rates.

Distinguishing growth rates across all open canopy sites, ten-times higher growth was found in west coast relative to southeast Everglades sites (Fig. 1.4). Maximum rates were recorded at the hurricane-disturbed site along the west coast (BR-O, $3.1 \pm 0.3 \text{ mm d}^{-1}$). At this site and in size class 4 at LSR-O, stem elongation rates were significantly greater than at any other sites ($P < 0.01$, Fig. 1.4). These two sites also exhibited maximum net leaf production rates (Fig. 1.5). Factors controlling net leaf production may have influenced high stem elongation rates in BR-O and LSR-O sites. Stem elongation rates were found to increase with leaf production (slope = 0.35; $P < 0.01$) and decrease with leaf fall across all open and closed canopy sites (slope = -0.36; $P < 0.01$). Slowest seedling growth rates were measured in southeast Everglades open canopy sites (0.03 to 0.13 mm d^{-1} , Fig. 1.4). These rates were lower than closed canopy sites along the west coast (0.14 to 0.47 mm d^{-1} , Fig. 1.3), although both groups had similarly low net leaf production rates (Fig. 1.5).

Rhizophora mangle stem elongation rates were regressed against soil characteristics across all open canopy sites (Table 1.3). Labile P in the upper and lower depth profiles were highly correlated to seedling growth rates ($r = 0.94$ to 0.99 , Table 1.3). Likewise, total P was directly correlated to growth rates among open canopy sites ($r = 0.96$ to 0.99 , Table 1.3). Despite the fact that soil N levels were similar among sites (Fig. 1.2), total N at 10-30 cm depth significantly correlated to seedling growth in upper size classes 3 and 4 (Table 1.3). Soil redox potentials at 30 cm depth explained a high amount of variance in average seedling growth rates. These data imply the importance of soil fertility, primarily P, and soil reducing conditions to *R. mangle* seedling

development.

Maximum, average, and minimum seedling growth rates extrapolated across size classes provide an estimate for seedling rates of development to the sapling stage (Fig. 1.6). Based on these estimates, seedlings at the BR site reach a sapling stage of 85 cm height in less than one year using maximum growth rates. A two-year development period is required to attain the sapling stage in the LSR-O and USR-O sites. Seedlings under closed canopies are estimated to take 6 to 9 years on average and up to 15 to 21 years to reach a sapling stage. In the SEEM site 27 to 61 years is required to reach the 85 cm height stage. Additional seasonal and inter-annual growth measurements are needed to reconcile the faster growth rates in SEEF versus SEEM site in the southeast Everglades. Nevertheless, slow growth rates estimated here correspond to minimum ages reported for *R. mangle* dwarf trees in the southeast Everglades (40 to 60 years) based on leaf scars and annual leaf turnover rates (Snedaker and Stanford unpublished notes, Teas 1974).

DISCUSSION

Light and nutrient resources

Canopy gaps are important for mangrove seedling development to the sapling stage. Canopy gaps stimulated *R. mangle* seedling growth two- to five-times relative to adjacent closed canopies with 85 and 74% PAR extinction. Similar levels of light extinction (80-95% reduction in PAR) lowered seedling survival and relative growth rates in three Australian mangrove species, *Avicennia marina*, *Ceriops tagal*, and *Rhizophora stylosa* (Smith 1987b). A majority of tropical forest species including mangroves are characterized as gap-dependent (Denslow 1987, Smith 1987ab, Jimenez 1988, Clarke and Allaway 1993, Ellison and Farnsworth 1993). Ellison and Farnsworth (1993) conducted a canopy removal experiment in a Belizean mangrove forest, increasing light availability to suppressed *R. mangle* seedlings. In their study, canopy gaps stimulated stem elongation rates two-fold and promoted biomass allocation to leaves. *Rhizophora mangle* growth and net leaf production responses found in ENP under natural canopy disturbances are consistent with growth responses from Belize. Light gaps have been shown to stimulate *R. mangle* in the field; however, *R. mangle* seedlings did not respond to increased light in a growth chamber experiment (McKee 1995b). Light treatments achieved in the growth chamber ($400 \mu\text{mol m}^{-2} \text{s}^{-1}$) were below photosynthetic light saturation levels found for *R. mangle* in South Florida ($>500 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Koch in prep.), and they are lower than light levels found in open canopy gaps in the field ($1000\text{-}2500 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Smith 1987b, this study). Thus, light level discrepancies probably account for the non-significant response of *R. mangle* to light treatments in growth chamber experiments.

Although mangrove seedlings require light for early recruitment into the sapling stage, soil nutrients also control growth responses to light. Hurricane Andrew in 1992 created a large open canopy gap providing light resources. The BR-O hurricane disturbed site had the highest soil extractable P levels among sites. Nutrient enrichment at the BR site cannot be directly related to Hurricane Andrew, but high resource availability promoted maximum seedling growth rates at this site. Nutrient amendments have been found to increase survivorship and stimulate *Avicennia marina* growth rates in an Australian mangrove forest (Clarke and Allaway 1993). Clarke and Allaway (1993) concluded that *A. marina* seedlings require establishment into a light and sediment resource regeneration niche to recruit into the sapling stage (50 cm). In South Florida, both high light and high nutrient resources promote maximum rates of *R. mangle* seedling development to the sapling stage.

Labile Pi was significantly correlated to seedling growth rates across all open canopy sites. Extractable labile Pi was also directly correlated to above-ground biomass in adult trees in Australia ($r = 0.85$, $P < 0.01$) (Boto and Wellington 1984). In the Everglades, high soil TN and TC content are an indication of highly organic soils. Australian soil TN (range = 0.16-0.40%, mean = 0.32%) and TC (range = 4-16%, mean = 11%) were low in comparison to Everglades

soils. Low bulk density soils in the Shark River sites also reflect highly organic soils. High bulk density (range = 0.38-0.45 g cm⁻³, mean = 0.42 g cm⁻³) mineral soils are characteristic of Australian mangrove soils reported by Boto and Wellington (1984). Although Australian and Everglades soils vary in many characteristics, P has been proposed to be an important determinant in the development of mangroves in both Australian and North American mangrove forests (Boto and Wellington 1983, 1984, this study). Phosphorus limitation was also concluded to be a major factor limiting *R. mangle* growth in Caribbean mangroves of Belize (Feller 1995). Thus, P from riverine, tidal, or biological inputs is an important resource for mangrove development where nitrogen and light are not limiting and stressors such as salinity and soil anoxia are not overriding factors. Soil N:P ratios in the southeast Everglades and upper ecotone site along the west coast support the P limitation hypothesis. However, tall-stature forests along the west coast may also be N limited, based on the low soil N:P ratios at the BR and LSR sites.

Stress factors

Porewater salinities measured in this study (0-27 ppt) were equivalent to or lower than salt concentrations where *R. mangle* dominates and attains greatest heights (Cintron et al. 1978, Twilley et al. 1986, McKee 1993). In fact, salinity was positively correlated to stem elongation rates in this study, although not significant at the $P < 0.05$ level. Soil salinities >65 ppt have been found to limit *R. mangle* development in the field (Cintron et al. 1978, Twilley et al. 1986). These data suggest that salinity is not a major factor limiting *R. mangle* growth in ENP and the southeast Everglades, although interannual measurements of interstitial salinity with seedling growth determinations including droughts are needed to substantiate this hypothesis.

In contrast to salinity stress, soil redox potential was significantly correlated to average stem elongation rates. Soils were moderately reducing in ENP, while those associated with lagoonal estuaries and minimal tidal fluctuations in the southeast Everglades were highly reduced. *Rhizophora mangle* fringe and mixed-species basin forests with tidal exchange are characterized as having moderately reducing (100 mV) soil conditions (McKee 1993). However, in interior monospecific *A. marina* basin forest sites, where tidal exchange is an infrequent event, soils become highly reduced (-100 to -200 mV). Although flooding and soil reducing conditions may directly influence mangrove development, soil anoxia and lack of tidal energy can indirectly influence nutrient uptake through several mechanisms: (i) minimize metabolic energy available for nutrient uptake because of the inefficiency of ATP production through fermentative pathways (McKee and Mendelssohn 1987); (ii) affect water potential by increasing stomatal resistance, thereby limiting water and nutrient uptake (Naidoo 1983, 1985); (iii) limit the development of small diameter roots with low oxygen storage capacity, subsequently decreasing the root surface area for nutrient absorption (Koncalova 1990, Youssef and Saenger in press); and (iv) minimize contact of root rhizospheres with oxygenated and nutrient-laden surface waters (Odum 1971, Carlson et al. 1983).

Conclusions

Rhizophora mangle seedling growth and rates of development into the sapling stage are dependent on the availability of light and soil nutrients. Growth responses to light are limited by regional variations in soil nutrients across the South Florida peninsula, particularly soil P. Porewater salinities during high-water years in the Everglades do not appear to influence *R. mangle* growth. However, soil hypoxia gradients from riverine-tidal estuaries on the west coast to the southeast Everglades are significant. Low soil P and highly reduced soils characterize the marsh-mangrove ecotone and the southeastern region of the Everglades. These site characteristics are contemporaneously found with the *R. mangle* dwarf form. Thus, a resource-flooding hypothesis is presented: without light limitation, soil fertility and flooding are the primary determinants limiting *R. mangle* seedling recruitment rates into the sapling stage in subtropical Florida.

Table 1.1. Soil phosphorus fractions ($\mu\text{g cm}^{-3}$) and descriptive soil characteristics from seedling growth study sites in Everglades National Park (Broad River, BR; Little Shark River, LSR; Upper Shark River, USR) and southeast Everglades sites (marine, SEEM; and fresh, SEEF). Means are presented with standard deviations ($n = 2; \pm \text{SD}$).

	Depth (cm)	BR	LSR	USR	SEEM	SEEF
<i><u>P fraction -Inorganic</u></i>						
NaCl Pi	0-10	2.7 $\pm$ 1.3	0.4 $\pm$ 0.1	0.5 $\pm$ 0.2	0.2 $\pm$ 0.2	0.1 $\pm$ 0.0
	10-30	3.8 $\pm$ 3.1	0.4 $\pm$ 0.1	0.1 $\pm$ 0.1	0.2 $\pm$ 0.1	0.1 $\pm$ 0.0
NaHCO ₃ Pi	0-10	44.0 $\pm$ 13.5	14.2 $\pm$ 0.6	3.8 $\pm$ 0.6	0.8 $\pm$ 0.1	0.3 $\pm$ 0.1
	10-30	25.5 $\pm$ 14.6	6.6 $\pm$ 0.3	2.1 $\pm$ 0.2	2.4 $\pm$ 0.4	3.0 $\pm$ 0.1
NaOH Pi	0-10	9.9 $\pm$ 0.0	16.7 $\pm$ 5.1	5.7 $\pm$ 0.0	1.3 $\pm$ 0.3	1.7 $\pm$ 0.2
	10-30	13.1 $\pm$ 0.2	14.9 $\pm$ 2.0	5.5 $\pm$ 0.0	2.0 $\pm$ 2.1	2.0 $\pm$ 1.4
HCL Pi	0-10	193.1 $\pm$ 7.0	67.3 $\pm$ 0.8	6.3 $\pm$ 1.0	6.2 $\pm$ 0.8	2.1 $\pm$ 0.3
	10-30	195.7 $\pm$ 10.9	81.5 $\pm$ 9.7	4.6 $\pm$ 0.0	5.0 $\pm$ 3.2	4.4 $\pm$ 0.8
Total Pi	0-10	249.5 $\pm$ 5.2	98.7 $\pm$ 5.0	16.2 $\pm$ 1.8	8.4 $\pm$ 0.8	4.2 $\pm$ 0.1
	10-30	238.0 $\pm$ 7.0	103.4 $\pm$ 11.5	12.4 $\pm$ 0.2	9.7 $\pm$ 4.7	9.5 $\pm$ 2.0
<i><u>P fraction -Organic</u></i>						
NaHCO ₃ Po	0-10	6.1 $\pm$ 8.6	9.0 $\pm$ 0.1	4.6 $\pm$ 0.1	2.5 $\pm$ 0.1	0.8 $\pm$ 0.1
	10-30	7.8 $\pm$ 2.1	7.2 $\pm$ 0.1	5.3 $\pm$ 0.7	1.2 $\pm$ 0.3	2.1 $\pm$ 0.3
NaOH Po	0-10	41.6 $\pm$ 0.8	93.0 $\pm$ 41.7	35.0 $\pm$ 7.5	1.1 $\pm$ 0.5	0.5 $\pm$ 0.0
	10-30	56.6 $\pm$ 9.0	89.1 $\pm$ 6.0	60.9 $\pm$ 0.6	2.3 $\pm$ 0.1	2.1 $\pm$ 0.2
Residual Po	0-10	138.0 $\pm$ 7.9	121.1 $\pm$ 5.9	43.1 $\pm$ 4.0	9.3 $\pm$ 2.1	4.0 $\pm$ 1.5
	10-30	156.7 $\pm$ 23.9	139.0 $\pm$ 16.2	69.0 $\pm$ 6.8	9.2 $\pm$ 0.2	9.7 $\pm$ 0.4
Total Po	0-10	185.7 $\pm$ 15.7	223.0 $\pm$ 47.5	82.7 $\pm$ 11.4	12.8 $\pm$ 2.7	5.4 $\pm$ 1.6
	10-30	221.2 $\pm$ 30.8	235.3 $\pm$ 22.3	135.1 $\pm$ 8.1	12.7 $\pm$ 0.7	13.9 $\pm$ 0.1
<i><u>Soil characteristics</u></i>						
Soil pH	0-10	7.67 $\pm$ 0.21	7.16 $\pm$ 0.12	7.14 $\pm$ 0.03	7.85 $\pm$ 0.01	7.54 $\pm$ 0.08
	10-30	7.70 $\pm$ 0.18	7.11 $\pm$ 0.02	7.10 $\pm$ 0.11	7.68 $\pm$ 0.12	7.28 $\pm$ 0.09
Bulk density (g cm ⁻³)	0-10	0.62 $\pm$ 0.08	0.24 $\pm$ 0.02	0.11 $\pm$ 0.00	0.39 $\pm$ 0.02	0.15 $\pm$ 0.03
	10-30	0.51 $\pm$ 0.02	0.23 $\pm$ 0.00	0.15 $\pm$ 0.01	0.33 $\pm$ 0.04	0.42 $\pm$ 0.02
Total Carbon (%)	0-10	12.19 $\pm$ 1.14	21.65 $\pm$ 1.42	36.71 $\pm$ 2.40	14.03 $\pm$ 0.01	20.99 $\pm$ 1.65
	10-30	11.80 $\pm$ 0.09	18.96 $\pm$ 2.26	32.42 $\pm$ 1.22	17.92 $\pm$ 0.98	15.18 $\pm$ 0.26
Water content (%)	0-10	52 $\pm$ 6	78 $\pm$ 1	89 $\pm$ 0	70 $\pm$ 1	84 $\pm$ 5
	10-30	61 $\pm$ 1	77 $\pm$ 1	86 $\pm$ 1	72 $\pm$ 3	64 $\pm$ 2

Table 1.2. Porewater nutrients (μM), interstitial salinity (ppt), and soil redox potentials (Eh in mV) at seedling growth study sites in Everglades National Park (Broad River, BR; Little Shark River open, LSR-O and closed, LSR-C; Upper Shark River open, USR-O and closed, USR-C) and southeast Everglades sites (marine, SEEM; and fresh, SEEF). Means ($n = 4$ for pore water; $n = 5$ for Eh) are presented with standard errors.

<i>Sites:</i>	BR	LSR-O	LSR-C	USR-O	USR-C	SEEM	SEEF
<u><i>Porewater nutrients (μM)</i></u>							
NH_4^+	4.2 $\pm$ 0.6	9.0 $\pm$ 3.1	1.5 $\pm$ 0.2	5.6 $\pm$ 1.8	4.7 $\pm$ 1.0	50.3 $\pm$ 17.3	73.3 $\pm$ 5.2
$\text{NO}_3^- + \text{NO}_2^-$	2.8 $\pm$ 0.52	7.1 $\pm$ 2.57	1.5 $\pm$ 0.11	1.9 $\pm$ 1.58	0.7 $\pm$ 0.09	0.6 $\pm$ 0.10	4.2 $\pm$ 0.41
SRP	3.0 $\pm$ 0.55	13.4 $\pm$ 2.35	14.5 $\pm$ 1.13	3.5 $\pm$ 2.89	3.2 $\pm$ 0.43	0.2 $\pm$ 0.07	0.1 $\pm$ 0.04
<u><i>Interstitial Salinity (ppt)</i></u>							
	17 $\pm$ 1	23 $\pm$ 1	27 $\pm$ 1	5 $\pm$ 4	6 $\pm$ 0	2 $\pm$ 1	0 $\pm$ 0
<u><i>Soil redox potential (mV)</i></u>							
Surface	153 $\pm$ 30	191 $\pm$ 32	216 $\pm$ 40	nd	126 $\pm$ 9	-60 $\pm$ 18	-50 $\pm$ 13
-5 cm	126 $\pm$ 34	165 $\pm$ 32	204 $\pm$ 24	nd	168 $\pm$ 14	-112 $\pm$ 9	-32 $\pm$ 6
-15 cm	199 $\pm$ 38	90 $\pm$ 22	266 $\pm$ 26	nd	127 $\pm$ 12	-137 $\pm$ 7	-49 $\pm$ 11
-30 cm	141 $\pm$ 20	40 $\pm$ 23	170 $\pm$ 41	nd	47 $\pm$ 17	-136 $\pm$ 11	-60 $\pm$ 7
Mean	155 $\pm$ 16	118 $\pm$ 33	214 $\pm$ 20		117 $\pm$ 25	-117 $\pm$ 16	-48 $\pm$ 6

nd = not determined

Table 1.3. Correlations between average stem elongation rates (X) in addition to each size class (1-4) and soil characteristics: Interstitial nutrients and salinity (40 cm depth), soil labile Pi (LPi = exchangeable + sodium bicarbonate extractable), total P (TP), total N (TN) from 0-10 and 10-30 cm depths, and redox potentials at four depths (0, -5, -15, and -30 cm). Bold coefficients represent significant correlations ($P < 0.05$). Data used in correlations are presented in Figures 2.2, 2.4 and Tables 2.1, 2.2.

					Soil									
Interstitial					LPi		TP		TN		Redox potentials			
					<i>cm</i>		<i>cm</i>		<i>cm</i>		<i>cm</i>			
NH ₄ ⁺	NOx	SRP	S‰		0-10	10-30	0-10	10-30	0-10	10-30	0	-5	-15	-30
<i>Size class</i>														
X	-0.70	0.24	0.36	0.78	0.98	0.94	0.97	0.97	0.80	0.90	0.74	0.61	0.83	0.89
1	-0.70	0.37	0.24	0.72	0.97	0.94	0.96	0.97	0.79	0.87	0.70	0.57	0.82	0.89
2	-0.64	-0.05	0.05	0.51	0.95	0.94	0.82	0.84	0.57	0.71	0.60	0.54	0.83	0.88
3	-0.67	0.24	0.34	0.77	0.99	0.95	0.96	0.96	0.80	0.91	0.71	0.58	0.80	0.86
4	-0.71	0.36	0.47	0.86	0.96	0.90	0.99	0.99	0.87	0.94	0.77	0.63	0.81	0.86

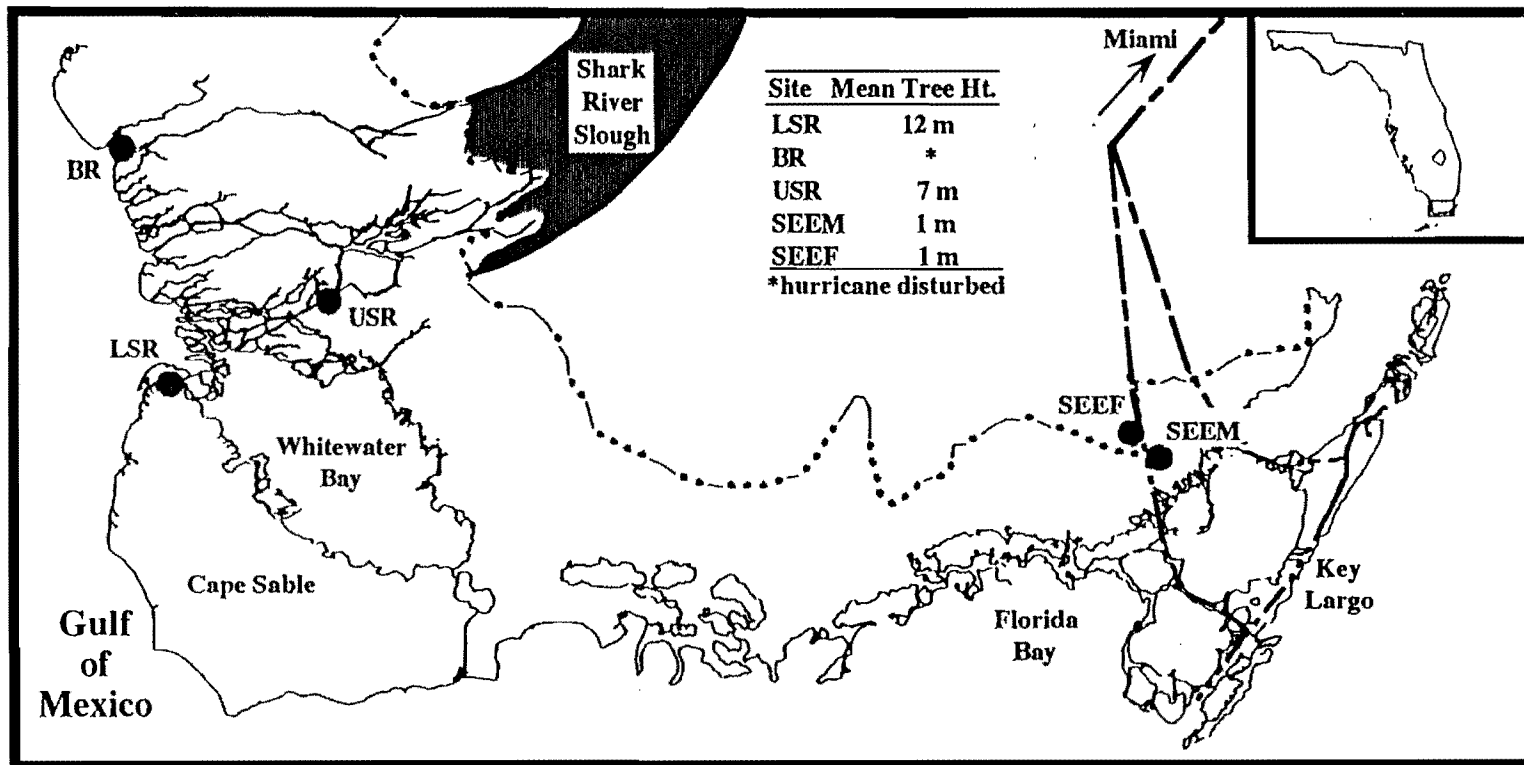


Figure 1.1. Study site locations in Everglades National Park on the west coast of South Florida: Broad River (BR), Little Shark River (LSR), Upper Shark River (USR); and sites in the southeast Everglades region: southeast Everglades Fresh (SEEF) and marine (SEEM). Adjacent open and closed canopy sites were established at LSR and USR (total sites = 7). Line with grass symbol approximates the landward extent of the marsh-mangrove ecotone. Table insert identifies forest structural gradient across the peninsula, showing the largest stature trees along the west coast decreasing in height toward the ecotone and the southeast Everglades region.

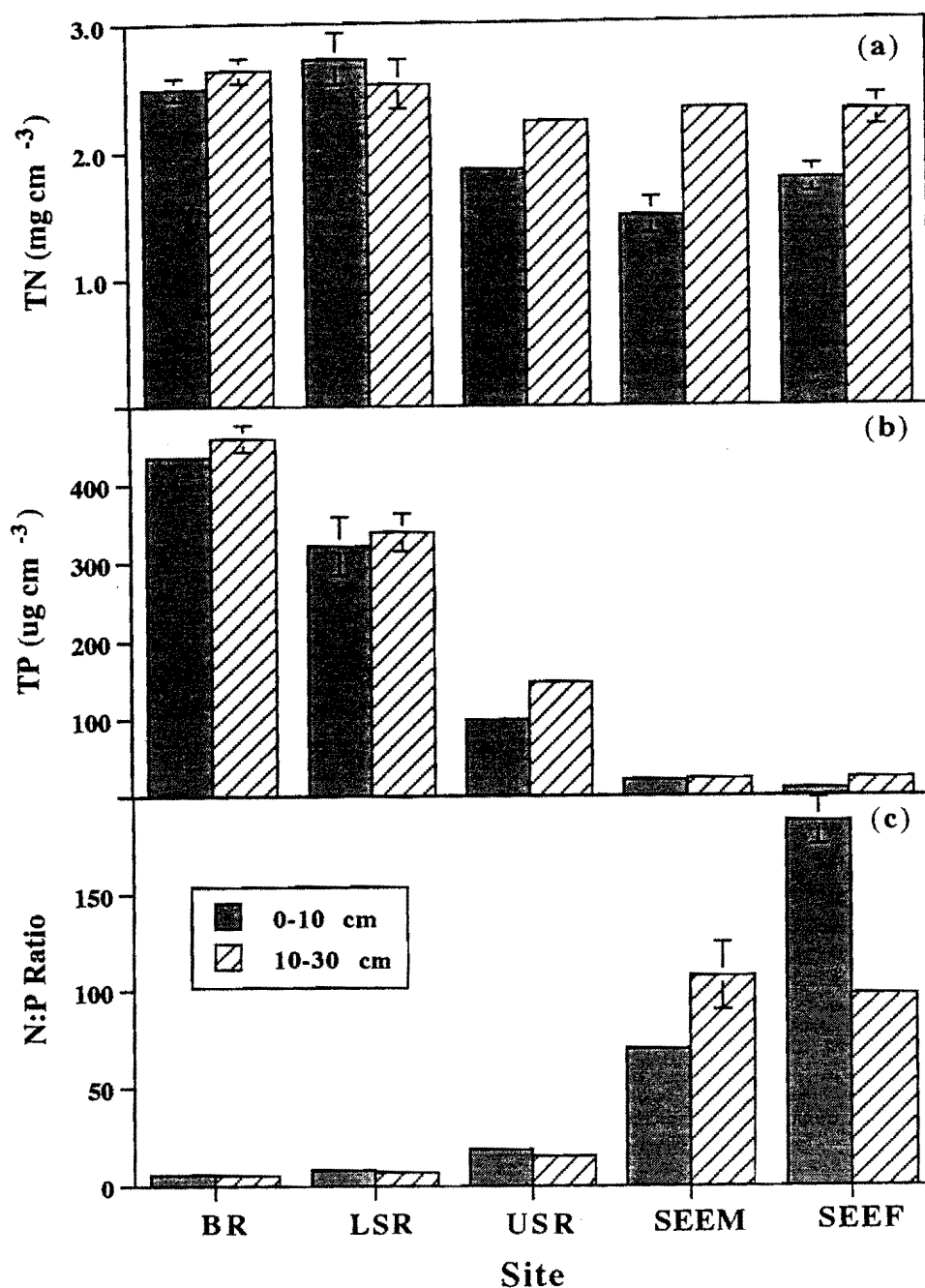


Figure 1.2. Soil TN, TP, and N:P ratios (0-10 and 10-30 cm depths) at sites across the south Florida peninsula. Three sites in Everglades National Park: a hurricane site at the mouth of Broad River (BR), undisturbed site at the mouth of Little Shark River (LSR), upper Shark River site close to the marsh-mangrove ecotone (USR). Two sites in the southeast Everglades: a marine dwarf mangrove site (SEEM), and a freshwater dwarf site (SEEF). Means given with standard errors (n=2).

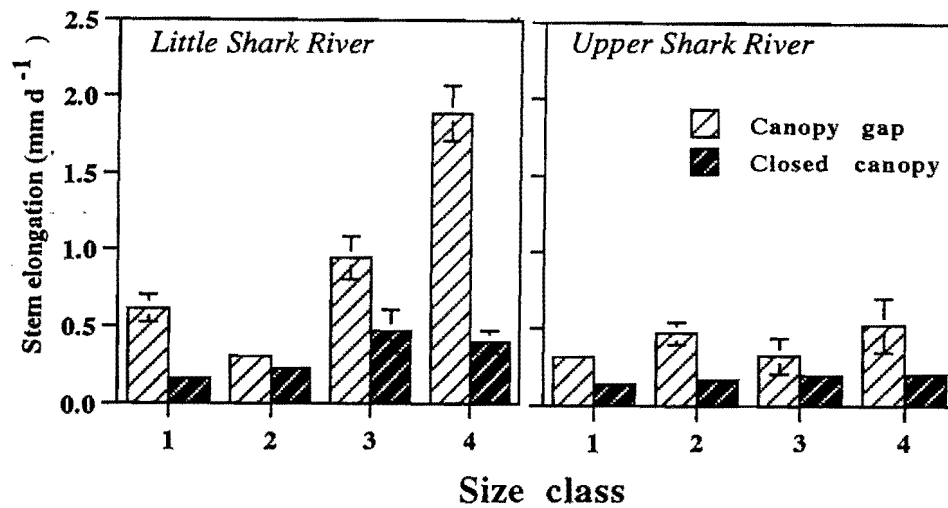


Figure 1.3. *Rhizophora mangle* main stem elongation rates in closed canopy versus canopy gaps at Little Shark River and Upper Shark River sites in Everglades National Park. Means are presented with standard errors (n=8).

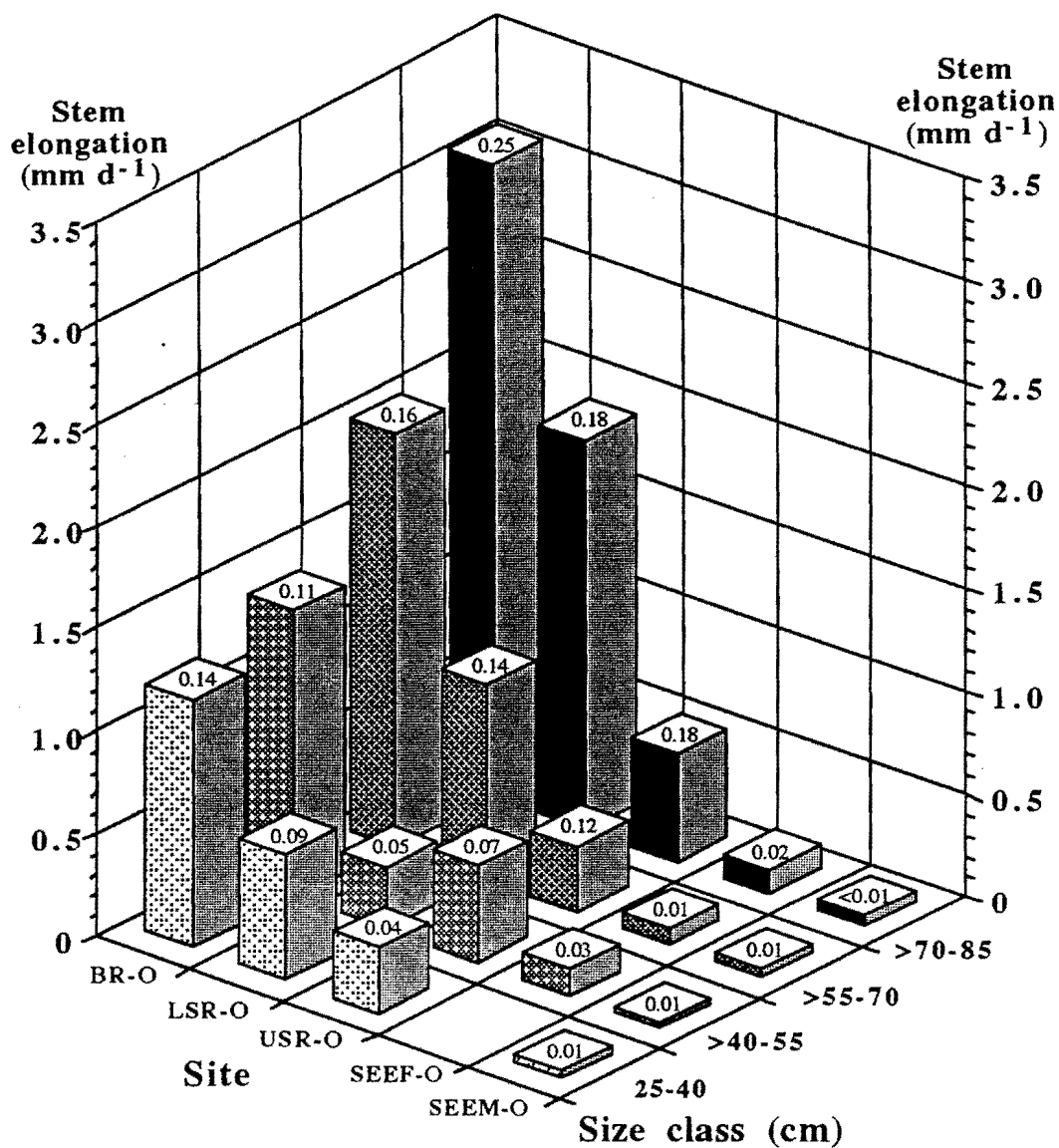


Figure 1.4. *Rhizophora mangle* stem elongation rates within four seedling size classes in open canopy sites: Broad River open (BR-O), Little Shark River open (LSR-O), Upper Shark River open (USR-O), Southeast Everglades Marine open (SEEM-O), Southeast Everglades Fresh open (SEEF-O). Standard errors shown on top of bars (n=8).

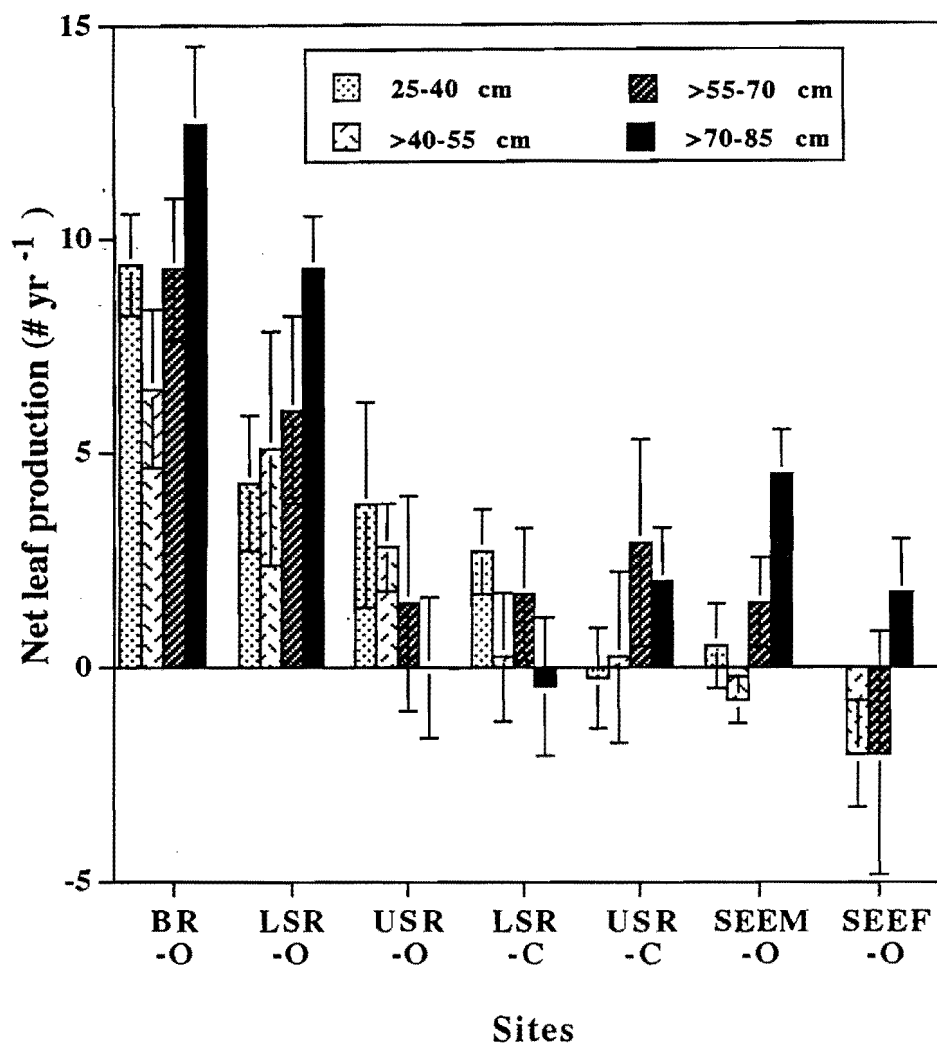


Figure 1.5. *Rhizophora mangle* main stem net leaf production rates within four seedling size classes in the Borad River open (B-O), Little Shark River open (LSR-O), Upper Shark River open (USR-O), Little Shark River closed (LSR-C), Upper Shark River closed (USR-C), and southeast Everglades marine open (SEEM) and fresh open (SEEF) canopy sites (N=8; SE).

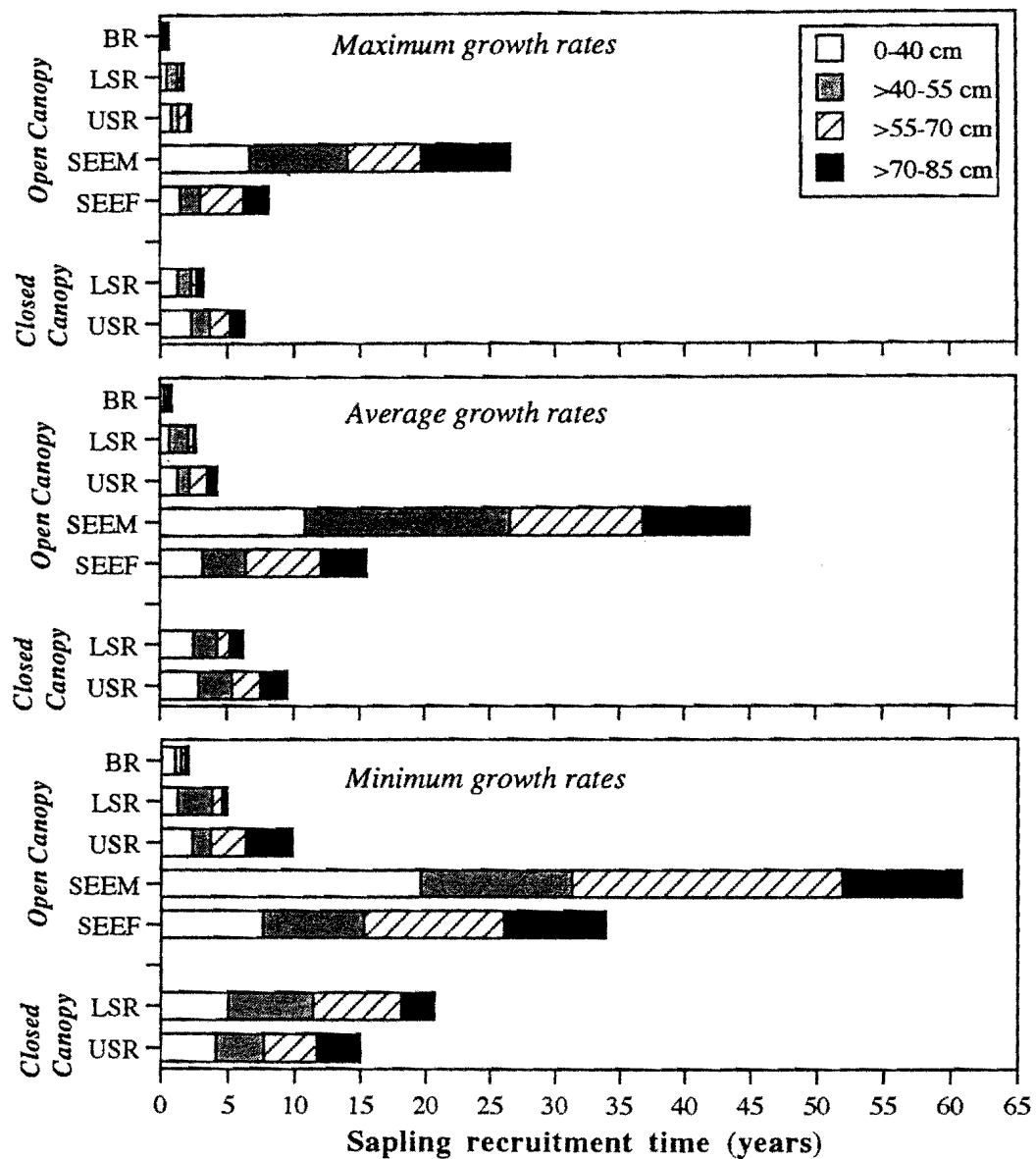


Figure 1.6. Estimates of *Rhizophora mangle* seedling (25 cm) development rates into the sapling stage (85 cm) based on maximum, average, and minimum growth rates within four size classes in open and closed canopied sites in Everglades National Park and the southeast Everglades.

CHAPTER 2

LIGHT AND SOIL NUTRIENT EFFECTS ON *RHIZOPHORA MANGLE* L. SEEDLING BIOMASS PARTITIONING AND C-FIXATION RATES

ABSTRACT

Patterns of biomass allocation and C-fixation rates in *Rhizophora mangle* seedlings were investigated in the Florida Everglades at sites with variable light and soil nutrients. Soil nutrient levels and light availability significantly influenced light-saturated C-fixation rates. Photosynthetic rates at light saturation decreased from 7.8 to 5.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with decreasing soil P. Low light under the canopy suppressed average daily photosynthetic rates 64% relative to an adjacent gap. Biomass allocation to photosynthetic tissue was also dependent on high light and soil nutrients. Photosynthetic tissue comprised approximately 50% of the total above-ground biomass in open canopied, high nutrient sites, whereas under low soil P, only 12-13% of the total biomass was allocated to leaf tissues. A general trend was found across size classes in open and closed canopied sites: biomass partitioning to leaves increased with size class in the gap, while under the canopy, leaf biomass increased initially, but subsequently decreased with increasing size. The inability of *Rhizophora mangle* to allocate increasing biomass to photosynthetic tissues to compensate for low C-fixation rates under closed canopies, identifies this species as shade intolerant. Whole plant C-fixation rates were strongly correlated to seedling growth rates in southwest Everglades sites. These results indicate the importance of both C-production and foliar biomass partitioning for early mangrove development. However, further study is needed to reconcile limited growth in response to C-production in dwarf mangrove forests in the southeast Everglades.

INTRODUCTION

Mangrove seedlings are influenced by a unique suite of factors at each stage in their development. Vivipary (Thomlinson 1986) results in direct seedling recruitment into adult mangrove forests without a dormant seed stage. Recruits establish within the forest along local gradients of abiotic and biotic influences according to species characteristics (Rabinowitz 1978a, Smith 1987ab, McKee 1995). Seedling buoyancy, angle of orientation upon establishment, and obligate dispersal time (Rabinowitz 1978a, McKee 1995) directly contribute to the sorting of propagules along gradients of water level, hydroperiod, and tidal buffeting (Chapman 1944, Hutchings and Saenger 1987, Jimenez 1988, Jimenez and Sauter 1991). Predation by crabs (family Grapsididae) and other herbivores can also influence species zonation and developmental patterns (Onuf et al. 1977, Smith 1987ab, Farnsworth and Ellison 1991). Although several abiotic and biotic factors influence seedling recruitment, these factors do not completely explain the variability in rates of seedling development to the sapling stage.

Carbohydrate reserves in propagules are critical to mangrove seedling survivorship over multiple years under low-light canopies (Burns and Ogden 1985, Jimenez and Sauter 1991). One year after recruitment, seedling half-lives correlated highly with propagule weight in four genera of Panamanian mangroves: *Avicennia*, *Rhizophora*, *Pelliciera*, and *Laguncularia* (Rabinowitz 1978b). In mixed species forests in Costa Rica, Jimenez and Sauter (1991) attributed *Rhizophora racemosa*'s large propagule, that provided greater carbohydrate reserves and height, to its greater growth and half-life relative to *A. bicolor*. This competitive advantage was found despite *R. racemosa*'s lower establishment rate relative to *A. bicolor*. These studies suggest propagule carbohydrate reserves are important for survival in the initial stages of mangrove development. However, once seedlings surpass the endogenous growth phase, environmental resources play a key role in seedling survivorship into the sapling stage (Jimenez 1988, Rabinowitz 1978b).

Resource acquisition strategies, such as plasticity in biomass allocation patterns, become important when propagule carbohydrate reserves are depleted. Most tropical forest shade-tolerant species partition above-ground biomass into photosynthetic components under low light compared to shade-intolerant gap associates (King 1991). This resource allocation strategy allows for the preferential allocation of photosynthate to leaf production, thereby supplementing limited resources (Chapin 1980, Chapin et al. 1987). Although greater leaf production could facilitate growth under a closed canopy, if mangrove seedlings are truly shade intolerant, low light may not provide the necessary photosynthate to support new leaf production. Ball (1980) defined mangroves with large seedling carbohydrate reserves, such as the genus, *Rhizophora*, as generally more shade-tolerant than genera with low mass propagules (Rabinowitz 1978b, Ball 1980, Jimenez and Sauter 1991). However, earlier work by the author identified both high light and soil nutrients as important factors influencing *Rhizophora mangle* seedling growth and rates of development into the sapling stage (Chapter 1). Low soil nutrient availability under field conditions may limit allocation of photosynthate to photosynthetic biomass as well as influence C-fixation rates.

In this chapter, biomass allocation patterns and C-fixation rates are examined between sites with contrasting light and soil nutrients. Above-ground biomass allocation to photosynthetic tissues is hypothesized to increase as light levels are reduced and decrease as nutrients become limiting. Alternatively, above-ground biomass compartmentalization remains constant between open and closed canopies, but C-fixation rates decline under low light and low soil nutrient environments. Low C-fixation rates can result from low photosynthetic rates at light saturation and/or low light levels limiting photosynthetic saturation. Photosynthetic-irradiance curves are defined at each site to address these two alternative mechanisms that may limit C-fixation in the field. Carbon-fixation rates at the leaf scale are extrapolated to the plant level based on total leaf area to establish a relationship between total C-fixed and *R. mangle* seedling growth rates.

METHODS

Study Sites

Rhizophora mangle C-fixation rates and photosynthetic versus non-photosynthetic above-ground biomass partitioning were investigated at sites with variable light and soil nutrients. Sites were chosen that represent the high and low range of light and soil nutrient environments in the South Florida Everglades based on data from a previous study (Chapter 2). Sites were located in Everglades National Park (ENP) and the southeast Everglades, approximately 50-100 km southwest of Miami, Florida, USA. Site locations, detailed soil chemistry, and seedling growth characteristics were previously described in Chapter two.

In summary (Table 2.1a), the Little Shark River closed canopy site (LSR-C) is characterized by low light transmission compared to the Little Shark River open canopy site (LSR-O) in an adjacent 25 m diameter gap. These adjacent LSR sites are primarily contrasted by light availability, having relatively high total soil and porewater nutrients, and low N:P ratios (Table 2.1a). The Broad River site that was impacted by Hurricane Andrew in 1992 (BR-O) and a dwarf mangrove (< 1m) site in the southeast Everglades (SEEM-O) are both open canopied sites with daily median light levels of approximately $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 2.1). The BR-O and SEEM-O sites are contrasted by their high and low soil phosphorus levels, respectively (Table 2.1a). Total soil and porewater nutrients inter-site differences are most notable in the N:P ratios (Table 2.1a). These ratios are at least one to two orders-of-magnitude higher at the SEEM site relative to the BR-O site.

Growth rates of *R. mangle* in four seedling size classes were determined at the same four sites from August to January in 1994 (Chapter 1; Table 2.1b). Growth rates were three-fold higher in the LSR gap relative to growth rates found under the canopy. Seedling growth rates were greatest in the high nutrient, hurricane disturbed, BR-O site. In extreme contrast, growth rates in the dwarf mangrove forest at the SEEM-O site were more than ten-times lower than rates at

the BR-O site. Seedling growth rates from high and low light and high and low soil nutrient sites that were determined in Chapter 1 (Table 2.1b) are related to C-fixation rates and photosynthetic biomass partitioning patterns in this Chapter.

Photosynthesis measurements

At each of the four sites, three *R. mangle* individuals in the four height classes (Table 2.1b) were randomly selected for photosynthetic measurements. Data were taken over consecutive cloudless days in May 1995. The second leaf pair below the main shoot apex were measured from 1000 to 1700 at 1- to 1.5-hr intervals. Photosynthetic rates were determined using an ADC-LCA3 open system infrared (4.26 μm band) CO_2 analyzer (Analytical Development Co., Herts, UK).

The open system 12 cm^2 leaf chamber was clamped onto each leaf until inlet and outlet CO_2 stabilized, approximately 10-30 sec. Photosynthetic rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, A) were calculated based on the flow rate, changes in CO_2 (ppm), and the water vapor of air passing through the chamber according to the following formula:

$$A = W \{ C_{\text{in}} - [C_{\text{out}}(P - e_{\text{in}})/(P - e_{\text{out}})] \} \quad [3.1]$$

where W is mass flow dry air per unit leaf area ($\text{mol m}^{-2} \text{ s}^{-1}$), e is vapor pressure water in air, P is atmospheric pressure (bar), and C is corrected CO_2 concentration for moisture, temperature, and pressure of cuvette air (μbar). Cuvette temperature ($^{\circ}\text{C}$) and the photosynthetic photon flux density incident on the cuvette (PPFD $\mu\text{mol m}^{-2} \text{ s}^{-1}$) were also recorded with each measurement.

Plant structural metrics and biomass partitioning

Ten replicate plants within the four size classes were harvested from each site. The number of primary, secondary, and tertiary branches were counted and their associated leaf numbers recorded, in addition to main stem leaves. Plant tissues were washed and separated into photosynthetic (leaf) and non-photosynthetic (stem + branches) components and dried (65°C) to constant weight before final weighing. Leaf areas were determined using a LI-COR LI-3000A area meter and LI-3050A belt conveyor. Leaf area-to-weight relationships were established for each site.

Statistical analyses

Plant biomass and metric data were assessed for normal distributions (Kolmogorov-Smirnov Test) and equality of variances (Bartlett Chi-square test). Although these data fit normal distributions, nonparametric tests were used because of non-homogeneous variances among means. The Mann-Whitney U test was applied to compare plant metrics (leaf number) and biomass (leaf and stem weight and ratios) between sites, and the Kruskal-Wallis and normal distributions with the Z statistic were used for among site comparisons. Photosynthetic rates were also compared among sites using nonparametric tests because of non-homogeneous variances among means. A nonlinear saturation model (StatSoft 1994) was applied to describe the photosynthesis-irradiance (PI) relationship:

$$P = b_0 - b_0/[1+(I/K)b_1] \quad [3.2]$$

where P is photosynthesis, I is irradiance, b_0 is Y at saturation, b_1 is the slope, and K is the half saturation constant. A nonlinear least squares estimation procedure was used to estimate the parameters of the saturation model (StatSoft 1994). The Marquardt algorithm was used to approximate the second-order derivatives of the least square function to select the best fitting parameter estimates (Marquardt 1963). All mean comparison and regression analyses were calculated using STATISTICA 4.1.

RESULTS

Photosynthesis

Even under conditions of light saturation, *R. mangle* leaves attained variable photosynthetic rates among sites with contrasting light and soil nutrients (Fig. 3.1, Table 2.2). Photosynthetic rates at light saturation were greatest at the high nutrient BR-O site. At this site, light levels that saturated photosynthesis were also high, $918 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 2.2). At the SEEM low nutrient site, photosynthetic rates followed a normal distribution and peaked at the mean photosynthetic rate of $5.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 2.1, Table 2.3). However, a PI curve could not be established from daily measurements of light and photosynthesis at this site. Light levels remained high throughout the afternoon because low stature forests did not promote shading. Average photosynthetic rates measured at the SEEM site were significantly lower than both average and saturation rates found at the BR-O site (Table 2.3). In addition, maximum photosynthetic rates were 20% higher at the BR-O compared to the SEEM-O site (Fig. 2.1).

Light levels were greater than $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ at both high and low nutrient sites and the LSR open canopy site (Table 2.3). In contrast, average and median light levels were less than 500 and $250 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, in the LSR closed canopy site (Table 2.1a, Table 2.3). These low light levels suppressed average daily photosynthetic rates in the LSR closed canopy site 64% relative to the adjacent gap (Table 2.3). The majority of photosynthetic measurements under the LSR canopy were taken at low irradiances (Fig. 2.1). When leaves under the canopy became exposed to sun flecks, as indicated by high light, photosynthetic rates remained low relative to photosynthetic rates under high irradiances in the gap (Fig. 2.1). As a consequence, average photosynthetic rates above light saturation (Table 2.3) were found to be significantly higher in the gap than under the canopy. Furthermore, the incremental response of photosynthesis to increased light in the LSR-C site resulted in a 50% higher light saturation level under the canopy relative to the adjacent gap (Table 2.2).

The closed canopy LSR site had significantly lower photosynthetic rates than all other sites with either high or low nutrients, based on daily averages or average rates at saturation (Table 2.3). In open canopied sites, average photosynthetic rates at saturation differed significantly among sites (Table 2.3) and decreased (BR-O > LSR-O > SEEM-O) along a soil P gradient (Table 2.1a). Ranked (Kruskal-Wallis test) comparisons of daily photosynthetic rates among sites found the SEEM-O site to be significantly greater than all other sites, resulting from high daily light availability (Fig. 2.1). Thus, although the dwarf mangrove forests have lower photosynthetic rates at saturation, high light availability over the entire day may compensate for low rates of C fixation at the leaf scale. Photosynthetic rates have been considered from the individual leaf scale, whereas photosynthetic to non-photosynthetic biomass allocation patterns need to be considered to relate total C-fixation rates to plant growth.

Structural metrics and Biomass partitioning

The BR-O high nutrient site exhibited not only the highest photosynthetic rates at light saturation, but also possessed the greatest number of leaves, the maximum number of branches, and a greater proportionment of above-ground tissue into photosynthetic biomass (Table 2.4). Conversely, the SEEM-O low nutrient site had six- to eleven-times lower leaf biomass and leaf area relative to the BR-O site (Table 2.4). Seedlings at the BR-O site developed a high degree of structural complexity, averaging 14 primary and 11 secondary branches from 35 and 18 individuals, respectively, including all size classes (Table 2.4). In contrast, plants from the SEEM-O site showed no primary or secondary branching in the first two size classes and half the number of branches found at the BR-O site in the upper two size classes. Although significant differences were found between the BR-O and SEEM-O sites for all branching and leaf parameters, stem biomass was not significantly different between sites for any of the four size classes (Table 2.4). Leaf biomass was close to unity with nonphotosynthetic tissues at the high

nutrient BR-O site (Fig. 2.2). At the SEEM-O low nutrient site, however, biomass allocation to leaves was consistently limited to 12-13% of the total above-ground biomass across all size classes (Fig. 2.2). Therefore, the BR-O site had significantly greater photosynthetic to nonphotosynthetic biomass ratios than SEEM-O in all size classes.

Under high nutrients in LSR, open and closed canopied sites showed no significant differences in structural metrics and biomass partitioning patterns in the first seedling size class (Table 2.4). In the second size class, stem weight was higher under the canopy and photosynthetic to nonphotosynthetic biomass ratios were significantly greater in the gap relative to under the canopy in the third size class (Fig. 2.2). Finally, in size class four, leaf numbers and biomass were significantly greater in the gap relative to the adjacent canopied site. Although leaf numbers and biomass were greater in the gap at LSR, the number of branches was similar (Table 2.4). In the upper size class photosynthetic to nonphotosynthetic biomass ratios were close to 50% in LSR gap, two-times the proportion allocated to leaves under the canopy (Fig. 2.2). A general trend was found across size classes in open and closed canopied sites at LSR: leaf partitioning increased with plant height in the gap, while under the canopy, leaf biomass increased initially but subsequently decreased with increasing size (Fig. 2.2).

Trends in leaf to stem biomass allocation patterns with increasing size class observed in LSR sites are in contrast to consistent biomass ratios among size classes in the BR-O and SEEM-O sites (Fig. 2.2). The BR-O site had significantly greater leaf biomass in all size classes relative to all other sites. Seedlings at this site may be partitioning the maximum amount of biomass to photosynthetic tissues. Allocation of photosynthate to leaf biomass was at a minimum in the SEEM-O site compared among sites. The differences in leaf to stem biomass allocation ratios among sites is primarily a function of increasing leaf biomass relative to stems with increasing plant height. In the case of the SEEM-O site, stem biomass did not differ from the BR-O site in any size class, however, seedlings did not maintain leaf production compared to the BR-O site. Similarly, the LSR canopied site increased stem mass relative to maintaining leaf biomass. Biomass partitioning to photosynthetic tissues is critical in the early stages of development because an exponential relationship exists between the percentage of leaves in one size class with those in the next growth phase (Fig. 2.3). In other words, leaf production in younger individuals may affect the plant's ability to develop additional photosynthetic tissue because a strong positive feedback exists in leaf allocation among size classes during development. The importance of maintaining leaf biomass is examined further through an estimation of total plant C-fixation and how C-production is related to seedling growth rates.

Integrating leaf-scale daily photosynthetic rates with total leaf area (Table 2.4), whole plant C-fixation rates were estimated. Plant C-fixation rates determined in this study were then related to previously measured plant growth rates at these same sites and size classes (Table 2.1b, Chapter 1). Two major findings emerge from comparing whole plant C-fixation rates to growth rates (Fig. 2.4). First, seedling growth rates along the South Florida west coast in both open and closed canopies are highly correlated to whole plant C-fixation rates ($r^2 = 0.95$, $P < 0.01$). If size class one is omitted from the correlation, perhaps eliminating propagule carbohydrate dependency, the linear fit increases, $r^2 = 0.98$. Note that stem elongation rates are greater than expected from C-fixation rates in size class one for all three open canopy sites, including the southeast Everglades. The second major finding was that growth rates based on C-assimilation were extremely low in individuals from the southeast Everglades. Individuals from this site did not follow the same trend as west coast plants (Fig. 2.4 insert). For example, the slope of the linear trend in growth as a function of whole plant C-fixation rates is an order-of-magnitude less in the SEEM-O site relative to all three sites in ENP. Normalizing for non-photosynthetic above-ground biomass did not improve the relationship between growth and C assimilation rates at any of the sites and accounting for below-ground biomass and respiration was not within the scope of the present study.

DISCUSSION

As evidenced in this study, *R. mangle* seedlings are shade-intolerant and require high light for photosynthetic saturation and allocation of maximum biomass to leaf tissue, both of which control seedling growth. Solar radiation in closed canopy forests in ENP and those reported for Australian mangrove forests, 100 to 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$, (Smith 1987b) are well below light levels 542-1028 $\mu\text{mol m}^{-2} \text{s}^{-1}$ estimated to saturate photosynthesis in *R. mangle*. Light levels of approximately 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ saturated carbon assimilation rates in adult leaves throughout a canopy in Australia (Clough and Sim, unpublished data in Clough and Sim 1989), which is within the range found for *R. mangle* in this study. In a separate field study of Australian mangroves, light saturated photosynthesis occurred between 600 and 750 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in *Bruguiera paviflora* for top of the canopy leaves (Cheeseman et al. 1991). Based on these data, it is concluded that high light saturation is important for maximum photosynthetic rates. However, intense solar radiation can be deleterious to C-fixation in tropical and subtropical climates (Ball et al. 1988).

Physiological studies have emphasized the importance of shade and low leaf temperatures ($< 30^\circ\text{C}$) in optimizing photosynthesis (Ball et al. 1988), particularly in high saline environments. Hypersaline and xeric conditions have been shown to decrease stomatal conductance (Clough and Sim 1989), negating the cooling effects of evaporative processes. Although shade may be important in hypersaline conditions, light gaps, intrinsically associated with high light and high temperatures in warm tropical and subtropical climates, are necessary for mangrove seedling development into a sapling stage (Smith 1987b, Jimenez 1988, Clarke and Allaway 1993, Ellison and Farnsworth 1993). Low soil salinities in ENP and the southeast Everglades sites (0-27 ppt, Chapter 1) may account for maximum photosynthetic rates at high field irradiances.

Evidently, light flecks recorded as saturated irradiances were ephemeral and low light conditions suppressed C-assimilation rates in the LSR closed canopy site. In contrast, under high light and high nutrient availability at the BR-O site, seedlings elicited high photosynthetic rates at light saturation. Phosphorus availability has been shown to promote greater photosynthetic capacity at the cellular level through influences on photo-phosphorylation and chloroplast lamellae development (Wong et al. 1979). Thus, soil nutrients may have facilitated the ranking of average photosynthetic rates at light saturation among open canopied sites (BR-O > LSR-O > SEEM-O) along a soil nutrient gradient. Although nutrients influenced average photosynthetic rates at saturation, light levels below saturation accounted for the greatest differences in average daily and saturated photosynthetic rates among sites.

Light gaps and open canopies not only accounted for high photosynthetic rates in *R. mangle*, but shifted biomass allocation patterns to leaf production. This biomass allocation strategy is contrary to shade-adapted species (King 1991), furthering the supposition that *R. mangle* is shade intolerant (Smith 1987b, Jimenez 1988, Ellison and Farnsworth 1993). Canopy gaps artificially created by Ellison and Farnsworth (1993) in Belize also stimulated *R. mangle* leaf biomass allocation. Earlier work by the author showed *R. mangle* net leaf production rates (leafing rates minus leaf fall) to be high in all four size classes in BR-O, increasing with size at LSR-O, and declining with size in LSR-C (Chapter 1). Biomass allocation patterns found in this study and earlier findings on net leaf production rates reiterate the importance of light availability for leaf allocation in *R. mangle*. The 1:1 ratio in photosynthetic to non-photosynthetic biomass in LSR-O was reduced 50% under the canopy with a disproportionate increase in stem mass over time. A shift to non-photosynthetic biomass would increase the respiration:photosynthesis ratio, and may contribute to slow growth (Chapter 1) and high mortality rates (Rabinowitz 1978b) of seedlings under closed canopied forests.

Although the SEEM-O site was exposed to high light, maintaining light saturated photosynthetic rates from 10:00 to 17:00, minimal biomass was allocated to photosynthetic tissues at this site. Non-photosynthetic tissue represented 86% to 88% of the total above-ground biomass at the southeast Everglades site across all size classes. Low nutrient availability at this site may

have inhibited the development of foliar tissue, in contrast to the BR-O site. High P retranslocation rates and nutrient use efficiencies have been reported for South Florida dwarf *R. mangle* forests compared to *Rhizophora* spp. from a wide geographic area (Snedaker and Brown 1981, Lugo 1990). In addition, a direct correlation was found between soil P and *R. mangle* seedling growth among southwest and southeast Everglades sites ($r = 0.97$, $P < 0.05$, Chapter 1). These data lend evidence to the hypothesis that P limitation may be an important factor restricting foliar development. Although leaf partitioning of photosynthate may be restricted as a result of nutrient limitation, stem elongation rates are slow in the southeast Everglades based on the relationship between whole plant C-fixation rates and stem growth in west coast sites.

One hypothesis to explain growth responses to C-fixation between sites, is that C being fixed at the SEEM-O site is lost through greater respiration rates relative to the west coast sites. An alternative hypothesis is that growth inhibition is the result of hormonal control, regardless of C-assimilation rates. Root-to-shoot ratios in the SEEM-O site increased from 47% in the 25-40 cm size class to 88% at 40-55 cm height (Koch in prep.), suggesting greater biomass allocation to roots over time and/or an inhibition of shoot development. Under conditions of low soil nutrients, extensive root versus leaf and above-ground biomass allocation can result in a substantial C-loss to the plant (Chapin et al 1987). However, the dwarf form persists at the marsh-mangrove ecotone with low *R. mangle* root biomass in response to macrophyte competition (Koch in prep.); additionally, mangroves characteristically allocate a large percentage of biomass to below-ground tissues (Lugo et al. 1988).

Rhizophora mangle biomass partitioning in the southeast Everglades may also be the phenotypic expression of physiological stress resulting from soil reducing conditions, in addition to P limitation. In wetland plants, flooding stimulates hormone production, that can adversely influence shoot growth by suppressing internode elongation, leaf development, leaf expansion, and induce leaf abscission (Kozlowski 1984). When plants are subject to persistent flooding, hormones that inhibit stem elongation such as ethylene increase, while those that promote growth decline (Reid and Bradford 1984). Chronic root hypoxia also induces anaerobic root metabolism, thereby lowering root energy status or ATP production and accelerate glucose consumption, creating an additional C-drain (McKee and Mendelssohn 1987). This reduction in metabolic energy production in the roots can further effect the problem of nutrient uptake, an energy requiring process.

Conclusion

Maximum light-saturated photosynthetic rates in *R. mangle* seedlings are dependent on both high light and high nutrient resource availability. Canopy gaps, although associated with high temperatures in the subtropics, promote maximum daily C-fixation rates relative to adjacent canopied forests. Low light under canopied forests, limit both photosynthetic rates at light saturation and average daily C-fixation rates. The inability of *R. mangle* under a closed canopy to allocate greater biomass to photosynthetic tissues to compensate for low C-fixation rates, identifies this species as shade-intolerant. Open canopy gaps are also necessary to promote maximum allocation of biomass to foliar tissue. Low nutrients may limit the allocation of photosynthate to leaf production, creating a negative feedback on further foliar development and C-fixation. Limited biomass allocation to leaves under low nutrient conditions, minimizes whole-plant C-fixation rates, even under high irradiances. Leaf area development and C-fixation rates in response to resource availability determine *R. mangle* seedling growth rates and development into the sapling stage in southwest Florida. However, further study is needed to reconcile limited growth in response to C-production in the dwarf mangrove forests of the southeast Everglades.

Table 2.1a. Summary data for sites with variable light (LSR-O and LSR-C) and nutrients (BR-O and SEEM-O): light, total soil phosphorus (TP, $\mu\text{g cm}^{-3}$), total soil nitrogen (TN, mg cm^{-3}), TN:TP mass ratios, and porewater (μM) N, P, and total inorganic Ni:Pi molar ratios. Median (n); means $\pm$ SE.

Sites	Light ^a	Nutrients ^{b,c,d}						
	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Total Soil			Porewater			
		TP	TN	TN:TP	SRP	NH_4^+	NO_3^-	Ni:Pi
LSR-O	1115 (141)	339 $\pm$ 24	2.5 $\pm$ 0.2	7 $\pm$ <1	13.4 $\pm$ 2.4	9.0 $\pm$ 3.1	7.1 $\pm$ 2.6	1 $\pm$ <1
LSR-C	246 (89)	-	-	-	14.5 $\pm$ 1.1	1.5 $\pm$ 0.2	1.5 $\pm$ 0.1	<1 $\pm$ <1
BR-O	1196 (116)	459 $\pm$ 17	2.6 $\pm$ 0.1	6 $\pm$ <1	3.0 $\pm$ 0.6	4.2 $\pm$ 0.6	2.5 $\pm$ 0.5	2 $\pm$ <1
SEEM-O	1239 (119)	22 $\pm$ 4	2.3 $\pm$ <0.1	108 $\pm$ 18	0.2 $\pm$ 0.1	50.3 $\pm$ 17.3	0.6 $\pm$ 0.1	258 $\pm$ 20

^aMedian daily light 1000 to 1700 hrs, this study.

^cSoil nutrient data, 10-30 cm depth, n=2.

^bPorewater from 4 replicate plots, 40 cm depth.

^dSoil nutrients sampled between LSR-O and LSR-C.

Table 2.1b. Summary data for *Rhizophora mangle* seedling growth rates (mm d^{-1}) at variable light (LSR-O and LSR-C) and nutrient (BR-O and SEEM-O) sites. Means $\pm$ SE (n=8).

Sites	Seedling height classes (cm)			
	(25-40)	(>40-55)	(>55-70)	(>70-85)
LSR-O	0.61 $\pm$ 0.09	0.30 $\pm$ 0.05	0.94 $\pm$ 0.14	1.89 $\pm$ 0.18
LSR-C	0.16 $\pm$ 0.04	0.23 $\pm$ 0.05	0.47 $\pm$ 0.14	0.40 $\pm$ 0.07
BR-O	1.21 $\pm$ 0.14	1.39 $\pm$ 0.13	2.01 $\pm$ 0.16	3.08 $\pm$ 0.25
SEEM-O	0.04 $\pm$ 0.01	0.03 $\pm$ 0.01	0.04 $\pm$ 0.01	0.05 $\pm$ <0.01

Table 2.2. Saturation model (eq. 3.2) parameters: b_0 is the photosynthetic rate at saturation, b_1 is the slope, and K is the half saturation constant. Data presented in Figure 3.1. Broad River open canopy (BR-O), Southeast Everglades open canopy (SEEM), Little Shark River open (LSR-O) and closed (LSR-C) canopy sites.

Site	b_0	b_1	K	n
BR-O	9.16	1.76	459	116
SEEM-O	-	-	-	-
LSR-O	6.56	2.41	271	141
LSR-C	5.67	1.39	514	89

Table 2.3. *Rhizophora mangle* average photosynthetic rates (A) above light saturation (K*2, Table 3.2) and daily averages. Cuvette temperature (T_{cuv}) and light (PPFD) data are also presented. Data are shown for Broad River (BR-O), Little Shark River open canopy gap (LSR-O), Little Shark River closed canopy (LSR-C), and Southeast Everglades site (SEEM-O). Means $\pm$ SE.

Site	n	T_{cuv}	PPFD	A
		$^{\circ}\text{C}$	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
<i>Light saturation</i>				
BR-O	75	39±0.2	1306±16	7.84±0.22
SEEM-O	118	37±0.1	1179±21	5.45±0.13
LSR-O	119	37±0.2	1139±23	6.30±0.18
LSR-C	11	34±0.2	1285±46	4.55±0.28
<i>Daily average</i>				
BR-O	116	39±0.2	1020±39	6.72±0.25
SEEM-O	119	37±0.1	1172±22	5.45±0.13
LSR-O	141	37±0.2	1009±32	5.87±0.18
LSR-C	89	33±0.1	458±42	2.14±0.18

Table 2.4. *Rhizophora mangle* structural metrics and biomass partitioning between photosynthetic (leaf) and non-photosynthetic (stem + branch) tissue in four height (cm) classes (25-40, >40-55, >55-70, and >70-85, respectively) from Broad River high nutrient site (BR-O), southeast Everglades low nutrient site (SEEM-O), high light open canopy Little Shark River site (LSR-O), and low light canopied Little Shark River site (LSR-C). Mean values are given with $\pm$ standard errors. Number of individuals possessing primary and secondary branches used to calculate mean leaf and branch numbers are shown in parentheses. Values presented without parentheses represent $n = 10$.

Site	Size Class	Number of leaves/branch				Number of branches		Biomass (g dry wt)		Leaf area (cm ² /plant)
		Main stem	1 ^o Branch	2 ^o Branch	Total	1 ^o Branch	2 ^o Branch	Leaf	Stem	
BR-O	1	9 $\pm$ 0.7	9 $\pm$ 2.9 (6)	0	14 $\pm$ 2.2	2 $\pm$ 0.2 (6)	0	6.7 $\pm$ 1.2	7.0 $\pm$ 0.9	5.2
	2	10 $\pm$ 0.5	24 $\pm$ 3.8 (9)	5 $\pm$ 1.5 (2)	33 $\pm$ 4.5	3 $\pm$ 0.5 (9)	2 $\pm$ 0.5 (2)	18.6 $\pm$ 2.6	17.2 $\pm$ 2.0	12.8
	3	10 $\pm$ 0.5	33 $\pm$ 4.0 (10)	17 $\pm$ 8.1 (6)	53 $\pm$ 8.8	4 $\pm$ 0.4 (10)	3 $\pm$ 1.1 (6)	28.2 $\pm$ 3.0	28.2 $\pm$ 2.4	19.0
	4	11 $\pm$ 0.6	40 $\pm$ 3.4 (10)	31 $\pm$ 8.8 (10)	81 $\pm$ 10.5	5 $\pm$ 0.4 (10)	6 $\pm$ 1.2 (10)	49.3 $\pm$ 6.8	47.0 $\pm$ 6.6	32.5
SEEM-O	1	5 $\pm$ 0.5	0	0	5 $\pm$ 0.5	0	0	0.8 $\pm$ 0.1	6.6 $\pm$ 0.6	0.7
	2	6 $\pm$ 0.5	0	0	6 $\pm$ 0.5	0	0	2.0 $\pm$ 0.3	16.2 $\pm$ 1.8	1.2
	3	7 $\pm$ 0.5	7 $\pm$ 1.1 (6)	11 (1)	12 $\pm$ 2.0	2 $\pm$ 0.4 (7)	2 (1)	4.1 $\pm$ 0.7	30.2 $\pm$ 2.7	2.1
	4	8 $\pm$ 0.5	13 $\pm$ 2.6 (6)	18 $\pm$ 6.9 (3)	21 $\pm$ 5.8	2 $\pm$ 0.4 (7)	3 $\pm$ 0.4 (4)	8.6 $\pm$ 2.7	61.8 $\pm$ 8.0	4.0
LSR-O	1	6 $\pm$ 0.6	2 (1)	0	6 $\pm$ 0.5	1 (1)	0	1.7 $\pm$ 0.4	4.3 $\pm$ 0.7	1.7
	2	9 $\pm$ 0.6	9 $\pm$ 1.0(2)	0	11 $\pm$ 1.6	2 $\pm$ 0.5 (2)	0	6.0 $\pm$ 0.9	7.8 $\pm$ 0.7	4.1
	3	10 $\pm$ 0.2	17 $\pm$ 2.6(9)	0	25 $\pm$ 2.9	2 $\pm$ 0.4 (9)	0	14.1 $\pm$ 1.8	16.0 $\pm$ 1.6	8.7
	4	11 $\pm$ 0.5	32 $\pm$ 2.7(10)	14 $\pm$ 3.5 (6)	51 $\pm$ 5.3	4 $\pm$ 0.4 (10)	2 $\pm$ 0.3 (6)	33.3 $\pm$ 3.9	34.5 $\pm$ 3.6	19.4
LSR-C	1	7 $\pm$ 0.5	0	0	7 $\pm$ 0.5	0	0	2.7 $\pm$ 0.6	5.6 $\pm$ 0.6	2.6
	2	8 $\pm$ 0.6	7 $\pm$ 1.5 (6)	0	13 $\pm$ 1.7	2 $\pm$ 0.2 (6)	0	5.7 $\pm$ 0.6	10.6 $\pm$ 1.1	4.5
	3	8 $\pm$ 0.6	16 $\pm$ 2.6 (8)	4 (1)	22 $\pm$ 3.3	2 $\pm$ 0.4 (10)	1 (1)	10.5 $\pm$ 1.5	23.5 $\pm$ 5.5	7.6
	4	7 $\pm$ 0.6	19 $\pm$ 2.5 (10)	17 $\pm$ 5.1 (6)	36 $\pm$ 4.7	4 $\pm$ 0.4 (10)	3 $\pm$ 0.8(6)	21.5 $\pm$ 3.4	51.3 $\pm$ 6.1	14.7

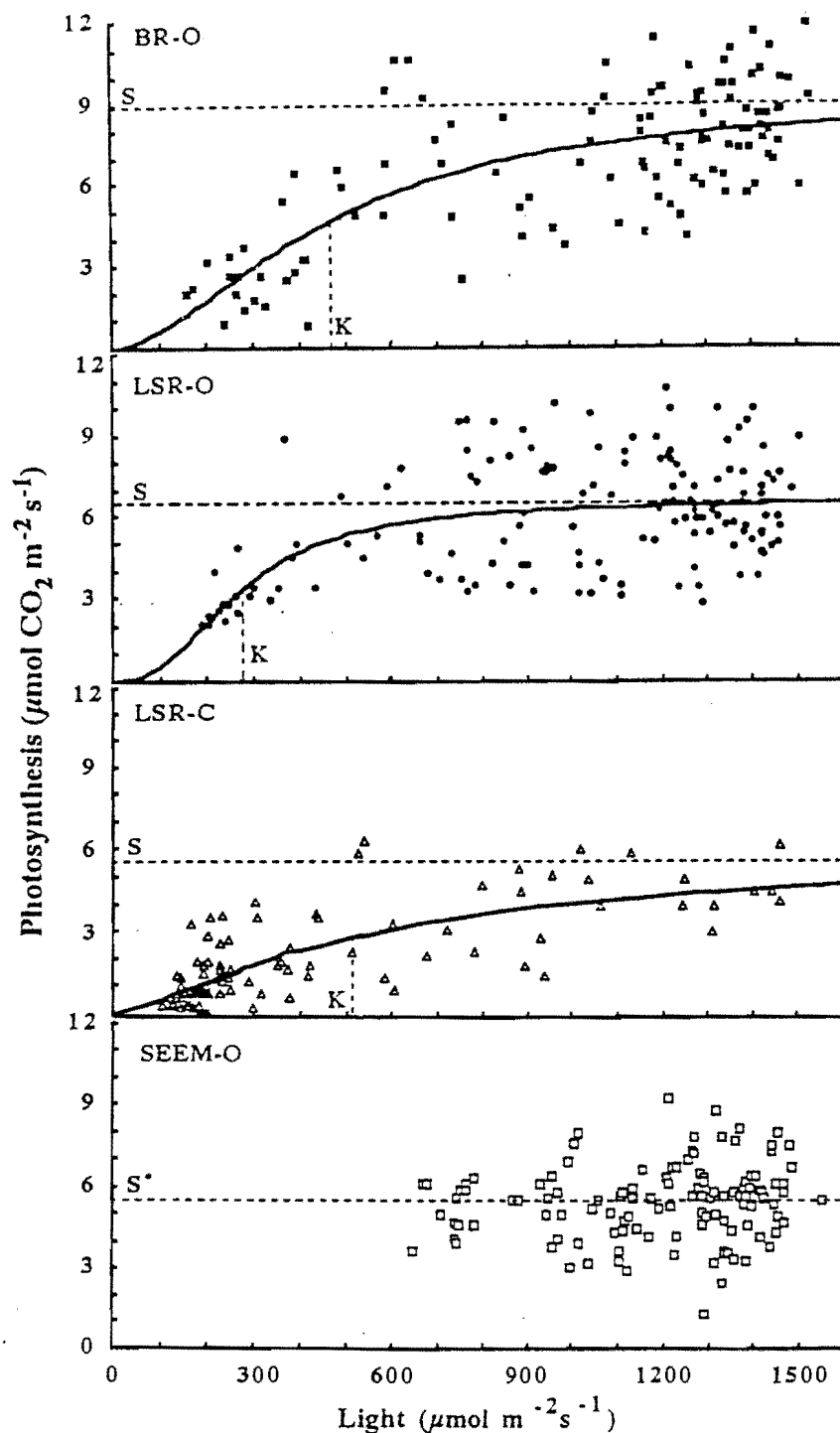


Figure 2.1. *Rhizophora mangle* seedling photosynthetic rates as a function of light (photosynthetic photon flux density; PPFD) in Everglades National Park sites: Broad River open canopy, BR-O; Little Shark River open canopy, LSR-O; Little Shark River closed canopy, LSR-C; and the southeast Everglades dwarf forest open canopy site, SEEM-O. A non-linear logarithmic function is presented with the expected photosynthetic rates at light saturation (S) and the half-saturation parameter (K).

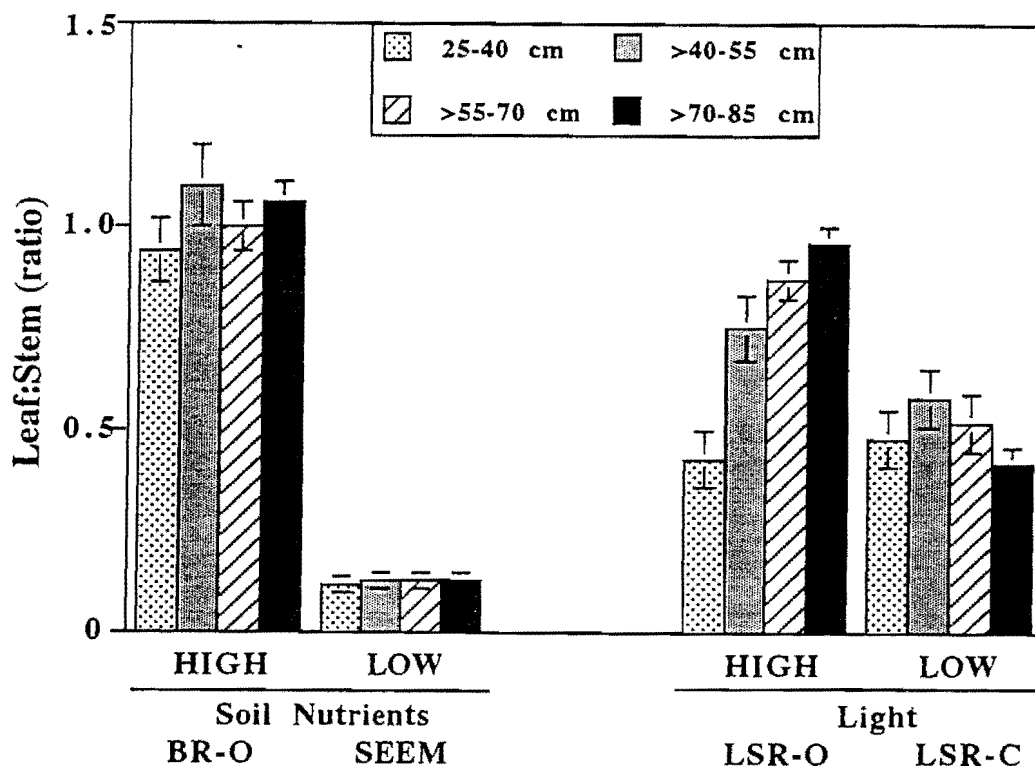


Figure 2.2. *Rhizophora mangle* photosynthetic (leaf) to non-photosynthetic (stem+branches) aboveground biomass (g dry wt) ratios at the high nutrient Broad River site (BR-O), low nutrient Southeast Everglades site (SEEM), high light Little Shark River gap site (LSR-O) and low light closed canopy Little Shark River site (LSR-C). Means shown with standard errors N=10.

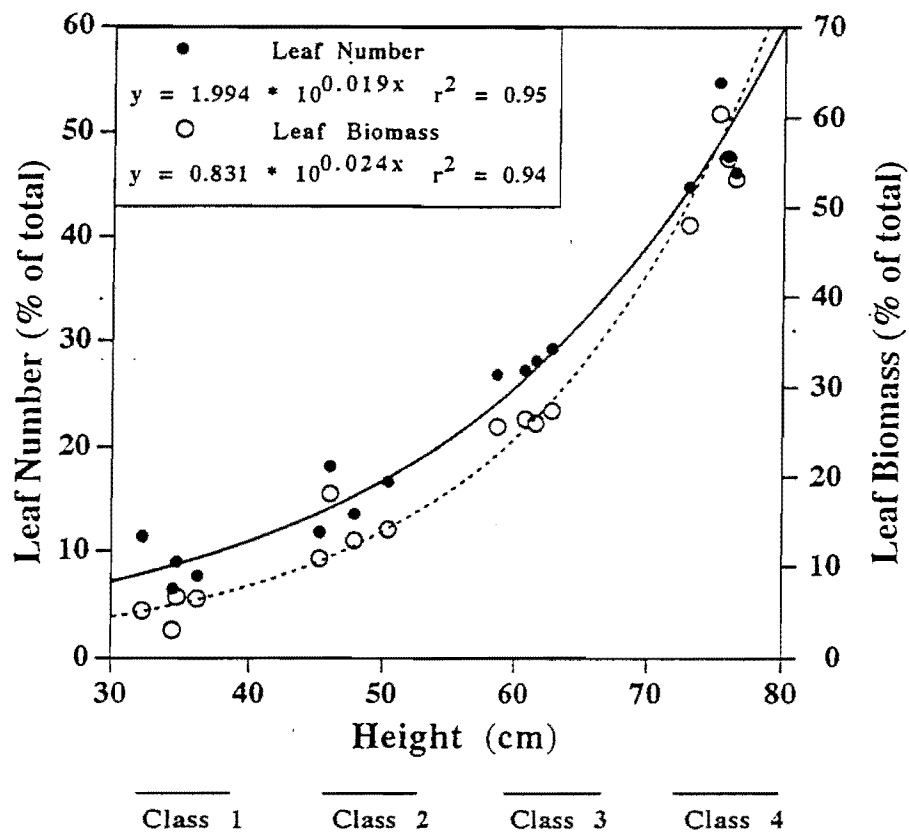


Figure 2.3. Exponential relationship between *Rhizophora mangle* plant height and the percentage of leaf numbers and leaf biomass for all four height classes combined. Percentages within each height class (25-40, >40-55, >55-70, and >70-85) are shown for all four sites.

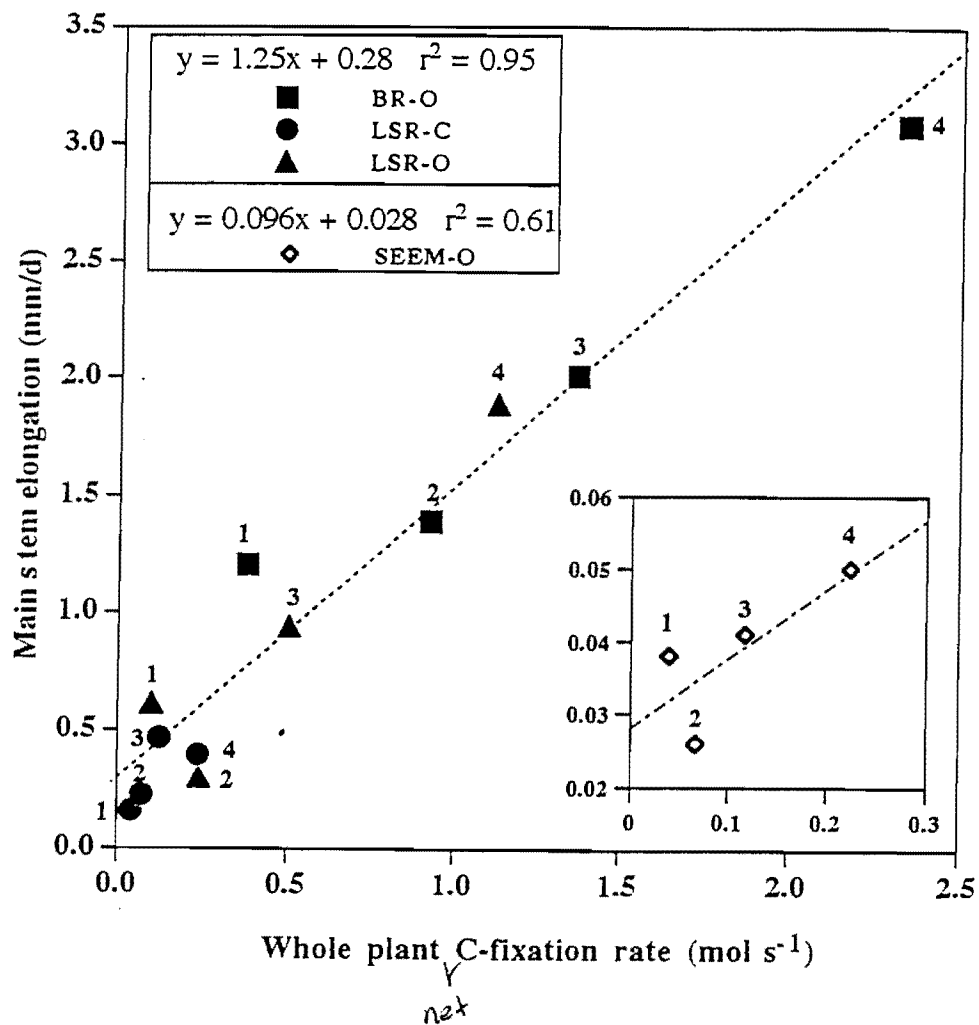


Figure 2.4. Stem elongation rates as a linear function of whole plant C-fixation rates in open and closed canopy sites in Everglades National Park and the southeast Everglades dwarf mangrove site (graph insert). Size classes are marked 1-4, see text for sizes.

CHAPTER 3

SOIL NITROGEN AND PHOSPHORUS AVAILABILITIES IN A MANGROVE LAND-MARGIN ECOSYSTEM

ABSTRACT

The spatial gradients of soil nitrogen (N) and phosphorus (P) mineralization rates, extractable N and P pools, and P fractionation were examined in a mangrove land-margin ecosystem along the Shark River estuary in the Everglades National Park. The mean tree height of mangrove forests linearly declined with distance from the mouth near the Gulf of Mexico to the oligohaline regions of the estuary. Mangrove forests along the estuary represented a landscape gradient of soil N and P availabilities. Higher amounts of extractable ammonium were found in the marine site of the estuary near the Gulf of Mexico. Mean rates of net ammonification and relative ammonification per unit of total N based on 45 d incubation periods decreased exponentially with distance from the estuary mouth to inland sites. N mineralization was positively correlated with total P and available P, but negatively with N:P ratio. Total P and available P increased from the oligohaline to marine sites. There was no net P mineralization in the marine sites based on 45 d incubation periods. Residual P was the largest P fraction in all soils and decreased from 70% in the oligohaline site to 45% in the marine site along the estuary. The percentage of Ca-bound-P increased from 3.3% at the oligohaline site to 32.3% at marine sites. Ca-bound-P pool was larger than Fe-Al-bound P pool in the marine sites, while the reverse was found in the mesohaline and oligohaline sites. The landscape gradient of P in the study area indicates that the Gulf of Mexico is the major source of P in this mangrove land-margin ecosystem rather than direct terrigenous input from inland watershed.

INTRODUCTION

Inputs from terrestrial runoff are generally considered the major nutrient source to support mangrove forest development (Lugo and Snedaker 1974, Day et al. 1987, Twilley 1995). This hypothesis predicts that nutrient availability in mangrove soils will decrease from the landward to seaward zones along the longitudinal axis of a tropical estuary (Carter et al. 1973, Odum et al. 1982, McIvor et al. 1994). The spatial gradient of nutrient availability is suggested as a critical determinant of plant community structure and development based on the inequality of resource utilization by plants along the gradient (Tilman 1982). Greenhouse experiments have demonstrated that seedlings of three Neotropical mangrove species differ significantly in their growth responses to the levels of nutrient availability (McKee 1995a). McKee (1995b) further showed that seedling recruitment patterns in mangrove forests were related to nutrient gradients. Nutrient enrichment experiments have revealed that the productivity and growth of mangrove forests in Florida (Onuf et al. 1977), Australia (Boto and Wellington 1983) and Belize (Feller 1995, Twilley 1995) can be limited by nutrient availability. These results suggest that studies of nutrient gradients along estuaries can provide valuable information on the effect of landscape patterns of soil nutrient availability on development of mangrove wetlands. However, little research has been performed on the spatial gradient of nutrient availability in a mangrove land-margin ecosystem along a tropical estuary.

Nitrogen (N) and phosphorus (P) availabilities are often implicated as the principal factors controlling forest stature and productivity of mangrove ecosystems (Lugo and Snedaker 1974, Boto and Wellington 1984, Lugo et al. 1988, Clough 1992, Twilley 1995). Soil N mineralization, the microbial transformation of organically combined N into inorganic forms, is an important determinant of N availability in mangrove wetlands. Soil remineralization can supply a major portion of the N required by plants for growth and reduce the requirement for new nutrients to

maintain high levels of productivity. N mineralization is generally used as an index of N availability in terrestrial ecosystems, which is strongly controlled by environmental factors (temperature and moisture), microbes, and substrate quality (Burke 1989, Binkley and Vitousek 1989, Nadelhoffer et al. 1991). Organic N content (Frank et al. 1994), C:N ratio (Wedin and Pastor 1993, Frank et al. 1994), P content (Pastor et al. 1984) and labile pool of mineralizable N (Wedin and Pastor 1993) in soils are recognized as potential factors controlling mineralization rates. In wetland ecosystems, these indices of substrate quality are a function of past and present hydrological processes and plant production (Lugo et al. 1988). Therefore, soil N mineralization in mangrove forests may change with the gradient of substrate quality along a tropical estuary.

Phosphorus availability depends on mineralization of organic matter and is constrained by inorganic chemical reactions (Binkley and Vitousek 1989). Although P has been found to be the primary nutrient limiting the development of mangrove forests (Boto and Wellington 1984, Feller 1995), P mineralization rates have not been measured in mangrove soils (Ellison and Farnsworth 1993). Mangrove soils contain a high proportion of organic P, but most of the organic P tends to be recalcitrant (Alongi et al. 1992). Moreover, most inorganic P is adsorbed and fixed by calcium, iron and aluminum minerals as different chemical forms in mangrove soils (Hesse 1962, 1963). Studies on P fractionation have indicated that the amount and proportion of P forms were related to the degree of weathering and soil development in a desert (Lajtha and Schlesinger 1988) and in Hawaiian islands (Crews et al. 1995). Hydrology is considered the single most important determinant of wetland processes such as soil deposition and erosion, and may determine the spatial gradients of P availability and P forms in mangrove soils along an estuary.

Vegetation can influence spatial patterns of soil nutrient availability by uptake of inorganic nutrients and return of organic materials to soil by litter fall (Pastor et al. 1984). The loss of biomass in canopy gaps may disrupt the spatial pattern of soil nutrient availability by reducing rates of uptake and increasing rates of decomposition and nutrient mineralization stored in living biomass (Canham and Marks 1985). Leaf fall and dead roots associated with canopy gaps caused by lightning strikes, storms and insect herbivory in mangrove forests (Jiménez et al. 1985, Smith 1992) result in a significant pulse of organic matter and associated nutrients to the forest floor and soil (Smith et al. 1994). These changes in nutrient pools and potential shifts in availability of nutrient resources can be important determinant of patterns and rates of mangrove forest regrowth (Clarke and Allaway 1993). Although considerable research has been conducted to measure the effect of enhanced light availability on the growth of mangrove seedlings in canopy gaps, relatively little information is available concerning soil nutrient availability in these disturbed patches of mangrove forest.

More than 60,000 ha of mangroves in southwest Florida including part of the Everglades National Park form one of the greatest land-margin mangroves in the Gulf of Mexico (Smith et al. 1994). The continuous distribution of mangrove forests in this broad coastal region represents an exceptional estuarine gradient, formed by the low energy mixing of fresh and salt water, to evaluate spatial gradients of soil N and P availabilities. I tested the hypotheses that the major N and P source is the direct input of terrestrial runoff in this estuary. I used this estuarine landscape gradient of mangrove forests to describe N and P availabilities by addressing the following questions: (1) Do N and P availabilities in mangrove soils decrease from the landward to seaward zones along the estuary? (2) Are there changes in the fractionation of P in mangrove soils along the estuarine gradient? (3) What is the relative effect of vegetation process in N and P availabilities along this estuarine landscape gradient?

MATERIALS AND METHODS

Study area

The study area was located in the Shark River estuary on the west coastal plain of the Everglades National Park (Fig. 3.1). Mangrove peats deposited over Miami Oolite formed in this

region about 3000 yrs ago, coinciding with the most recent rise in sea level at the mid to late Holocene epoch (Scholl 1964a, b). The Everglades area is topographically flat with an average gradient of 2.8 cm/km from the inland region to the coast (SFWMD 1992). Mangrove forests consisting of three mangrove species, *Rhizophora mangle* L., *Avicennia germinans* (L.) Stearn and *Laguncularia racemosa* (L.) Gaertn., form a continuous band and extend from the Gulf of Mexico to the upland limit of periodic salt water influence, a distance of about 10-20 km. *Conocarpus erecta* L. is also found in coastal forests where the salinity does not exceed 10 g/kg.

The Shark River is one of the largest coastal streams to carry freshwater from the upland Everglades region through the Shark River Slough to the Gulf of Mexico. Mangrove wetlands in this region receive most of the surface fresh water from the Everglades through this Slough. Depending on timing, duration, and magnitude of regional meteorological conditions, the velocity of sheet flow in the Shark River Slough may vary from zero to 480 m/d (SFWMD 1992). The present quantity and quality of water input to the Shark River Slough is modified by human land-use in northern part of the Everglades. Water delivery has been determined to be a function of rainfall, evaporation, and water level in the water conservation areas and the previous week's discharge (Light and Dineen 1994). Tides within the Everglades National Park are predominantly diurnal with a mean amplitude of 1.1 m (Provost 1973, Wang et al. 1994). Monthly sea levels are above the mean annual height from May to November in the Gulf Coast of Florida (Provost 1973). This results in highly seasonal tidal inundations of mangrove wetlands in southwestern Florida, with peak number of tides occurring in the forest from August to October (Twilley 1985).

Mean annual air temperature in the Everglades National Park is 24°C with little seasonal change (Thomas 1974, Duever et al. 1994). Mean monthly air temperatures range from a January low of 19°C, to a high in August of 28°C (Thomas 1974). Average annual precipitation in the Everglades National Park is 1320 mm with distinct wet and dry seasons (Thomas 1974). Precipitation in the wet season (June to September) is approximately 60% of annual precipitation, and is produced primarily by thunderstorms. About 25% of the annual precipitation falls during the dry season (November to April), which results from the passage of warm and cold air masses. Rainfall in May and October tends to be transitional.

Field sampling and vegetation measurement

Vegetation and soil properties were examined at four mangrove forests along a natural gradient of the Shark River estuary from the Gulf of Mexico to the inland mangrove-marsh ecotone (Fig. 3.1). The four sites ranged from 25°19'N, 81°08'W to 25°25'N, 80°58'W and are located about 1.4, 4.1, 9.9 and 18.2 km inland from the estuary mouth, respectively. These mangrove sites represent a salinity gradient from tide-dominated inundation near the estuary mouth to fresh water runoff from the Shark River Slough in the upstream region. According to Duke's (1992) classification of mangrove habitats and the terminology of Odum et al. (1984) for salinity zones of an estuary, S1 and S3 sites are downstream locations in marine zone of the Shark River estuary, while S4 is in an intermediate location in the mesohaline zone and S6 is an upstream location in the oligohaline zone (Fig. 3.2). Since mangrove forests in this region are recovering from destruction by Hurricane Donna in 1960 (Craighead and Gilbert 1962), mangrove forests at each site along the Shark River region are assumed approximately even aged.

A 20 x 20 m plot about 10 to 20 m inland from the estuary was established at sites S1, S3 and S4. A smaller plot (10 x 15 m) about five m from the estuary was set at S6, due to the restricted band of mangroves along the river in this upstream region. DBH (diameter at breast height) of all trees >2 cm was measured in each plot in January 1995. Fifteen to 20 trees were randomly chosen for measurement of tree height by range finder in each plot. The relationship between DBH and tree height was fitted by regression for each species. Mean tree height at each site was determined for all trees in each plot based on this regression.

To assess nutrient availability in surface soils without a canopy (less vegetation effect), a canopy gap less than 30 m from the intact forest plot in sites S1, S3, and S4 was used for

comparisons. The gap in S1 was apparently caused by a lightning strike, while the gaps in S3 and S4 were associated with storm-related treefall. The sizes of gaps in S1, S3 and S4 were 502 m², 48 m² and 37 m², respectively. The ages of gaps were estimated to be at about three yrs based on ages of seedlings under the gaps (Duke and Pinzón 1992).

Soil property determination

The timing of three sampling trips was based on seasonal climatic and hydrological regimes. January represents the dry season with low rainfall and fewer tidal inundations. August represents the wet season with high rainfall and high tidal flooding frequencies. May corresponds to a transient season between dry and wet seasons. Three randomly chosen stations in each intact forest plot and canopy gap were marked in August 1994 for repeated measures of soil properties and mineralization rates in August 1994, January and May 1995. Soils were collected with a 5.0 cm diameter corer at each site from surface to 40 cm depth. Soil samples at 10 cm interval were stored on ice in polyethylene bags in the field, and stored at 4°C in the laboratory prior to analysis. Recognizable plant litter and coarse root material were removed. Subsamples of soils were oven-dried to constant weight at 60°C and ground with a Wiley Mill to pass through a 250 µm mesh. Cores with a 15.2 cm diameter were used to estimate soil bulk density since the wider diameter eliminated compaction. Carbon (C) and N contents were determined on two replicates of each sample with a LECO CHN analyzer using standard protocols. Total P was extracted from soils with 1N hydrochloric acid after ignition at 550°C (Aspila et al. 1976) and determined using molybdenum blue, and ascorbic acid as reducing agents (Parsons et al. 1984). Extractable PO₄-P (P_{ext}) was determined by dilute acid-fluoride extraction of fresh soil samples (Olsen and Sommers 1982). The extract was analyzed colorimetrically for soluble reactive phosphorus. Amount of P extracted by this method is generally used as the available P index in plant ecology (Vitousek and Denslow 1986, Lajtha and Schlesinger 1988, Binkley and Vitousek 1989, Walbridge 1991).

N and P mineralization

Numerous techniques for measurements of soil mineralization have been developed, but no one method provides accurate estimates of N and P, thus all methods should be considered an index of nutrient availability for comparative purpose (Binkley and Vitousek 1989). The potential problems caused by field measures are that net mineralization may reflect treatment differences in microclimate rather than differences in the quality or quantity of soil organic matter (Wedin and Pastor 1993). Laboratory incubation can provide information on the amount of mineralizable N and P at the time of sampling. I used an anaerobic incubation of soil cores in the laboratory to determine net N and P mineralization. This allows a comparison of soil quality across a range of sites in the mangrove land-margin ecosystem under comparable conditions. Intact soil cores were collected in glass tubes to maintain soil structure, which can be an important factor that influences soil microbial activity (Robertson et al. 1988). Glass tubes (2.5 cm diameter and 10 cm length) were placed in a soil recovery probe and driven into the soil. The end of each tube was capped with a rubber sleeve immediately after collection to avoid aeration, and the tube was stored on ice in a cooler. Paired tube samples at each depth of 0-10 and 10-20 cm intervals were collected at each sampling station. After samples were transported to the laboratory, one tube from each pair was anaerobically incubated in the dark in an environmentally controlled chamber at 25°C for 15 d. The other tube was kept at 4 °C until extracted with 1 mol/L KCl within 7 d of collection.

Soils were extracted with 1 mol/L KCl (1:10 mass/volume). The extract was centrifuged and analyzed for NH₄-N by colorimetric method (Parsons et al. 1984), and for NO_x-N and PO₄-P with an ALPKEM autoanalyzer using standard techniques. Ammonium and nitrite+nitrate extracted from initial soils was treated as extractable ammonium (NH₄-N) and extractable nitrite+nitrate (NO_x-N), respectively. Rates of net nitrification, ammonification and P mineralization for each soil depth were determined by subtracting the initial concentration of

respective nutrients ($\text{NO}_x\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{PO}_4\text{-P}$) from concentrations at the end of the incubation period. Mineralization rates were converted to a soil area basis with respective bulk density values.

P fractionation

The sequential extraction scheme selected was developed by Hieltjes and Lijklema (1980) and a modification of P fractionation scheme has been successfully used to characterize P in Everglades wetland soils (Koch and Reddy 1992, Gale et al. 1994) and estuarine sediment (Zwolsman 1994). Soil samples for P fractionation were collected in August 1994. Fresh soil samples were sequentially extracted with 1 mol/L KCl (1:10 w/v) with 2 h of shaking at 250 rpm; 0.1 mol/L NaOH with 16 h of shaking; and 0.5 mol/L HCl with 24 h of shaking. After each step, the suspensions were centrifuged and the supernatants were analyzed colorimetrically for inorganic P (soluble reactive phosphate) using an ascorbic acid reduction method (Parsons et al. 1984). A subsample of the NaOH extract was digested by the Kjeldahl procedure (US EPA 1979) to determine total P in the extract. The portions of P in extractions with KCl, NaOH and HCl solution are defined respectively as: labile P, Fe-Al bound P, and Ca-bound P (Gale et al. 1994). Organic P determined as the difference between total P and inorganic P in the NaOH-extract is defined as hydrolyzable organic P. Residual P is the difference between the total P as determined by ignition-acid extraction method (Aspila et al. 1976) and the sum of P extracted.

Statistical analysis

My primary objectives were to compare substrate quality of mangrove soils along the longitudinal gradient of the Shark River estuary and to determine the effect of substrate quality on soil nutrient availability. I used linear regression models to test the dependencies of total soil C, N and P pools at four mangrove forests on distance from the mouth of the estuary. A repeated-measures ANOVA was used to analyze the effects of site and season on P_{ext} , $\text{NH}_4\text{-N}$, $\text{NO}_x\text{-N}$, ammonification and P mineralization in soils from intact forests. I also used one way ANOVA to test the effect of site on $\text{NH}_4\text{-N}$, $\text{NO}_x\text{-N}$ and P_{ext} pools, net N and P mineralization, and P fractionation at each sampling date. In these ANOVAs of soil parameters, I restricted the tests for the effects of site along the estuary to soils taken under intact mangrove forests. When a main effect was significant, tests based on the ANOVA model were used to make multiple comparisons of means using Tukey's test. I also used t-tests to look for the effect of vegetation (canopy gap vs. intact forest) on P fractions at each site and a repeated-measures ANOVA on other nutrient variables. All statistical tests were done by using either original data or log-transformed data in order to meet assumptions of parametric analysis. I used SAS (SAS 1989) to perform all statistical tests.

RESULTS

Tree height, salinity and soil nutrient content

Mean water salinity of three sampling days in Shark River estuary increased from 1.4 g/kg in S6 to 27.2 g/kg in S1 (Fig. 3.2). Mean tree height of the even-aged mangrove forests in the land-margin transition increased from 5.4 m at S6 to 10.1 m at S1 (Fig. 3.2). The correlations between salinity, tree height and distance from the mouth of the estuary were highly significant. Both total C and N concentrations in the top 40 cm of mangrove soils showed a significant linear decrease along the Shark River estuary from S6 (C=43.3%, N=2.33%) to S1 (C=14.3%, N=0.7%) (Table 3.1). However, P concentrations showed an inverse relation with distance from the estuary mouth, increasing from 0.06% in S6 to 0.11% in S1 (Table 3.1). When nutrient pools were expressed as mass per unit area, C and N pools were not correlated with distance along the estuary (Fig. 3.3). However, P pools exponentially increased from 26.3 g/m² in S6 to 152.2 g/m² in S1 along the estuary ($r^2=0.95$, $P<0.05$). The total P pool in mangrove soil was six times

greater in S1 than in S6 (Fig. 3.3). The consistent relation between C and N concentrations in these mangrove soils was reflected in atomic C:N ratios between 22:1 and 25:1 along the entire longitudinal axis of the estuary. Atomic N:P ratios exponentially increased with distance from the estuary mouth from 15:1 at S1 to 102:1 at S6 ($r^2=0.99$, $P<0.05$).

Soil N and P availabilities along the estuary

Extractable N and P pools. - The repeated measures ANOVA showed significant effects of site on the amount of $\text{NO}_x\text{-N}$ without showing season effects (Table 3.2). Multiple comparisons of means in each sampling season showed a significant site effect on $\text{NO}_x\text{-N}$ only for January (Fig. 3.4). Results of $\text{NH}_4\text{-N}$ and $\text{NO}_x\text{-N}$ extracted by KCl indicated that most of the inorganic N in these mangrove soils was dominated by $\text{NH}_4\text{-N}$ (Fig. 3.4). The repeated measures ANOVA showed significant effects of site and season on the amount of $\text{NH}_4\text{-N}$ with a significant interaction factor (Table 3.2). Amounts of $\text{NH}_4\text{-N}$ were generally high at S1 during all three sampling seasons (Fig. 3.4). Mean $\text{NH}_4\text{-N}$ pools within the 0-20 cm soil for three seasons increased significantly along the estuary at 0.35, 0.36, 0.55 and 0.97 g/m² from the oligohaline to marine sites (Fig. 3.5).

The repeated measures ANOVA showed significant effects of site and season on the amount of P_{ext} with a significant interaction factor (Table 3.2). This site difference for P_{ext} was more pronounced in January 1995 with less site differences in August 1994 (Fig. 3.4). The P_{ext} pool was significantly greater in S1 for all sampling dates, but not significantly different between S4 and S6 at August and May samplings (Fig. 3.4). Mean P_{ext} pools within the 0-20 cm soil for all three seasons were 1.60, 0.98, 0.48 and 0.42 g/m² in S1, S3, S4 and S6, respectively. Thus both P_{ext} and $\text{NH}_4\text{-N}$ pools exhibited an increase from the oligohaline to marine zones in this mangrove land-margin ecosystem (Fig. 3.5).

Nitrogen mineralization. - The production of $\text{NO}_3\text{-N}$ from the remineralized $\text{NH}_4\text{-N}$ in the soil incubations was negligible for all sites and seasons (data are not shown). Repeated ANOVA tests of ammonification indicated significant effects of site and sampling season with significant interactions (Table 3.2). Multiple comparisons of means in each sampling season revealed significant site effects only in January and May (Fig. 3.6). Net $\text{NH}_4\text{-N}$ production occurred in January and May, but net immobilization was found in August for all sites. Mean daily net ammonification rates within the 0-20 cm depth for three seasons decreased exponentially with distance from the downstream (182 mg·m⁻²·d⁻¹ in S1 and 135 mg·m⁻²·d⁻¹ in S3) to intermediate and upstream sites (46 mg·m⁻²·d⁻¹ in S4 and 17 mg·m⁻²·d⁻¹ in S6) (Fig. 3.5). Therefore soils in S1 can potentially supply more than 10 times the amount of $\text{NH}_4\text{-N}$ mineralized in S6.

P mineralization. - Net P mineralization rates measured as the difference in extractable P (by KCl) during an incubation period were more variable than N mineralization (Fig. 3.6). There was a significant effect of site in January with a significantly higher net P mineralization in S4 and S6 (Fig. 3.6). Repeated measures ANOVA showed that the season effect on P mineralization was significant (Table 3.2). Mean daily rates of net P mineralization averaged over the three seasons within the 0-20 cm soil were positive at S4 (4.78 mg·m⁻²·d⁻¹) and S6 (1.28 mg·m⁻²·d⁻¹), compared to negative values reflecting immobilization at S1 (-1.43 mg·m⁻²·d⁻¹) and S3 (-0.04 mg·m⁻²·d⁻¹).

P fractionation. - There were significant differences in absolute amounts of labile-P, Fe/Al-bound-P, hydrolyzable-organic-P, Ca-bound-P and residual P at 0-20 cm depths at sites along the estuary (Table 3.3). The amount of labile P was significantly higher in S1 than other sites and was not significantly different among S3, S4 and S6 (Table 3.3). Labile P never exceeded 2% of

the total amount of P among all sites within the 0-20 cm depth, and the percent of labile P was higher in S6 (1.9 %) than in S3 (0.7%) and S1 (0.8%) (Fig. 3.7).

Fe/Al-bound-P pools increased from S6 (1.24 g/m²) to S1 (5.58 g/m²) (Table 3.3). However, the percent of Fe/Al-bound-P in the total P ranged from 8.2% to 10.5% and did not exhibit a significant trend along the estuary (Fig. 3.7). The amount of hydrolyzable-organic-P ranged from 2.39 to 7.64 g/m² and was significantly higher in S1 and S3 than in S4 and S6 (Table 3.3). The highest percent of hydrolyzable-organic-P fraction of the total P was in S4 (21%), and this contribution was similar among S1, S3 and S6 (Fig. 3.7). Except in S1, hydrolyzable-organic-P was the second largest pool of P in these mangrove soils.

Ca-bound-P pools ranged from 0.50 to 21.33 g/m² and had the most significant increase from S6 to S1 in the estuary, which indicated there was 40 times more Ca-bound-P in S1 than in S6 (Table 3.3). The percentage of Ca-bound-P also increased significantly, from 3.3% in S6 to 32.6% in S1 (Fig. 3.7). Ca-bound-P pool was larger than Fe-Al-bound P pool in S1 and S3, while Fe-Al-bound P pool was larger than Ca-bound-P pool in S4 and S6. Residual P was the largest P fraction in all sites, with a significant increase in percentage from 45% in S1 to 70% in S6 along the estuary (Fig. 3.7). However, the amount of residual P increased significantly from S6 toward S1 (Table 3.3).

Soil N and P availabilities in canopy gaps and forests

The repeated ANOVA indicated a significant vegetation effect on P_{ext} with a mean of 1.31 g/m² in canopy gaps compared to 1.02 g/m² in the intact forests (Fig. 3.3, Table 3.4). The repeated ANOVA also showed there was a significant effect of vegetation and season with interaction factor for NO_x-N. Mean NO_x-N was 20.9 mg/m² in the intact forests compared to 12.4 mg/m² in the canopy gaps (Fig. 3.3, Table 3.4). There were no significant differences in NH₄-N, net ammonification and P mineralization rates between canopy gaps and forests. Paired comparisons revealed that there were no significant effects of vegetation on any of the P fractions in sites S1, S3 and S4 (Table 3.3).

DISCUSSION

The effect of vegetation on N and P availabilities

Amounts of extractable soil P, nitrate and nitrite were higher in canopy gaps than intact forests in this study. Vitousek and Denslow (1986) have reported that P availability was slightly higher in crown-fall zones than in intact forests of a lowland tropical rainforest. Mladenoff (1987) also found higher soil P concentrations in canopy gaps of a northern hardwood-hemlock forest and suggested that the higher P content in gaps was due to the reduced uptake of N. Loss of vegetation in gaps also may directly reduce the uptake of P by plants. Mangrove vegetation can transport oxygen through roots into soil and enhance soil redox potential (McKee 1993). Therefore oxidized soil may promote transformation of ammonium to nitrate+nitrite. Overall, canopy gaps had no effect on N and P mineralization (Table 3.4). The laboratory incubation method for mineralization in this study did not reflect the effects of environmental factors such as changes of temperature and moisture, which are influenced by absence of a forest canopy. These results only compare the effect of an absence of plant biomass on substrate quality. Although large scale disturbances such as hurricanes can dramatically increase the detrital pool in mangrove forest (Smith et al. 1994), the effect of small gaps on nutrient availability may depend on gap age, gap size and vegetation structure (Vitousek and Denslow 1986, Mladenoff 1987, Zhang and Zak 1995). The size of gaps in this study ranged from 37 to 502 m². In addition, tidal flooding in mangrove wetlands may reduce the gap effects on nutrient availability by redistributing detritus in mangrove forests.

Landscape trends and control of N availability

Total soil N (0.7 to 2.3%) in the mangrove land-margin ecosystem studied here is higher than global estimates of total N concentrations in mangrove soils, which range from 0.02 to 0.4% (Alongi et al. 1992). In contrast to soil P concentrations, soil N concentrations decreased from 2.3% at the oligohaline site to 0.7% at the marine site of the estuary. However, the soil N pool per unit area was fairly constant across this mangrove land-margin at about 1.0 kg/m² within 0-40 cm depth. The tendency of soil N concentrations along the estuary associated with total C concentrations suggests that there is an accumulation of recalcitrant organic matter that is resistant to decomposition. Walbridge (1991) suggested that soil organic N accumulates as soil P availability decreases in P-deficient systems. Two possible mechanisms may involve this biogeochemical process. P mineralization from organic matter is often the direct result of phosphatases produced by plants and microbes without the microbial oxidation of organic matter and associated N (McGill and Cole 1981). The selective reabsorption of P relative to N by plants during leaf senescence reduces the relative uptake of P compared to N and accelerates the cycling of N between soil and plants (Walbridge 1991). In addition, the higher bulk density in the marine zone of the Shark River estuary may dilute N concentration.

In this study, N existed mostly as organic N, with the small amount of inorganic N comprised primarily of ammonium. This is consistent with other studies of mangrove soils showing that the extractable nitrate+nitrite pool is a small proportion of the total amount of inorganic N (Boto and Wellington 1984, Rivera-Monroy et al. 1995). However, nitrate can be an important source of inorganic N for mangrove growth (Boto et al. 1985).

Seasonal changes in ammonification rates can be the result of variation in substrate quality. This study showed that net ammonification was negligible with evidence of immobilization in August; however, net ammonification rates in January (35-239 mg·m⁻²·d⁻¹) and May (18-70 mg·m⁻²·d⁻¹) are comparable to other macrophyte systems such as subtropical seagrasses (28-294 mg·m⁻²·d⁻¹) (Boon et al. 1986), tidal freshwater marsh (44 mg·m⁻²·d⁻¹) (Bowden 1984), and marine sediment (24-106 mg·m⁻²·d⁻¹) (Blackburn and Henricksen 1983). In all of these studies net ammonification rates were measured under controlled conditions. In a case study measuring seasonal variation of ammonification in coastal wetlands, Abd. Aziz and Nedwell (1986) also found that the ammonification rate under controlled condition was minimal during summer. They suggested that seasonal changes in the rates were related to the variation in available mineralizable organic N. The latter accumulates during winter due to low temperature and is gradually depleted from spring to summer with increased mineralization rates.

The mineralizable organic N is a small proportion of the total N in mangrove soils, not only due to higher annual temperature, but also to the temporal pattern in litter production and export. Litter production in south Florida generally peaks during August to October (Pool et al. 1975, Twilley et al. 1986). Surface litter mass on the forest floor in a basin mangrove forest of southwestern Florida remains high from October or November to May, and is significantly lower from July to September (Twilley et al. 1986). This temporal pattern of litter mass on the forest floor is coincident with the tide flooding frequency (Twilley 1985). There are less than eight tides per month in a Florida basin mangrove forest from December to April, compared to over 30 when seasonal sea level peaks exceed mean sea level in September (Twilley 1985). Thus, litter mass is accumulated after peak litter production because of the decreasing tidal flooding frequency and relatively low temperature. The higher soil ammonification rate in January under controlled conditions corresponds to the accumulation of potential mineralizable organic N during this period. When tidal flooding frequency and temperature increase starting in late spring, fresh organic matter is exported by tidal exchange and consumed by microbial decomposition.

Mangroves have a maximal growth during summer in Florida (Gill and Tomlinson 1971). Plant roots are able to absorb almost all available N from soil, which causes a strong competition between plants and microbes for inorganic nutrients. When live roots are excluded from sampling

cores under controlled conditions, microbial communities can absorb the N released from mineralization. Immobilization occurs when there is insufficient mineralizable organic N due to depletion by microbes and tidal export during spring to summer. This suggests that mangrove growth in this region may be more limited by N availability in summer than in the other seasons.

The method of core-sampling with glass tubes to measure ammonification rates under controlled laboratory conditions provides an estimate of net $\text{NH}_4\text{-N}$ production. N mineralization was not correlated with either total C and N pools or C:N ratios (Table 3.5). This suggests that ammonification rates in this mangrove region are independent of the total N concentration. Mean rates of net ammonification were significantly correlated with initial extractable phosphate and ammonium pools, while being negatively related to N:P ratios (Table 3.5), suggesting that N mineralization is regulated by phosphate and ammonium supply. Highly significant correlations of microbial activity with P components in New Guinea mangrove muds indicate that microbial activity is probably P-limited in mangrove soils, which then may limit N mineralization (Alongi et al. 1993). Pastor et al. (1984) also found inorganic N and P supply limiting N mineralization in terrestrial forests.

Relative N mineralization (N mineralization per unit of total N) is a useful index to compare overall substrate quality as a factor determining N mineralization rates (Schimel et al. 1985, Pastor et al. 1987, Hart and Gunther 1989, Polglase et al. 1992). Relative N mineralization decreased exponentially with distance from the mouth of the estuary (Fig. 3.8). This indicates that the proportion of recalcitrant organic N in mangrove soils increases rapidly with distance from the Gulf of Mexico to inland mangrove-marsh ecotone. A decrease in rates of N mineralization associated with declines in organic matter quality with increasing soil age has been observed in a prairie (Schimel et al. 1985) and old fields (Pastor et al. 1987).

In addition to the composition of soil organic matter, the species composition of forests has been suggested as an important factor influencing soil N mineralization through quality and quantity of litterfall (Pastor et al. 1987, Hart and Gunther 1989). Wedin and Tilman (1990) have experimentally demonstrated that differences in the tissue N concentration, below ground lignin concentration and below-ground biomass of grass species resulted in differences in annual net N mineralization. There are only three mangrove species in the study area, however their distribution is distinct among sites with *L. racemosa* and *A. germinans* dominating in the downstream location and *R. mangle* dominating in the intermediate and upstream locations (Chapter 4). It is well documented that *Avicennia* litter decomposes more quickly than that of other species due to high nutritive quality and lower concentration of tannin (Twilley et al. 1986, Alongi et al. 1992). *R. mangle* leaves have higher concentrations of condensed tannins than *A. germinans* and *L. racemosa* (McKee 1995a, b). Tannin and other polyphenolic compounds can inhibit microbial activity in mangrove soils (Benner et al. 1986, Alongi et al. 1992). Lacerda et al. (1995) found that there is an increase in the contribution of carbohydrates and amino acids to the soil organic pool in *Avicennia* soils but not in *Rhizophora* soils. They further suggested that organic matter associated with *Avicennia* soil is more degradable than with *Rhizophora*. Thus, P availability, substrate and litter quality can potentially control the spatial gradient of N availability in mangrove soils. In addition, spatial trends in soil P gradients coupled to N availability could in turn strongly influence mangrove forest development and composition.

Landscape trends and control of P availability

The concentrations of total P (0.06-0.12%) in the mangrove soils along the Shark River estuary are within the values (0.01-0.16%) for mangrove soils in the world (Alongi et al. 1992). However, more than half of the total P in this study area existed in a residual form. Available source of inorganic P to mangrove soils include mineralization of organic P matter, solubilization of mineral-P, and external flooding of tidal waters (Alongi et al. 1992). Mangroves absorb these pools of inorganic P and return them as organic-P through litterfall to the forest floor. Anaerobic mangrove soil limits the oxidation of organic matter by microorganisms and a greater proportion of

P remains in the residual P pool. This pool of organic P becomes chemically recalcitrant and is not available for mangrove utilization (Boto 1991).

Rates of net P mineralization measured in this study are based on the net change in the concentration of the labile P pool. This net change is a balance between P release from the mineralization of organic P and dissolution from minerals, and uptake by microbes and adsorption by minerals during the incubation. The 1 mol/L KCl solution used in this study mildly extracts labile P, which constitutes less than 2% of the total P pool in these mangrove soils. The results revealed a small release of P from soil mineralization in the mesohaline and oligohaline sites, but no net P mineralization in the sites close to the mouth of the Shark River estuary. These data suggest that strong immobilization of labile P occurs in mangrove soils with higher rates of N mineralization. Bacteria in mangrove soils are highly productive and they can sequester much of the labile nutrients in sediment (Alongi et al. 1993, Robertson and Phillips 1995). Microbes are able to immobilize almost all of the labile P produced from organic mineralization in acid organic soils (Walbridge and Vitousek 1987, Walbridge 1991). Rapid immobilization of amended inorganic phosphorus (30 mg/kg) suggests that P adsorption by minerals in mangrove soils can strongly immobilize soluble reactive phosphate (Hesse 1962, 1963). Adding 400 kg P/ha to mangrove soils in Australia increased the concentration of extractable P to only ~65 µg/g above ambient levels of 20-30 µg/g (Boto and Wellington 1983, Alongi et al. 1992). Higher Ca-bound-P was found in the marine sites than in the oligohaline site along the Shark River estuary, indicating the relative influence of carbonate processes at the mouth of the estuary. It has been demonstrated that carbonate can rapidly adsorb the inorganic P released from mineralization of organic matter (DeKanel and Morse 1978, Binkley and Vitousek 1989). Therefore, both the carbonate fixation of P and microbial immobilization may contribute to the absence of net P mineralization at the downstream mangrove sites in the Shark River estuary. KCl extraction is too mild to desorb phosphate adsorbed by Ca, Fe and Al minerals, but P in these minerals may be partly available to mangroves. Thus, P mineralization rates in this study probably underestimate the concentration of biologically available P in mangrove soils.

Changes in the chemical forms of P can be a function of soil development as demonstrated in soils of desert (Lajtha and Schlesinger 1988) and Hawaiian islands (Crews et al. 1995). In both case studies, Ca-bound-P decreased with increasing soil age, but residual P showed a reverse trend. In my study, sequential extractions of P indicate a significant increase in Ca-bound-P and decrease in residual-P as percentage of total P from the oligohaline to marine sites of the estuary. This landscape trend in P distribution is probably not related to soil age, since known mangroves have existed in this region for more than 3000 yrs (Scholl 1964a, b). Forms of soil P in mangroves with open nutrient cycles may depend on the source of P input. A significantly higher Ca-bound-P as the percentage of total P near the mouth of the estuary suggests that the greater bulk density concentration of P in the marine sites may be related to the deposition of carbonate sediment from the Gulf of Mexico. Upstream mangroves at the head of the estuary receive less mineral sediment and show a greater proportion of organic P.

Geomorphology, topography and hydrology play important roles in determining the spatial gradient of P availabilities. The environmental setting in this mangrove land-margin ecosystem was identified by Thom (1984) as a mainland carbonate platform, in which terrestrial sediment supply is low but calcareous sediment production dominates. Mangrove soils in the study area consist of mangrove residuals and carbonate sediment (Scholl 1964a, b), and thus weathering of minerals in parent rock material is not an important source of nutrients (Fourqurean et al. 1993). The other external sources of phosphorus in this carbonate setting are water and sediment from the Everglades and the Gulf of Mexico, or precipitation. Upstream marshes in the Shark River Slough effectively reduce surface water P concentrations to levels near detection limits, which leads to relatively low P inputs to the Everglades National Park, despite the increased loading of P into marshes (Davis 1994). The results from the Shark River estuary indicate that tidal water and suspended sediments from the Gulf of Mexico represent a major source of nutrients to the

mangroves. When a tide transports dissolved and suspended P from the Gulf of Mexico into the Shark River estuary, the availability of this imported P to the mangroves will depend on the tidal elevation relative to the topography of the mangroves. There is no direct measurement of P flux in this mangrove wetland, but other studies on the exchange of P between vegetated coastal wetland and adjacent waters have suggested that marsh (Wolaver and Spurrier 1988) and mangroves (Boto and Wellington 1988) are a sink of P. Long-term P accumulation is linked with external inputs in mangrove wetlands (Lynch et al. 1989, Twilley et al. unpublished manuscript), saltmarsh (DeLaune et al. 1981) and fresh-water wetlands (Craft and Richardson 1993*a,b*, Reddy et al. 1993). Lynch et al. (1989) found higher accretion rates in riverine and fringe mangroves than in basin mangroves of Florida and Mexico. P accumulation was negatively correlated with distance from upland inflows in the Everglades fresh-water wetlands (Craft and Richardson 1993*a,b*, Reddy et al. 1993). Total P and available P in mangrove soils had a significant landscape trend with an increase from oligohaline to marine zones along the Shark River estuary. These results support the hypothesis that the major source of P in mangrove wetlands distributed along an estuary in a carbonate mainland environment is from the marine source of the estuary, and not directly from terrestrial runoff. The hypothesis that freshwater sources of nutrients control the supply of P in mangrove estuaries is specific to those geomorphological settings with terrigenous sediments (Thom 1982).

Table 3.1. Soil C, N and P concentrations and bulk density along the Shark River estuary. Data are means of three seasons $\pm$ SE. Correlation coefficients are between respective soil variables for each site and distance from the mouth of the Shark River estuary (* $P < 0.05$, ** $P < 0.01$).

Variables	Sampling position	S1	S3	S4	S6	Correlation coefficient (r)
Distance from the estuary mouth (km)		1.8	4.1	9.9	18.2	
Total C (%)	Forest	14.3 $\pm$ 0.3	22.2 $\pm$ 1.2	32.5 $\pm$ 1.5	43.3 $\pm$ 1.1	0.985*
	Gap	20.0 $\pm$ 0.7	22.9 $\pm$ 1.2	33.3 $\pm$ 1.7		
Total N (%)	Forest	0.70 $\pm$ 0.07	1.15 $\pm$ 0.09	1.55 $\pm$ 0.07	2.33 $\pm$ 0.10	0.990**
	Gap	0.97 $\pm$ 0.07	1.26 $\pm$ 0.04	1.59 $\pm$ 0.10		
Total P (%)	Forest	0.11 $\pm$ <0.01	0.12 $\pm$ <0.01	0.09 $\pm$ <0.01	0.06 $\pm$ <0.01	-0.960*
	Gap	0.09 $\pm$ <0.01	0.10 $\pm$ <0.01	0.09 $\pm$ <0.01		
Bulk density (g/cm ³)		0.462	0.212	0.148	0.135	-0.751

Table 3.2. Summary of F statistics from repeated measures ANOVA of site and season effects on nutrient availability. Statistical tests were conducted using univariate tests. Effect of sampling station was not significant ($P>0.05$).

Sources	df	NH ₄ -N	P _{ext}	NO _x -N	Ammonification	P mineralization
Site	3,8	26.85***	108.5***	8.15**	7.53*	4.10*
Season	2,16	17.28***	10.88***	2.68	75.70***	8.38**
Site*season	6,16	3.84*	4.10*	1.91	7.88***	8.83***

* $P\leq 0.05$, ** $P\leq 0.01$, or *** $P\leq 0.001$

Table 3.3 Phosphorus fractionation at 0-20 cm depth in sediments from intact mangrove forests and canopy gaps. Data are means $\pm$ SE (n=3). The superscript letters indicate significant differences (Tukey's $P < 0.05$) among sites in P components under intact forests.

Sampling Position	Site	Soil P components (g/m ²)				
		Labile-P	Fe/Al-bound-P	Hydrolyzable organic-P	Ca-bound-P	Residual P
Forest	S1	0.54 ^a $\pm$ 0.04	5.58 ^a $\pm$ 0.21	7.64 ^a $\pm$ 0.39	21.33 ^a $\pm$ 1.60	30.36 ^a $\pm$ 5.68
	S3	0.26 ^b $\pm$ 0.06	3.32 ^b $\pm$ 0.37	6.55 ^a $\pm$ 0.52	5.87 ^b $\pm$ 1.21	23.32 ^{ab} $\pm$ 2.28
	S4	0.30 ^b $\pm$ 0.03	2.66 ^b $\pm$ 0.34	5.40 ^b $\pm$ 0.40	0.92 ^c $\pm$ 0.04	16.14 ^{ab} $\pm$ 2.07
	S6	0.29 ^b $\pm$ 0.02	1.24 ^c $\pm$ 0.03	2.39 ^c $\pm$ 0.16	0.50 ^c $\pm$ 0.03	10.69 ^b $\pm$ 0.59
Site effect $P=$		0.003	<0.001	<0.001	<0.001	0.013
Canopy gap	S1	0.84 $\pm$ 0.13	5.61 $\pm$ 0.60	6.64 $\pm$ 0.24	16.74 $\pm$ 2.67	20.92 $\pm$ 1.66
	S3	0.34 $\pm$ 0.02	3.26 $\pm$ 0.28	5.33 $\pm$ 1.00	8.03 $\pm$ 0.97	17.26 $\pm$ 1.69
	S4	0.24 $\pm$ 0.02	2.36 $\pm$ 0.12	4.57 $\pm$ 0.43	0.81 $\pm$ 0.04	15.55 $\pm$ 1.69
Vegetation effect $P=$		ns	ns	ns	ns	ns

Table 3.4. Summary of F statistics from repeated measures ANOVA of vegetation (intact forest vs canopy gap) and season effects on nutrient availability. Statistical tests were conducted using univariate tests. Effect of sampling station was not significant ($P>0.05$).

Sources	df	NH ₄ -N	P _{ext}	NO _x -N	Ammonification	P mineralization
Vegetation	1,4	1.74	41.3**	37.0**	0.88	0.44
Season	2,44	1.47	2.69	3.66*	37.09**	5.85**
Vegetation*season	2,44	2.25	0.33	5.41**	0.22	1.42

* $P\leq 0.05$, ** $P\leq 0.01$, or *** $P\leq 0.001$

Table 3.5 Linear correlations among N mineralization ($N_{\min}$), P mineralization ($P_{\min}$) and other soil properties within the 0-20 cm depth in mangrove forests and gaps. (Mean values over three seasons were used for correlative analysis). (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

	$N_{\min}$ mg·m ⁻² ·d ⁻¹	$P_{\min}$ mg·m ⁻² ·d ⁻¹	NH_4 -N g/m ²	P_{ext} g/m ²	Total C kg/m ²	Total N g/m ²	Total P g/m ²	Atomic C:N
$P_{\min}$	-0.700							
NH_4 -N	0.853*	-0.716						
P_{ext}	0.926**	-0.668	0.960***					
Total C	0.332	-0.393	0.770*	0.623				
Total N	0.314	-0.390	0.698	0.610	0.918**			
Total P	0.883**	-0.757*	0.906**	0.852*	0.563	0.431		
C:N	0.270	-0.321	0.576	0.379	0.671	0.328	0.626	
N:P	-0.876*	0.472	-0.672	-0.727	-0.146	0.030	-0.826*	-0.449

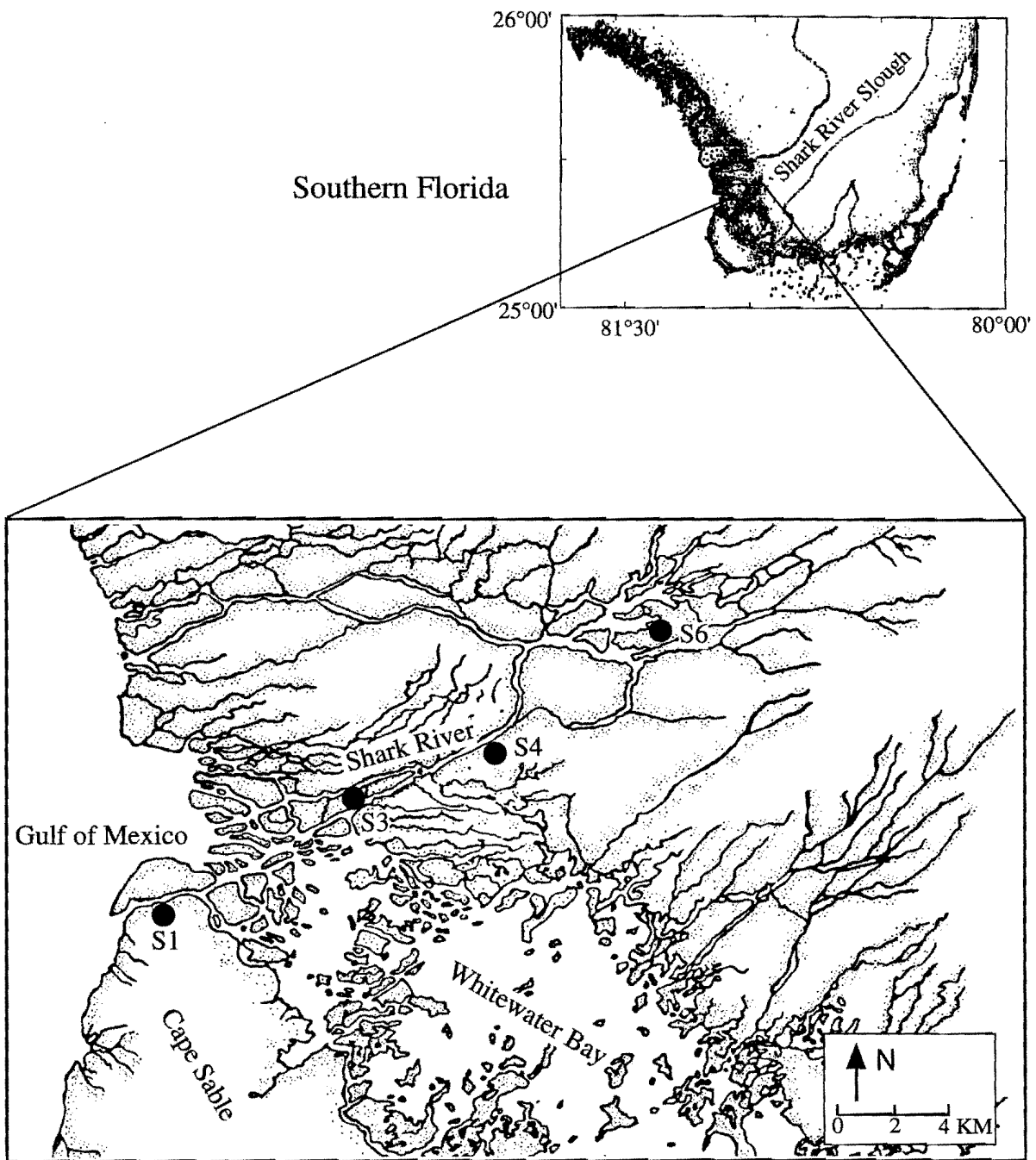


Figure 3.1. Study site locations along the Shark River estuary in the Everglades National Park.

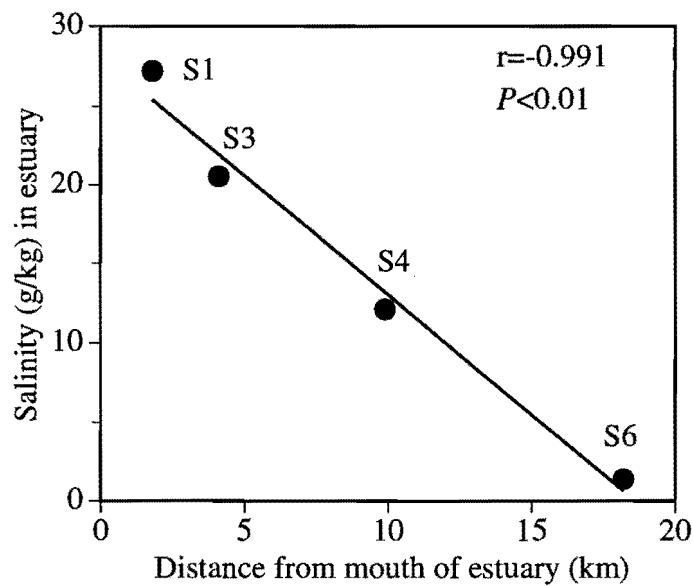
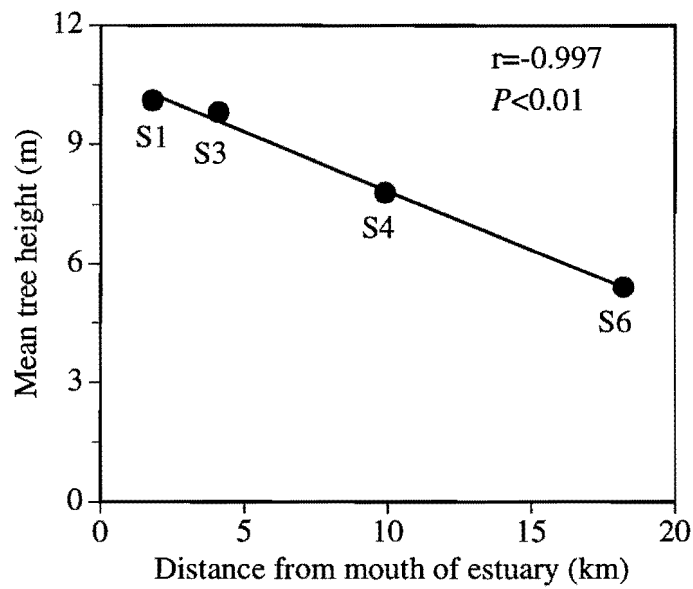


Figure 3.2. Changes of mean tree height of mangrove forests and salinity from the marine site (S1) to the oligohaline site (S6) along the Shark River estuary of the Everglades National Park.

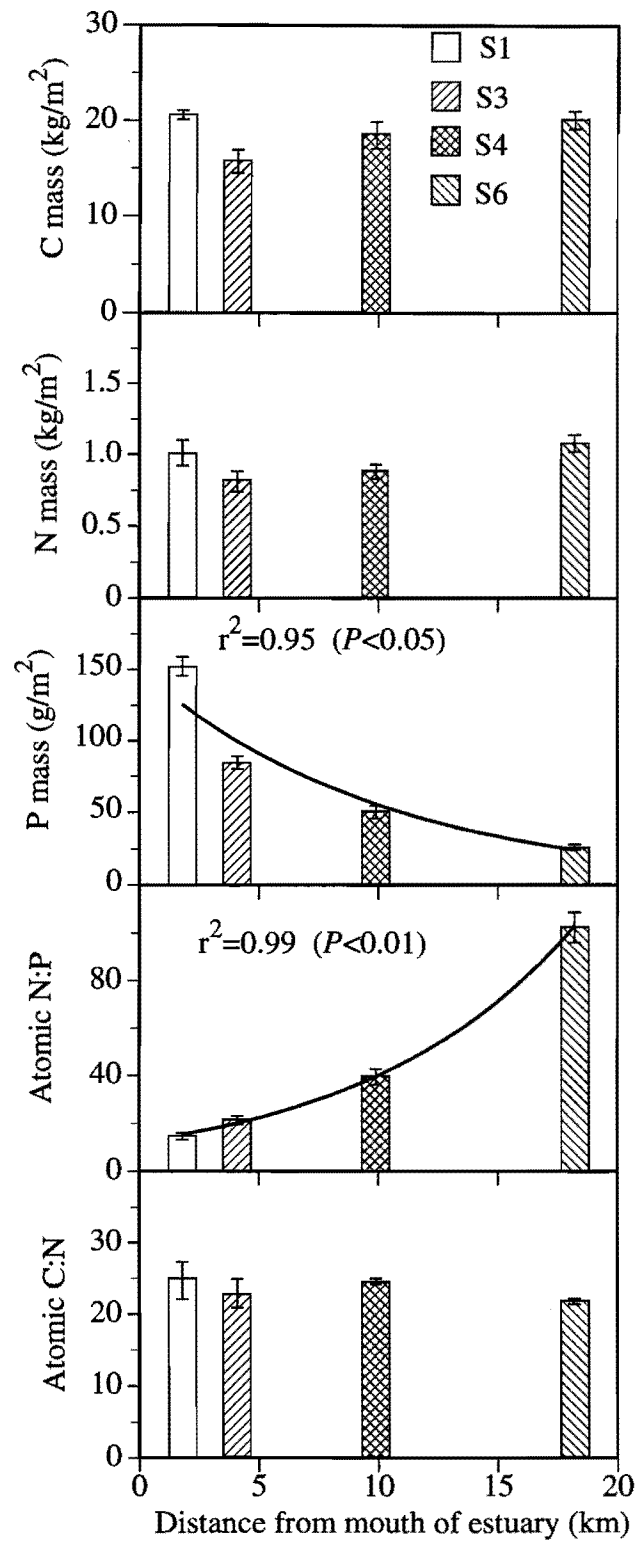


Figure 3.3. Changes of soil C, N and P within 0-40 cm soil in mangrove forests from the marine site (S1) to the oligohaline site (S6) along the Shark River estuary of the Everglades National Park. Data are mean of three seasons $\pm$ SE.

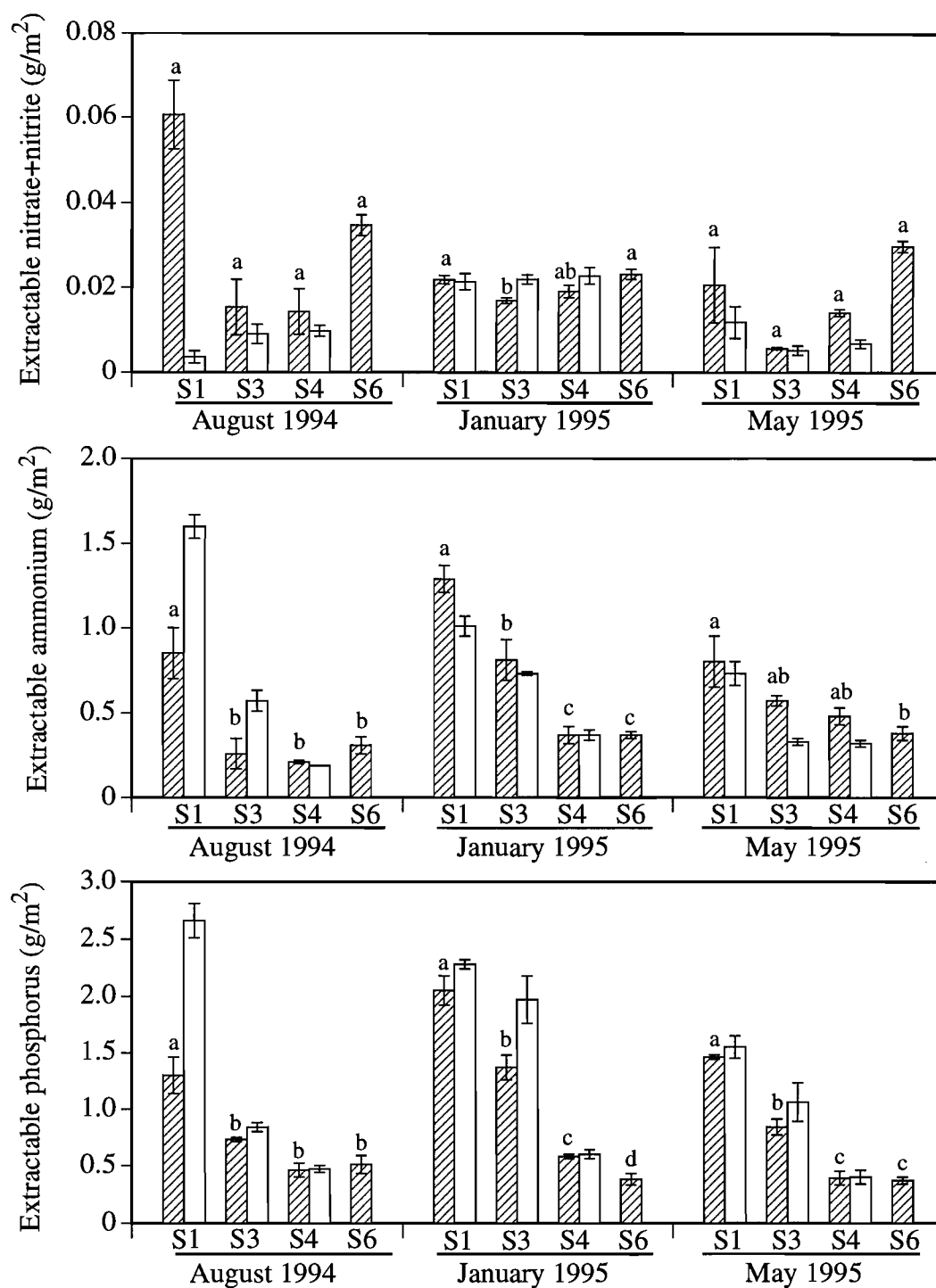


Figure 3.4. Extractable nitrate+nitrite, ammonium and phosphorus within the 0-20 cm soil at four mangrove sites along the Shark River estuary in August 1994, January and May 1995. Hatched bar and open bar represent sampling stations under intact forests (S1 - S6) and under canopy gaps (S1 - S4), respectively. Each value is the mean ($\pm$ SE) of three stations. The values for intact forests from different sites at each sampling date with the same letter are not significantly different ($P>0.05$; Tukey's test).

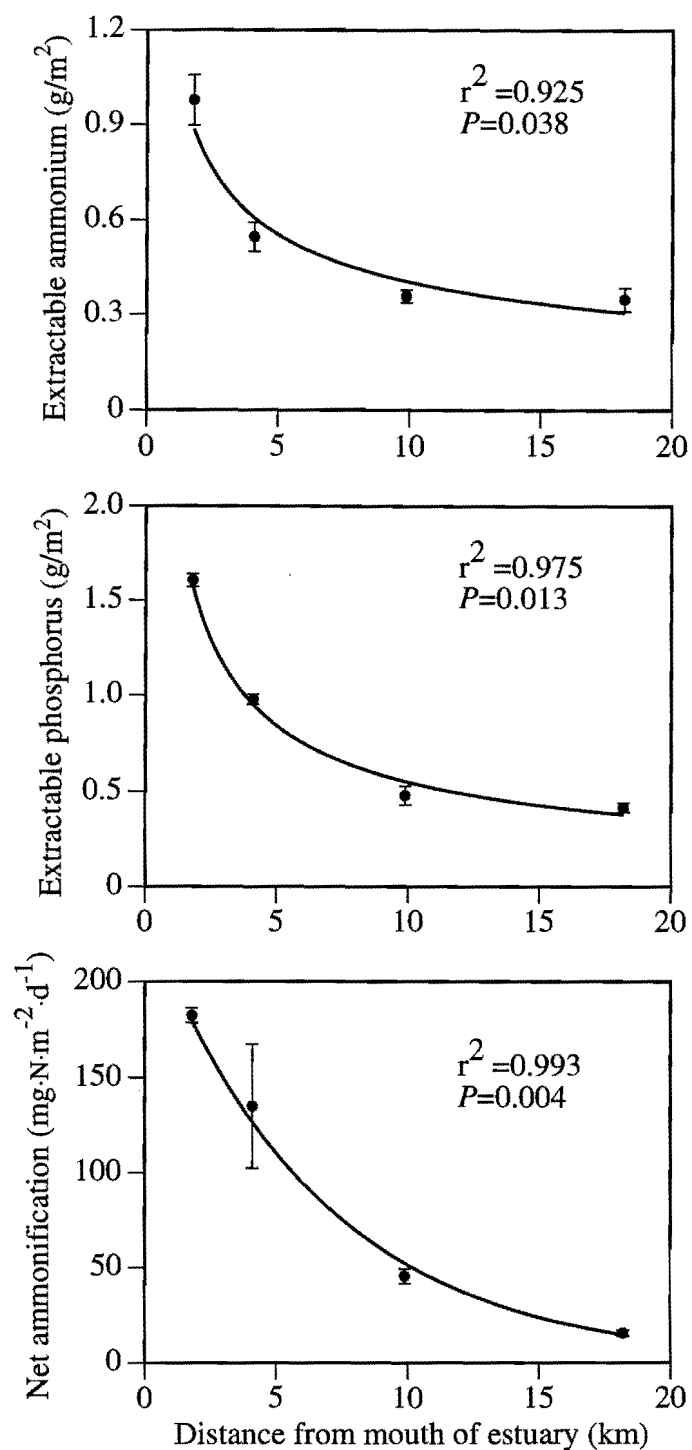


Figure 3.5. Relationship between mean extractable ammonium, extractable phosphorus, net ammonification, and the distance from the mouth of the Shark River estuary. Values are mean $\pm$ SE (n=3). Curves have been fitted to the relationship: $y = ax^b$ for extractable ammonium and phosphorus; $y = \exp(a+bx)$ for net ammonification.

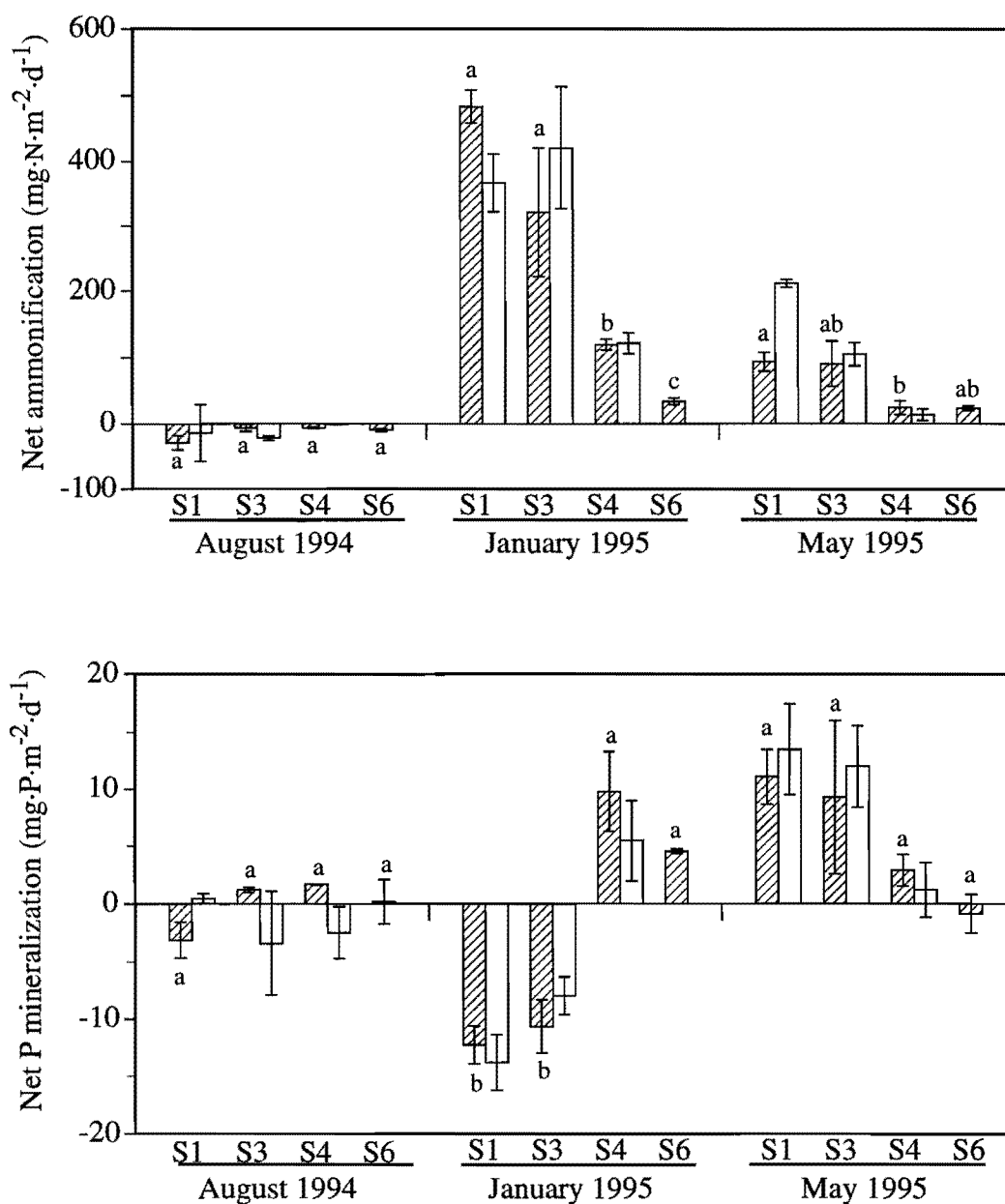


Figure 3.6. Net ammonification and phosphorus mineralization within the 0-20 cm soil at four mangrove sites along the Shark River estuary in August 1994, January and May 1995. Hatched bar and open bar represent sampling stations under intact forests (S1 - S6) and under canopy gaps (S1 - S4), respectively. Each value is the mean ($\pm$ SE) of three stations. The values for intact forests from different sites at each sampling date with the same letter are not significantly different ($P>0.05$; Tukey's test).

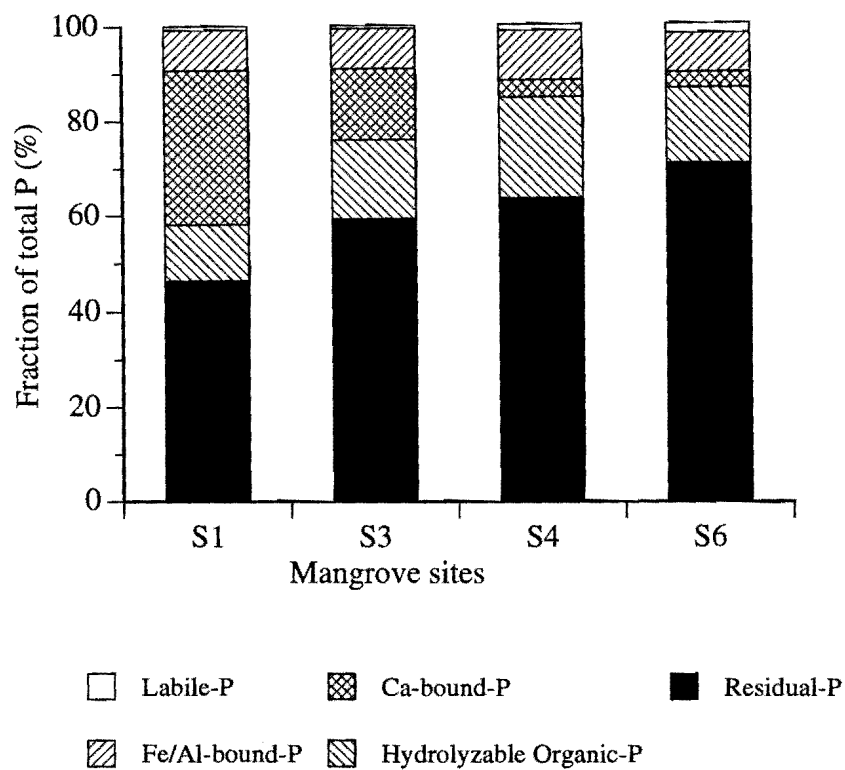


Figure 3.7. Changes in P fractionations in percent of total P within the 0-20 cm soil at four mangrove sites along the Shark River estuary.

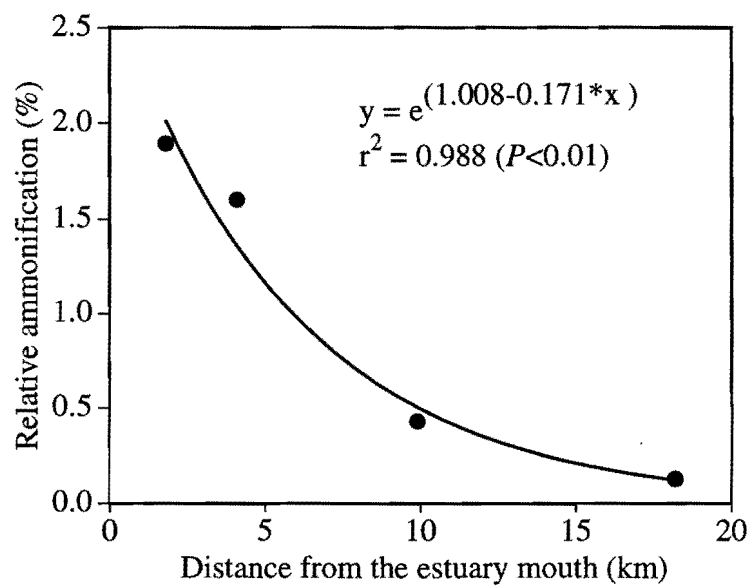


Figure 3.8. The relative ammonification rate of mangrove sediments in relation to the spatial gradient of the Shark River estuary. Relative ammonification is calculated as the net total amount of ammonium mineralized (0-20 cm) during three periods of 15-d incubation as a percentage of mean total N present initially.

CHAPTER 4

LANDSCAPE PATTERNS OF MANGROVE FOREST STRUCTURE AND SOIL CHARACTERISTICS ALONG THE SHARK RIVER ESTUARY, FLORIDA

ABSTRACT

Mangrove forest structure, growth, soil nutrient resources and pore water stressors were examined along the longitudinal gradient of the Shark River estuary in the Everglades National Park. Patterns of forest structure were based on 34 yrs of growth since Hurricane Donna destroyed most of the mangrove resources in this region in 1960. Forest basal area increased from lower values at the upstream and intermediate locations of the estuary (19.61 and 20.72 m²/ha, respectively) to nearly double these values at two downstream locations (40.36 and 39.67 m²/ha) near the mouth of the estuary. Tree density with dbh >10 cm was 1900/ha in the downstream location, which indicated a more mature stand than in the upstream location where only 334 trees/ha were >10 cm dbh. *Laguncularia racemosa* had a higher importance value in the downstream location, whereas *Rhizophora mangle* dominated in the intermediate and upstream locations. Biomass increments were higher at the downstream sites (10.73 and 11.96 Mg·ha⁻¹·yr⁻¹) than at the lower stature forest in the upstream and intermediate sites (3.23 and 4.20 Mg·ha⁻¹·yr⁻¹). Pore water salinities in mangrove soil were < 35 g/kg at all three sampling seasons and sulfide concentrations were generally < 0.15 mmol/L. There was no spatial trend of total C and N contents per unit soil volume, nor in C:N ratios among the sites. However, total P, extractable P and extractable ammonium contents increased from the upstream sites to the sites at the mouth of the estuary. Soil properties in the downstream marine region of the Shark River estuary include high levels of nutrient resources and low concentrations of toxic stressors supporting a region of optimum growth of mangroves. A regression of mangrove basal area on concentrations of soil total P per unit volume suggest that the landscape gradient of mangrove forest development is associated with soil P resources along this subtropical estuary.

INTRODUCTION

Global trends of mangrove structural complexity and biomass show a decrease toward higher latitude, however, above ground biomass among mangrove forests can vary greatly within a specific latitude (Twilley et al. 1992, Saenger and Snedaker 1993). Variation in forest structure among mangroves can be linked to the geophysical processes and geomorphology of a regional setting. Factors influencing variation in mangrove stature among specific geomorphic settings have been proposed to include the distribution of toxic stressors (such as salinity and hydrogen sulfide) and resources (such as nutrients and light) within the intertidal zone. In areas of increasing soil salinity mangroves may be considered as an ecosystem under stress due to the limitation of hypersaline soils on the growth of mangroves (Lugo and Snedaker 1974), changes in species composition, and increasing scrubbyness (Macnae 1968). Cintrón et al. (1978) correlated the specific decrease in basal area and tree height with increased soil salinity in mangroves among the dry coasts of Puerto Rico. As a result of strong salinity gradients (35-300 g/kg), mangroves along the dry Pacific coasts of Central America exhibited significant differences in structural development within the same forest region (Jiménez 1990). In contrast, hypersaline soils have less effect on mangrove forest development along humid tropical coasts where rivers provide a source of freshwater to dry coastal environments (Blasco 1984).

The growth of mangroves is not only constrained by variations in soil salinity, but also by highly toxic compounds such as hydrogen sulfide. Hydrogen sulfide is transformed from sulfate

in reduced soil. Concentrations of sulfide exceeding 3 mmol/L have been recorded in mangrove soils (Nickerson and Thibodeau 1985, McKee 1993), and sulfide is considered a factor limiting growth and distribution of mangrove species. Boto and Wellington (1984) found that above ground biomass of mangroves decreased at sites with more reduced soils in an Australian mangrove forest. In a greenhouse study, McKee (1993) demonstrated that reduced soil conditions caused a 20 to 40% decrease in total biomass of *Avicennia germinans* seedlings relative to drained soil controls.

Nitrogen (N) and phosphorus (P) have been implicated as the nutrients most likely limiting primary productivity of mangrove ecosystems (Twilley 1995). Based on field observations, Lugo and Snedaker (1974) hypothesized that dwarf mangroves in Florida suffer from nutrient limitation because they usually occur in an environment lacking obvious external nutrient sources. Biomass and productivity increased as nutrient inputs were increased in simulations of an ecosystem model of mangrove wetlands (Lugo et al. 1976). Surveys of forest structure and soil characteristics among natural mangrove communities in Australia indicated that above ground biomass was positively correlated with extractable P (Boto and Wellington 1984). Day et al. (1987) observed that riverine forests in Términos Lagoon had much greater biomass and productivity than fringe and basin mangroves along a tidal creek, Estero Pargo. The first direct evidence that nutrients may influence the structure and productivity of mangrove wetlands was by Onuf et al. (1977), who measured the growth of overwash mangroves naturally enriched by bird guano in Florida. They found greater leaf production and branch growth in those mangroves relative to those at sites without bird guano. Field fertilization studies by Clarke and Allaway (1993) showed that higher nutrients enhanced the growth and survival of seedlings in gaps and under the canopy of forests in Australia. Furthermore, Feller (1995) and Twilley (1995) manipulated nutrient levels in organic soils of a dwarf mangrove in Belize and revealed that *Rhizophora mangle* trees responded quickly and grew vigorously following fertilization with P.

More than 50 yrs ago, Davis (1940) suggested that mangrove forests in the downstream region of the estuaries in southwestern Everglades are "probably the optimum growth of mangroves in the Americas". However, this hypothesis has not been tested with synoptic surveys of forest structure and environmental factors in this specific land-margin ecosystem. Coastal forested wetlands in the southwestern Everglades of south Florida extending from the Whitewater Bay region to Ten Thousand Islands include one of the greatest mangrove areas in the Gulf of Mexico (Davis 1940, Smith et al. 1994). Mangrove wetlands extend about 10-20 km inland bordering several estuaries that drain the Everglades, such as the Shark River Slough. Several studies of mangrove forests have been carried out in this region including zonation (Davis 1940), hurricane disturbances (Craighead and Gilbert 1962, Craighead 1971, Smith et al. 1994, Wanless et al. 1994, Doyle et al. 1995), organic export and trophic dynamics (Heald 1969, Odum and Heald 1972), and structure and litter production of ecological types (Pool et al. 1975, 1977). However, the landscape gradient of mangrove forests along the estuary as a function of environmental conditions has received far less attention. It has been observed that mangrove forest stature along the more marine regions of the estuary is about 25 m, and tree height decreases toward the mangrove-marsh transition zone (Davis 1940, Smith et al. 1994, Chapter 3). Specifically, it has not been shown whether these changes in forest structure are associated with either increased stressors or reduced nutrient resources.

In this paper, I described patterns of mangrove forest structure relative to distribution of soil resources and toxic stressors along the Shark River estuary in the Everglades National Park. This study was undertaken 34 yrs after Hurricane Donna destroyed most of the mangrove resources in this region in 1960 (Craighead and Gilbert 1962). The objective of this study was to investigate the relationships between landscape gradients of mangrove forest structure and soil characteristics. I quantified the structure and biomass increments of mangrove forests, soil and pore water nutrient pools, and pore water salinity and sulfide concentrations along the longitudinal gradient of the Shark River estuary. Understanding spatial patterns of soil nutrient resources and

stressors is crucial to the interpretation of mangrove forest dynamics in the face of natural disturbance, such as hurricanes. In addition, these environmental constraints on forest structure and function are linked to human land-use patterns in the Everglades watershed, particularly those associated with the Shark River Slough.

MATERIALS AND METHODS

Study area

The study sites are located along the Shark River estuary on the west coastal plain of the Everglades National Park (Fig. 3.1). An elevation gradient of the coastal Everglades region of only 2.8 cm/km (SFWMD 1992) along with a low-energy environment results in the development of extensive mangrove wetlands. Three mangrove species, *Rhizophora mangle* L., *Avicennia germinans* (L.) Stearn. and *Laguncularia racemosa* (L.) Gaertn., form a continuous band of forested wetlands that extend from the Gulf of Mexico to the inland limit of periodic salt water influence. *Conocarpus erecta* L. is also found in this coastal region where the salinity is lower than 10 g/kg and soils are frequently inundated. This study area was previously destroyed by Hurricane Donna in 1960, with an instant mortality of mangroves reported at 50 to 70%, but the eventual tree mortality was higher (Craighead and Gilbert 1962). Because tree destruction in this region by Hurricane Donna was so widespread, mangrove forests at each site along the Shark River estuary are considered to be approximately even aged.

Four sites of mangrove forests were selected for measurements of species composition, density, tree height and basal area along the Shark River estuary. The sites were located between 25°19'N, 81°08'W and 25°25'N, 80°58'W at about 1.4 (S1), 4.1 (S3), 9.9 (S4) and 18.2 (S6) km inland from the mouth of the estuary (Fig. 3.1). Following the terminology of Duke (1992), mangrove habitats in S1 and S3 sites are categorized as downstream locations of the Shark River estuary, while S4 is intermediate and S6 is an upstream location. This region consists of 1-4 m deep peats accumulating above a mainland carbonate Oolite platform, which is unique among geomorphological groups of mangroves (Davis 1940, Scholl 1962 a,b, Thom 1984, Woodroffe 1992).

Permanent plots were established at each of the four sites to study dynamics of mangrove vegetation along the estuary. A 20 x 20 m plot about 10 to 20 m inland from the estuary was divided into four 10 x 10 m quadrats at sites S1, S3 and S4. A smaller plot 10 x 15 m plot about 5 m inland from the estuary was divided into three 10 x 5 m quadrats at S6 due to the restricted band of mangrove vegetation along the estuary in this upstream region. Three stations were randomly selected in each forest plot and marked in August 1994 for repeated measures of soil and pore water properties in August 1994, January and May 1995.

Forest structure and growth

All trees with diameter at breast height (dbh) > 2 cm in each plot were tagged and measured in January 1995 and remeasured in February 1996. I also measured dbh of dead trees in January 1995. Fifteen to 20 trees were randomly chosen in each plot for the measurements of tree height using a range finder. I also measured tree height and dbh in a disturbed mangrove forest at the mouth of Broad River, which is recovering from Hurricane Andrew in 1992, to analyze the relationship between tree height and dbh. Regression between dbh and tree height was estimated for each species.

Total above-ground biomass of *R. mangle* and *L. racemosa* was calculated using published allometric equations from Cintrón and Schaeffer-Novelli (1984) and of *A. germinans* from Day et al. (1987). Annual net biomass growth was estimated as the difference between the initial and final biomass of each individual tree using species-specific equations. The sum of these differences was used to estimate biomass production for each plot. There is no allometric equation for *C. erecta* so I used the allometric equations of *L. racemosa* as a reference to estimate biomass of *C. erecta*.

because their growth forms are similar at this site.

Pore water analyses

Pore water samples were collected at the three soil stations in each plot using a plastic siphon with syringe as described by McKee et al. (1988). I was able to collect pore water at 20 cm depth using this method in May 1995 and August 1994, but collections were at 40 - 50 cm in January 1995 due to lower water level. One aliquot of pore water was assayed for salinity using a portable Labcomp Instruments Model SCT analyzer and for pH using a HANNA HI9025 pH meter. A second aliquot of the pore water sample was filtered and immediately added to an equal volume of antioxidant buffer in the field, then brought to the laboratory to be analyzed for sulfide concentrations with a LAZAR Model IS-156 sulfide sensing electrode (McKee et al. 1988). A third aliquot of pore water was used to measure nutrient concentrations by filtering through a GF/F filter and storing the sample frozen until assayed for inorganic nutrients. Ammonium concentrations were measured by colorimetric method (Parsons et al. 1984). Nitrite, nitrate and phosphate in pore water samples were determined by ALPKEM Autoanalyzer using standard techniques (Strickland and Parson 1972).

Soil nutrients

Soils were collected with a 5.0 cm diameter corer at the three stations to a depth of 40 cm. Soil samples at 10-cm intervals were stored on ice in polyethylene bags in the field, and stored at 4°C in the laboratory prior to analysis. Index of available P was determined by a dilute acid-fluoride extraction of fresh soil samples (Olsen and Sommers 1982). The extract was analyzed colorimetrically for soluble reactive phosphorus. Fresh soils were extracted with 1 mol/L KCl (1:10 mass/volume) to measure extractable ammonium. The extract was centrifuged and analyzed for $\text{NH}_4\text{-N}$ by colorimetric method (Parsons et al. 1984). Recognizable plant litter and coarse root material were removed from soil samples prior to extractions. Soil subsamples were oven-dried to constant weight at 60°C and ground with a Wiley Mill to pass through a 250 μm mesh. Total C and N content of two replicates of each sample were determined with a LECO elemental analyzer using standard protocols. Total P in soils was extracted from soils with 1N HCl after ignition at 550°C (Aspila et al. 1976) and determined by using molybdenum blue, and ascorbic acid as reducing agents (Parsons et al. 1984). Another 15.2 cm diameter soil core from each site was used to estimate soil bulk density. Nutrient concentrations were multiplied by bulk density to obtain nutrient contents expressed per unit soil volume.

Statistical analysis

Repeated measures ANOVAs were used to test the effects of site, depth and sampling date on soil C, N and P concentrations and contents. I also used repeated measures ANOVAs to test the effect of site and sampling date on pore water variables including salinity, sulfide and inorganic nutrients. One way ANOVA was used to test for differences in concentrations of pore water variables among the sites for each sampling date. All statistical tests were done by using either original data or log-transformed data to meet assumptions for parametric analysis. SAS was used to perform all statistical tests (SAS 1989).

RESULTS

Forest structure and growth

The landscape patterns of mangrove forest structure along the Shark River estuary exhibited differential recovery from Hurricane Donna disturbance in 1960, assuming that these stands are even-aged. The highest density of trees among the four sites was 7333 trees/ha at S6, compared to 3725, 3600 and 2578 trees/ha at S1, S3 and S4, respectively (Fig. 4.1). However, density of trees >10 cm dbh increased significantly from 334 trees/ha at S6 to 1900 trees/ha at S1,

with intermediate values of 850 and 1600 trees/ha at S4 and S3, respectively (Fig. 4.2). S6 was characterized by a high density of small trees (5534 trees/ha) with dbh <6 cm. Size class distribution of trees at S6 showed an exponential decrease of tree density with an increase in dbh, however, frequency of size-class distribution at S1 was bell-shaped (Fig. 4.2).

R. mangle, *A. germinans*, and *L. racemosa* were found in the plots at S1, S3 and S4, but *A. germinans* was replaced by *C. erecta* at S6. *R. mangle* was found in all sites and this species represented 35% to 90% of total tree density among the study sites. The dominance of *R. mangle* was restricted to the size-class <8 cm dbh, except at S4 where *R. mangle* dominated in all size-classes (Fig. 4.2). At S3, *L. racemosa* dominated in size-class >14 cm dbh, while no *R. mangle* above this size-class was found in the plot. All three species were co-dominant in size-class >14 cm at S1.

Basal areas were similar at S1 and S3 with values of 40.36 and 39.67 m²/ha, respectively. However, basal areas at S4 and S6 were only 20.72 and 19.61 m²/ha, respectively, which was about half of the values at S1 and S3 (Fig. 4.1). Basal area indicated that the structural complexity of mangroves increased from the oligohaline zone to the marine sites of the estuary.

Mangrove forests were mixed-species communities at S1 and S3, where *L. racemosa* had the highest importance value (42.1 and 48.5%, respectively in S1 and S3) and *A. germinans* the least (Fig. 4.1). The S4 site was dominated by *R. mangle* with an importance percentage of 72%. *R. mangle* was co-dominant with *C. erecta* at S6.

Regression equations relating tree height and dbh were obtained for each species:

R. mangle - $\log(\text{height}) = 0.2162 + 0.7434 \cdot \log(\text{dbh})$, ($r^2 = 0.83$, $n=73$);

L. racemosa- $\log(\text{height}) = 0.2931 + 0.7465 \cdot \log(\text{dbh})$, ($r^2 = 0.96$, $n=35$);

A. germinans- $\log(\text{height}) = 0.2069 + 0.746 \cdot \log(\text{dbh})$, ($r^2 = 0.87$, $n=30$).

Mean tree heights of mangrove forests in the four sites increased from 5.4 m in the oligohaline location (S6) to 10.1 m in the downstream location (S1). Tree heights at S4 and S3 were 7.8 and 9.8 m, respectively.

Biomass of individual trees was calculated with tree height and dbh using the species-specific allometric equations described above. Total above ground biomass at each of the four sites was estimated by summing the individual tree biomass values. Organic matter storage was higher in mangrove forests at S1 and S3 rather than S4 or S6. Total above ground biomass in 1994 was estimated at 245.7, 250.8, 127.4 and 78.7 Mg/ha in S1, S3, S4 and S6, respectively (Fig. 4.1). The contribution of each species to total biomass was similar to that of total basal area (Fig. 4.1). *L. racemosa* was the major component of total biomass in S1 and S3, whereas *R. mangle* was dominant in S4 and S6.

Average tree growth rates, calculated as an increase in basal area (cm²·tree⁻¹·yr⁻¹) and in biomass (kg·tree⁻¹·yr⁻¹), varied among sites and species (Table 4.1). *A. germinans* had the greatest basal area increase and biomass production at S1, whereas *L. racemosa* growth rate exceeded those of the other species in S3, S4 and S6. The average tree growth rates of *R. mangle* were lower than those of *A. germinans* and *L. racemosa* in all sites.

Annual increments of total biomass in S1 and S3 were twice the levels of those in S4 and S6 during the interval from January 1995 to February 1996 (Table 4.1). Although average tree growth rate of *R. mangle* were low, this species contributed 78% and 87% of total biomass increment in S4 and S6, respectively, due to higher density of *R. mangle* in these sites. *L. racemosa* dominated total biomass increments at 46% in S1 and 86% in S3.

Pore water characteristics

There were significant effects of site and season on pore water salinity with a significant interaction of site * season (Table 4.2). Pore water salinity decreased from S1 to S6 at all sampling dates and peak concentrations at each station occurred during August (Fig. 4.3). The highest pore water salinity occurred at S1 in August at 33.5 g/kg, compared to 8.2 g/kg at S6

during this season. Pore water salinities were generally lower in January at 23.2 g/kg and 1.6 g/kg at S1 and S6, respectively. The sites with the greatest seasonal change in salinity were S3 and S4 that ranged from 8.2 and 4.4 g/kg in January to 26.1 and 26.5 g/kg in August, respectively.

There were significant effects of site and season on the pore water sulfide with a significant interaction of site * season (Table 4.2). Multiple comparisons of means in each sampling season exhibited a significant site effect only in August, with the highest concentration at S6 compared to no differences among S1, S3, and S4 (Fig. 4.3). No sulfide concentrations could be detected at any of the sites in January when the ground water level was 40 cm below the surface. The highest mean sulfide concentration was 0.46 mmol/L at S6 in August, compared to 0.15 mmol/L at the other sites. Pore water pH was near neutral at all sites with the mean of sites ranging from 6.6 to 6.9.

Nitrite and NO_3^- concentrations were $<1 \mu\text{mol/L}$ and $<0.5 \mu\text{mol/L}$, respectively, at all sites during the three sampling seasons (Fig. 4.4). The repeated measures ANOVA showed significant effects of site and season on the pore water NO_2^- with a significant interaction (Table 4.2). Significant site effects were only observed in January with higher concentrations of NO_2^- at S6 and S4 than at S1 and S3 (Fig. 4.4). There were no significant site and season effects on NO_3^- (Table 4.2, Fig. 4.4). NH_4^+ concentrations were significantly different among sampling seasons (Table 4.2), with the highest mean in August and no difference in concentrations between January and May. However, there were no significant site effects on pore water NH_4^+ concentrations (Table 4.2). Mean PO_4^{3-} concentrations were $<2 \mu\text{mol/L}$ at all sites during the three sampling seasons, except at S3 in January. There were significant effects of season and significant interaction between site and season, but there was no site effect on pore water PO_4^{3-} concentrations (Table 4.2).

Soil nutrients

There were significant effects of site, depth and season on contents of available P and extractable NH_4^+ expressed as per unit volume (Table 4.3). Available P contents usually decreased from surface to 40 cm depth. The spatial trend of available P contents was an increase from S6 to S1 along the estuary (Fig. 4.5). The decrease in extractable NH_4^+ contents with depth was more significant at S1 than other sites (Fig. 4.5). The mean NH_4^+ content was the highest at S1 in the 0-10 cm depth. Soil extractable NH_4^+ contents did not show a significant spatial trend as measured in available P.

There were significant effects of site, depth and season on concentrations (per dry mass) of total soil C, N and P (Table 4.3). Significant interactions among site, depth and season precluded further statistical testing of site, season and depth effects on these soil variables. However, in general, landscape trends in nutrient concentrations were not similar for each nutrient. Total C and N concentrations showed a landscape trend with a decrease from S6 to S1 (Fig. 4.6). In contrast, total P concentrations decreased from S1 and S3 to S6 (Fig. 4.6). Generally, the concentrations of C, N and P decreased slightly with depth, however, the effects of depth on these nutrient concentrations were less than that of site (Table 4.3). Nutrient contents were calculated as a per unit volume and also compared among the sites. There were significant effects of site and season on contents of C, N and P (Table 4.3). C and N contents did not show a landscape trend along the estuary, however, P contents increased significantly from S6 to S1 (Fig. 4.6).

There was a significant effect of site on C:N ratios. Overall mean atomic C:N ratio was 24.7, 22.9, 24.6 and 21.8 in S1, S3, S4 and S6, respectively, without a landscape trend with distance from the mouth of the estuary (Table 4.3, Fig. 4.6). N:P ratios decreased significantly from S6 to S1 with an overall mean atomic N:P ratio of 102.2 (S6), 39.5 (S4), 21.6 (S3) and 14.8 (S1) among sites (Table 4.3, Fig. 4.6). Like N:P ratios, overall mean atomic C:P ratios also decreased from S6 to S1 at 2224, 969, 487 and 355 in S6, S4, S3 and S1, respectively. N:P and

C:P ratios decreased significantly with depth at S6.

DISCUSSION

Soil sulfide and salinity stress along the estuarine gradient

Previous studies report that mangrove and salt marsh sulfide concentrations in Florida are highest in late summer and lowest in winter (Carlson et al. 1983, Rey et al. 1992). Measurements of sulfide concentrations showed a similar pattern with highest values in August and undetectable concentrations in January along the Shark River estuary. Peak sulfide concentrations in summer have been attributed to higher inputs of organic detritus and high evapotranspiration (Rey et al. 1992). High inputs of organic detritus lead to higher oxygen consumption by microbes and enhanced evapotranspiration concentrates sulfide in pore water. Twilley (1985) reported maximum rates of evapotranspiration in August of a basin mangrove forest in southwestern Florida. Undetectable sulfide concentrations at all sites in January corresponded with a decrease in seasonal sea level (Provost 1973) and tidal flooding frequency (Twilley 1985), which enhances rates of oxygen diffusion into sediment and drains reduced pore water from upper soil strata (Rey et al. 1992).

Significant differences in sulfide concentrations among the sites were only found in August with the higher value in the upstream location. This pattern may result from several factors related to hydrology, soil texture and plant aeration. Tidal inundation can flush out sulfides in mangrove soils and contribute reactive iron (King et al. 1982); however, this effect may decrease with increased distance of the wetland from the Gulf shore. Significantly higher soil concentrations of C (43%) in the upstream site of the Shark River estuary may reduce water flow in mangrove soils given that lower water conductivity occurs in wetland soils with higher organic matter content (Mitsh and Gosselink 1993). Furthermore, mangrove roots can have a significant feedback effect on reduced mangrove soils by transporting oxygen to the surrounding soil matrix (McKee 1993). The magnitude of this effect depends on plant biomass and root density (Boto and Wellington 1984, McKee et al. 1988). Although the above-ground mangrove biomass at S6 was only half of the amount at the downstream sites, implying a lower oxidation potential by roots into sediment, the relative amount of below-ground biomass among the sites was not clear.

The species-specific tolerance of mangroves to pore water sulfide concentrations has been associated with patterns of mangrove species zonation. Carlson et al. (1983) measured sulfide concentrations ranging from <0.01 mmol/L to 1.5 mmol/L in an east Florida mangrove. Nickerson and Thibodeau (1985) reported that values ranged from 0.68 to 4.1 mmol/L in Bahamian mangrove soils. McKee and her colleagues, using the same method as I did, found that pore water sulfide concentrations ranged from 0.24 to 3.36 mmol/L (McKee et al. 1988) and 0 to 2.46 mmol/L (McKee 1995a) in a Belizean mangrove, compared to 0.14 to 3.08 mmol/L in a southwestern Florida mangrove (McKee 1993). Mangrove soils along the Shark River estuary can be characterized as only slightly reducing with most concentrations of sulfide less than the lower range of these other studies. The lower concentrations of sulfide (0-0.46 mmol/L) compared to these other reported values indicate that this stressor is not responsible for the landscape gradient of decreased forest stature of mangrove wetlands in the Shark River estuary.

Hypersalinity has been frequently suggested as one of the major factors limiting mangrove forest stature and growth (Lugo and Snedaker 1974, Cintrón et al. 1978, Boto and Wellington 1984). Pore water salinity in mangrove wetlands along the Shark River estuary during both the dry and wet seasons did not exceed 35 g/kg, below the critical value that influences mangrove complexity (see Lugo et al. 1988). Heald (1969) and Powell (1989) also reported that salinities in the North River estuary and the Shark River estuary were lower than 30 g/kg in mangrove regions based on monthly measurements. There were increases to the marine zone in both the landscape gradients of pore water salinity and basal area of forest along the axis of the Shark River estuary, indicating that forest development along the estuary was not limited by soil salinity. Based on

correlation of tree height and soil salinity, Cintrón et al. (1978) suggested that a soil salinity of 65 g/kg was a threshold above which would cause an increase in mangrove tree mortality in Puerto Rico. Day et al. (1987) found that mangrove structure and productivity in Mexico was not affected by salinities under 50 g/kg. Therefore, mangrove wetlands in the Shark River estuary are characterized as lacking any significant stress effects of either soil salinity or sulfide concentrations.

Soil N and P resources along the estuarine gradient

Concentrations of pore water ammonium and phosphate were lower in the study sites of the Shark River estuary compared to reported values for other mangrove soils. Pore water ammonium concentrations are lower than reported for mangroves in Florida Bay (Rosenfeld 1979a), Missionary Bay of Australia (Smith et al. 1991), Papua New Guinea (Alongi et al. 1993), and Belize (McKee 1995a), but are similar to those reported for mangroves in the Indian River of Florida (Carlson and Yarbrow 1988) and dwarf mangroves in Belize (Feller 1995). Pore water phosphate values in the study sites of the Shark River estuary are lower than those reported by Rosenfeld (1979a), Carlson and Yarbrow (1988), McKee (1995a) and Feller (1995) for mangroves in a carbonate setting and by Smith et al. (1991) for Australian mangroves, but are higher than those reported by Alongi et al. (1993).

The presence of detectable pore water NO_3^- and NO_2^- in the Shark River study sites over three sampling periods coincides with the significance of aerobic zones around mangrove roots that can enhance nitrification (Joye and Hollibaugh 1995), which may lead to lower ammonium concentrations in pore water. It is interesting that NO_2^- was higher than NO_3^- during January at S3, S4 and S6, when ground water level was lowest and sulfide concentrations were undetectable. This suggests a seasonal coupling of nitrification with the hydrology of these forests mediated by increased aeration of the upper soil strata. In general, there was no consistent spatial gradient of pore water ammonium, nitrate, nitrite, and phosphate in the mangrove soils along the Shark River estuary. Factors controlling these pore water values are complex, including decomposition and mineralization (Chapter 3), adsorption and dissolution by mineral and organic matter (Rosenfeld 1979b), fluxes across the sediment-water interface (Alongi et al. 1993, Rivera-Monroy et al. 1995a), plant uptake (Boto and Wellington 1984), microbe immobilization (Alongi et al. 1993), redox potential (Boto and Wellington 1984) and bioturbation (Smith et al. 1991). The interactions of these factors probably have more significant effects on pore water nutrients within mangrove sites than among sites along the estuary.

Alongi et al. (1992) reviewed concentrations of total soil N and P in mangrove wetlands around the world. Total N concentrations ranged from 0.02 to 0.4 % and most of P concentrations were between 0.011 to 0.067%, except in a mangrove in West Africa where total P ranged from 0.08 to 0.16%. Several recent studies in mangroves reported total soil N concentrations ranging from 0.03 to 1.7% and P concentrations ranging from 0.043 to 0.085% (Lynch 1989, Alongi et al. 1993, Alongi 1996). Compared with these data, mean concentrations of soil total N (0.7 to 2.3%) and P (0.06 to 0.12%) in mangrove wetlands along the Shark River estuary are higher than in most of the mangroves world-wide.

There is an increased concern that accelerated nutrient loadings, especially P, from anthropogenic sources can change the vegetation characteristics of oligotrophic regions of the Everglades. Intensive studies have been conducted on N and P distribution and accumulation in soil and plants in Water Conservation Area 2A, adjacent to Everglades Agricultural Area, in the northern Everglades (Davis 1991, Koch and Reddy 1992, Craft and Richardson 1993a,b, Reddy et al. 1993, DeBusk et al. 1994). Results of these studies showed that there was a spatial gradient of soil P decreasing from areas proximal to surface inflows to regions south in WCA2A. Surface soil concentrations of total P in the nutrient enrichment area occurred at levels of 0.12-0.16% (DeBusk et al. 1994) and 0.14-0.16% (Craft and Richardson 1993a), compared to about 0.05% in areas south of the enrichment in WCA2A to 0.07% in WCA3 (Craft and Richardson 1993b). Both

southern areas are in the immediate vicinity of the upstream extent of the Everglades National Park. Total P concentrations in the oligohaline mangrove site (0.057%) of the Shark River estuary are similar to reported concentrations in WCA2A and WCA3, upstream of the Shark River Slough. However, P concentrations near the mouth of the estuary (0.12%) are similar to the upper limits of total soil P in the marsh adjacent to areas of agriculture effluent. If bulk density is taken into consideration, P contents per unit volume soil in the downstream locations (0.212 and 0.381 mg/cm³ in S3 and S1, respectively) are even higher than those in the enriched area in WCA2A where P contents are < 0.12 mg/cm³ (Koch and Reddy 1992), 0.2 mg/cm³ (Reddy et al. 1993), and 0.16 mg/cm³ (Craft and Richardson 1993a). These comparisons indicate that increased loading of P to the northern Everglades marsh from the agriculture area has not yet affected mangroves in this study area, because upstream marshes in the Shark River Slough effectively reduce surface water P concentrations which leads to relatively low P inputs to the Everglades National Park (Davis 1994).

Total C and N concentrations increased from the mouth of the Shark River estuary to oligohaline site, resulting in similar ratios of C:N; however, there was no landscape trend of total C and N contents per unit volume along the estuary. In contrast to the spatial trend in total C and N concentrations, both total P concentrations (per unit dry mass) and contents (per unit volume) showed a reduction in mangrove soils from the mouth of the estuary to the oligohaline zone along the Shark River estuary. The gradient in soil P concentrations coincides with higher bulk densities at the downstream locations. Soil extractable P contents exhibited the same trend as total P content. The major source of freshwater to the estuary is the Shark River Slough, and the gradient of soil salinity along the estuary represents the relative importance of terrestrial runoff and Gulf water to the chemical composition of soils among the study sites. Increased contents of both total and extractable P with salinity suggests that the Gulf of Mexico is the major source of P for mangrove growth. Fourqurean et al. (1992) reported higher P availability in the northwest region of Florida Bay and hypothesized that P is transported in dissolved and suspended forms to this region from the Gulf of Mexico to Florida Bay. Therefore, P from the Gulf source appears to have a stronger impact on mangroves along the Shark River estuary than freshwater input from the Shark River Slough, at least in the recent time scale.

Forest structure

It has been suggested that mangrove wetlands in south Florida can recover from large scale disturbances, such as hurricanes, and achieve maturity in 20-30 yrs (Lugo and Snedaker 1974, Lugo et al. 1976, Lugo 1980). Such large scale disturbances have a significant impact on the structure and function of mangrove ecosystems throughout the Caribbean (Craighead and Gilbert 1962, Roth 1992, Smith et al. 1994, Wanless et al. 1994, Doyle et al. 1995). On September 10, 1960, Hurricane Donna passed throughout the Shark River region with a wind speed at 220 km/hr and gusts higher than 288 km/hr (Craighead and Gilbert 1962). The initial mortality of mangroves caused by the hurricane was 50 to 70% (Craighead and Gilbert 1962), however, mortality probably was higher due to delayed mortality (Smith et al. 1994). After 34 yrs of regeneration, mangrove forests in the downstream locations of the estuary have grown into a mature forest with the highest basal area among mangrove forests in Florida and Puerto Rico (Table 4.4). Mangrove forests in Florida and Puerto Rico lie in the hurricane tracking zone, whereas mangrove forests in Mexico and Costa Rica are less influenced by hurricanes and these forests have a lower density but larger trees and higher basal area (Pool et al. 1977).

The bell-shaped pattern of size-class distribution of mangroves in S1 represents a relative mature forest, compared to distributions in S6 and S4 that have a much higher density of smaller trees. Since mangroves in this region regenerated from the disturbance of Hurricane Donna, I assume that all sites are of similar age with a possibility that the forest in S6 is older than in S1, given that the central path of Hurricane Donna was located in the downstream region of the estuary (Craighead and Gilbert 1962). Thus, size-class distribution, an index of age structure, of

mangrove forests in these study sites may be related to the gradient of nutrient resources.

Davis (1940) recorded that the relative abundance of three mangrove species in the downstream zone of the Shark River was 60% for *R. mangle*, 30% *A. germinans* and 10% *L. racemosa*. Results indicate that forests in the downstream locations (S1 and S3) are mixed-species community with a relative higher importance value of *L. racemosa*. *L. racemosa* had a greater growth rate and dominated in the larger size (dbh > 8 cm) cohort in sites with high P availability (S1 and S3). This implies that *L. racemosa* recovers faster than *R. mangle* and can dominate the mangrove canopy in fertile sites. McKee (1995b) compared the growth characteristics of seedlings under the control of light intensity and nutrient availability, and suggested that the order of success of three mangrove species was *L. racemosa* > *A. germinans* > *R. mangle* at either higher nutrient or light availability. Not only can *L. racemosa* have a higher growth potential under high light and nutrient availability, this species may become dominant in the downstream locations of the estuary because it recovers rapidly by trunk sprout after stem damage (Wadsworth 1959). In my study plots, *A. germinans* were the largest specimens of live and dead trees with dbh > 30 cm in all plots. These trees are survivors from Hurricane Donna in 1960 and this species may be the most resistant to hurricane disturbance. Smith et al. (1994) surveyed the mortality of mangroves in south Florida after Hurricane Andrew in 1992 and also found that *A. germinans* had significantly less mortality than the other two mangrove species. The widespread occurrence of *R. mangle* through the study area and its dominance in the smaller tree cohort (dbh < 8 cm) indicate that *R. mangle* has a relatively higher tolerance to shade and nutrient stress. The density of dead trees of *L. racemosa* was the highest at 83% in S1, 72% in S3 and 69% in S6 for total dead trees, with an exception in S4. The closed canopy and self-thinning of forest will probably replace *L. racemosa* with *R. mangle* due to the lower tolerance of *L. racemosa* to shading (Ball 1980). Therefore, hurricane disturbance may have an impact on the species richness of a region by resetting the processes of mangrove succession.

Forest biomass accumulation in relation to nutrient limitation

Biomass production of mangroves in my study sites increased from the oligohaline to marine zones along the Shark River estuary. Biomass production at two downstream locations (S1 and S3) was 10.73 and 11.96 Mg·ha⁻¹·yr⁻¹, which is comparable with that of a riverine mangrove (12.06 Mg·ha⁻¹·yr⁻¹) and higher than a fringe mangrove (7.7 Mg·ha⁻¹·yr⁻¹) in Laguna de Términos, Mexico (Day et al. 1987). The annual increment of biomass was lower at the intermediate and upstream locations of the estuary dominated by *R. mangle* and similar to an estimate (3.07 Mg·ha⁻¹·yr⁻¹) of *Rhizophora* forests in Puerto Rico (Golley et al. 1962). However, these values are higher than that of a basin (0.68 Mg·ha⁻¹·yr⁻¹) and a fringe mangrove (1.2 Mg·ha⁻¹·yr⁻¹) in southwestern Florida (Warner 1990). In the absence of a toxic stress, soil nutrient availability is often implicated as the principle factor determining variation in forest structure and biomass production. Comparative analysis of mangrove forests and soil characteristics in Australia revealed that concentrations of extractable P decreased with tidal height and extractable P was one of the major factors limiting annual biomass accumulation (Boto and Wellington 1984). P fertilization resulted in a positive leaf production in elevated mangrove areas (Boto and Wellington 1983). Experimental additions of P to dwarf mangroves in Belize significantly stimulated the growth of trees, which increased biomass accumulation (Feller 1995, Twilley 1995). Silver (1995) further pointed out that soil P availability is important to humid tropical forest functions, such as litterfall production. My study shows that the landward decline of forest structure among even-aged mangrove forests can be associated with a decrease in soil P concentration, suggesting that P availability is a major factor influencing the gradient of forest development in the Shark River estuary. In addition, the mean N:P ratio of mangrove soil varied along the estuary from <10 in the downstream locations, 18 in the intermediate zone, to >40 in the upstream location. This gradient in relative availability of N and P indicates the importance of P as a limiting nutrient in the

oligohaline zone of this estuary.

A study of mangrove productivity and soil characteristics in tropical Australia and Papua New Guinea showed that forests with lower productivity were associated with soils that have decreased concentrations of P (Boto et al. 1984). Boto (1991) further suggested that tropical mangroves in Australia are P-limited. I used a Monod model (Bridgham et al. 1995) to analyze the specific nature of P-limitation of mangrove forest development in Florida and the Caribbean. The relationship between forest development and nutrient resource availability in mangroves was examined by the following model (Bridgham et al. 1995):

$$PR = \frac{(R_{ac} - R_{min})PR_{max}}{R_{ac} - R_{min} + \alpha}$$

where PR is production, PR_{max} is the maximum production, R_{ac} is the amount of resource acquired, R_{min} is nutrient availability at zero production and α is half-saturation constant with respect to R_{ac} (see Bridgham et al. 1995 for details). To apply this Monod model to results in this study, I used basal area as an index of biomass production and total P (per unit area soil) as an estimate of nutrient availability (Bridgham et al. 1995). Basal area is a more direct estimate of forest production than biomass, because errors can be introduced by different allometric equations used to calculate biomass in different geographical areas (Day et al. 1987). Basal areas were regressed against respective contents of soil P using the Monod model above and a nonlinear fitting technique (SAS 1989) by minimizing residual sum of squares. There was a significant range in total P concentrations among the mangrove sites, and basal area was strongly correlated with total soil P (Fig. 4.7). The fit of the Monod model was significant ($r^2=0.80$), and R_{min} was positive with an optimum soil P content of 36.3 g/m² to a depth of 40 cm. The half-saturation constant of soil P based on the nonlinear model was 29.3 g/m².

These data suggest that basal area increased asymptotically with soil P content among these even-aged mangrove forests along the Shark River estuary. Lower soil P resources in the oligohaline zone of the estuary limit the basal area development of mangrove wetlands. Basal area development approached the asymptote in the marine zone near the mouth of the Shark River estuary where maximum soil P concentrations exist. These results suggest that the landscape pattern of mangrove forest recovering from hurricane disturbance may depend on availability of soil P resources. Therefore, results in this study indicated that soil properties in the marine region of the Shark River estuary can be characterized as lacking any effects of stress in terms of either nutrient resource or toxic compounds (salinity and sulfide). Thus Davis's (1940) hypothesis that the coastal forest in this region is the optimum growth of mangroves in the Americas can be related to these soil attributes.

Table 4.1 Average basal area (BA) increment and biomass increment per tree, and total annual basal area increment and woody growth per unit area of mangroves along the Shark River estuary, the Everglades National Park.

	S1	S3	S4	S6
Average BA increment (cm ² ·tree ⁻¹ ·yr ⁻¹)				
<i>Avicennia germinans</i>	5.57	7.16	0.57	-
<i>Laguncularia racemosa</i>	3.84	10.90	12.07	1.94
<i>Rhizophora mangle</i>	3.19	0.94	1.51	1.32
<i>Conocarpus erecta</i>	-	-	-	0.39
Average biomass increment (kg·tree ⁻¹ ·yr ⁻¹)				
<i>Avicennia germinans</i>	4.03	4.81	0.37	-
<i>Laguncularia racemosa</i>	3.09	9.17	8.59	1.15
<i>Rhizophora mangle</i>	2.35	0.60	1.04	0.69
<i>Conocarpus erecta</i>	-	-	-	0.11
BA increment (m ² ·ha ⁻¹ ·yr ⁻¹)				
<i>Avicennia germinans</i>	0.24	0.06	0.01	-
<i>Laguncularia racemosa</i>	0.65	1.11	0.09	0.04
<i>Rhizophora mangle</i>	0.51	0.12	0.36	0.71
<i>Conocarpus erecta</i>	-	-	-	0.07
Total	1.40	1.29	0.46	0.83
Total woody growth (Mg·ha ⁻¹ ·yr ⁻¹)				
	10.73	11.96	3.23	4.20

Table 4.2. Summary of F statistics from repeated measures ANOVA of site and season effects on pore water chemistry. Statistical tests were conducted using univariate tests. Effect of sampling station was not significant ($P>0.05$).

Sources	df	Sulfide	Salinity	NH ₄ ⁺	NO ₂ ⁻	NO ₃ ⁻	PO ₄ ³⁻
Site	3, 8	31.62***	167.8***	NS	12.2**	NS	NS
Season	2, 16	50.82***	445.7***	30.3***	33.4***	NS	5.17*
Site*season	6, 16	13.30***	28.9***	NS	7.3***	NS	2.93*

* $P\leq 0.05$, ** $P\leq 0.01$, or *** $P\leq 0.001$, NS no significance.

Table 4.3 Summary of F statistics from repeated measures ANOVA of site, depth and season effects on soil C, N and P. Statistical tests were conducted using univariate tests for between-subject factors (site, depth) and multivariate tests for within subject factors (season, season*site, season*depth, season*site*depth). Effects of season*depth, season*site*depth were not significant ($P>0.05$).

Variables	Sources				
	Between subject (F-values)			Within subject (Wilks' value)	
	Site	Depth	Site*Depth	Season	Site*Season
df	3, 32	3, 32	9, 32	2, 31	6, 62
Available P ($\mu\text{g}/\text{cm}^3$)	270***	88.7***	8.4***	0.47***	NS
Extractable NH_4^+ ($\mu\text{g}/\text{cm}^3$)	72***	73.0***	2.7*	0.39***	0.33***
C(%)	2317***	24.2***	6.3***	0.30***	0.63*
N(%)	1637***	21.6***	7.8***	0.22***	0.21***
P(%)	205***	9.5***	9.3***	0.60***	0.62*
C (mg/cm^3)	22***	NS	NS	0.36***	NS
N (mg/cm^3)	22***	3.1*	NS	0.24***	0.20***
P (mg/cm^3)	501***	3.5*	3.7**	0.78*	0.63*
C:N	20***	NS	3.6**	0.14***	0.12***
N:P	372***	14.0***	21.8***	0.69**	0.63*
C:P	375***	15.3***	21.6***	NS	0.61*

* $P\leq 0.05$, ** $P\leq 0.01$, or *** $P\leq 0.001$, NS=no significance

Table 4.4 Structural characteristics of mangrove forests of southern Florida, Puerto Rico, Mexico and Costa Rica.

Site	Latitude (N)	Number of trees >2.5 cm	Basal area (m ²) >2.5 cm	Reference
<u>Florida</u>				
Shark River (S1)	25°20'	3725	40.4	This study
Shark River (S3)	25°21'	3600	39.7	This study
Shark River (S4)	25°22'	2575	20.7	This study
Shark River (S6)	25°24'	7333	19.6	This study
Ten Thousand Islands	25°50'	4000	38.5	Pool et al. 1977
	25°50'	2800	23.5	Pool et al. 1977
	25°50'	1800	15.0	Pool et al. 1977
Rookery Bay	25°55'	5900	20.3	Pool et al. 1977
	25°55'	2600-9400	12.9-35.5	Lugo et al. 1980
Turkey Point	25°25'	25030	6.0	Pool et al. 1977
<u>Puerto Rico</u>				
Piñones	18°27'	1380-3210	15.8-21.6	Pool et al. 1977
Vacia Talega	18°27'	1890	20.9	Pool et al. 1977
Ceiba	18°15'	5690	16.7	Pool et al. 1977
Mona Island	18°06'	2930	35.0	Pool et al. 1977
Aquirre	17°57'	3670	22.6	Pool et al. 1977
Jobos Bay	17°57'	11650-47330	14.3-15.5	Pool et al. 1977
Punta Gorda	17°57'	1780	6.9	Pool et al. 1977
<u>Mexico</u>				
Roblitos	22°31'	2240	29.6	Pool et al. 1977
Isla La Palma	22°35'	2360	60.8	Pool et al. 1977
Isla Roscell	22°30'	1480	28.5	Pool et al. 1977
El Calón	22°44'	3120	15.2	Pool et al. 1977
Rio de las Cañas	22°31'	1790	57.8	Pool et al. 1977
Laguna de Términos	18°40'	3360	34.2	Day et al. 1987
Laguna de Términos	18°40'	7510	23.3	Day et al. 1987
<u>Costa Rica</u>				
Moin	10°00'	1370	96.4	Pool et al. 1977
Boca Barranca	09°58'	1100	32.9	Pool et al. 1977
Santa Rosa	10°45'	1050	23.2	Pool et al. 1977

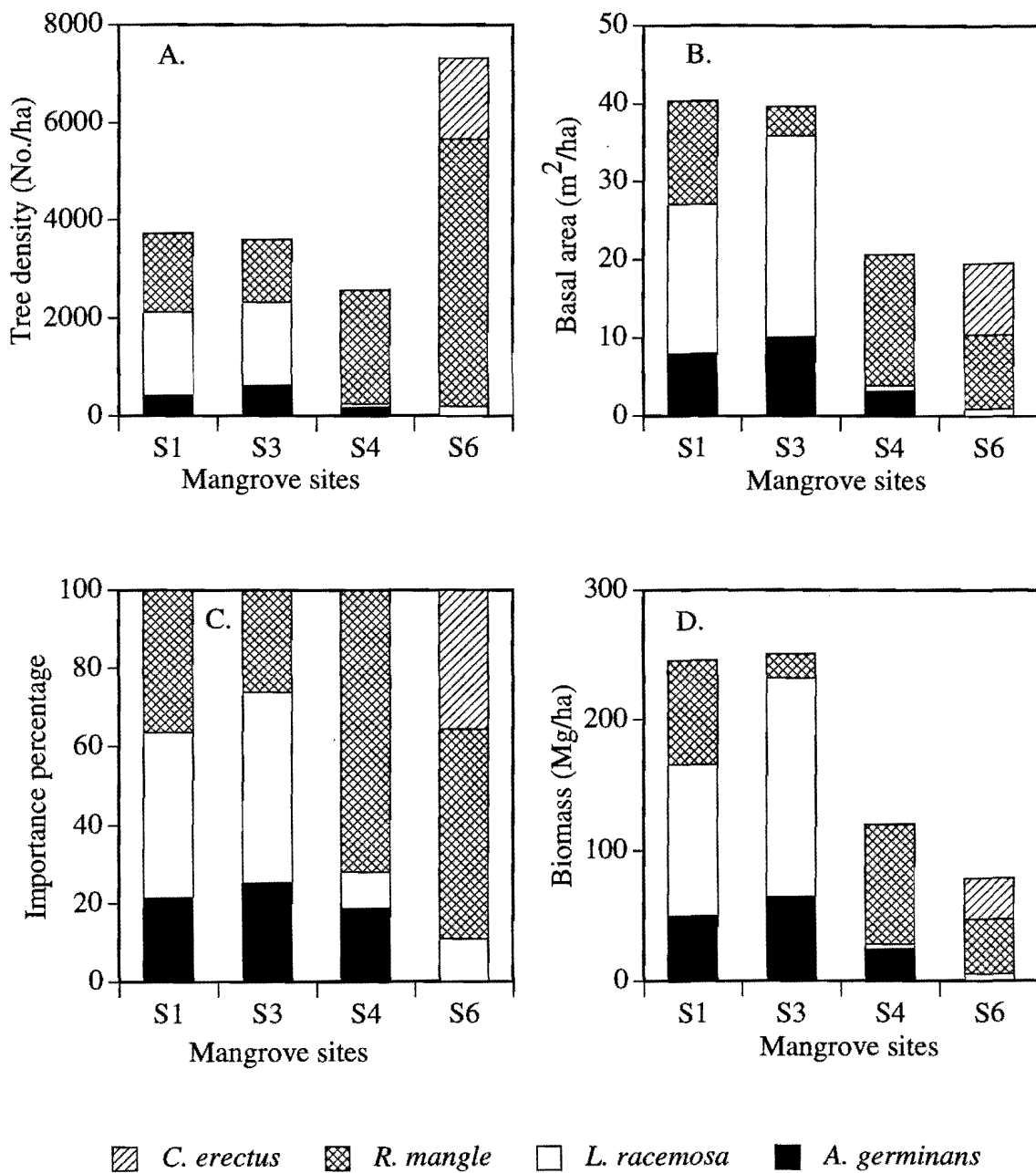


Figure 4.1 Mangrove forest structure by species at sites along the Shark River estuary from the downstream location (S1) to the upstream location (S6) including:
A) Density, B) Basal area, C) Importance values, and D) Biomass.

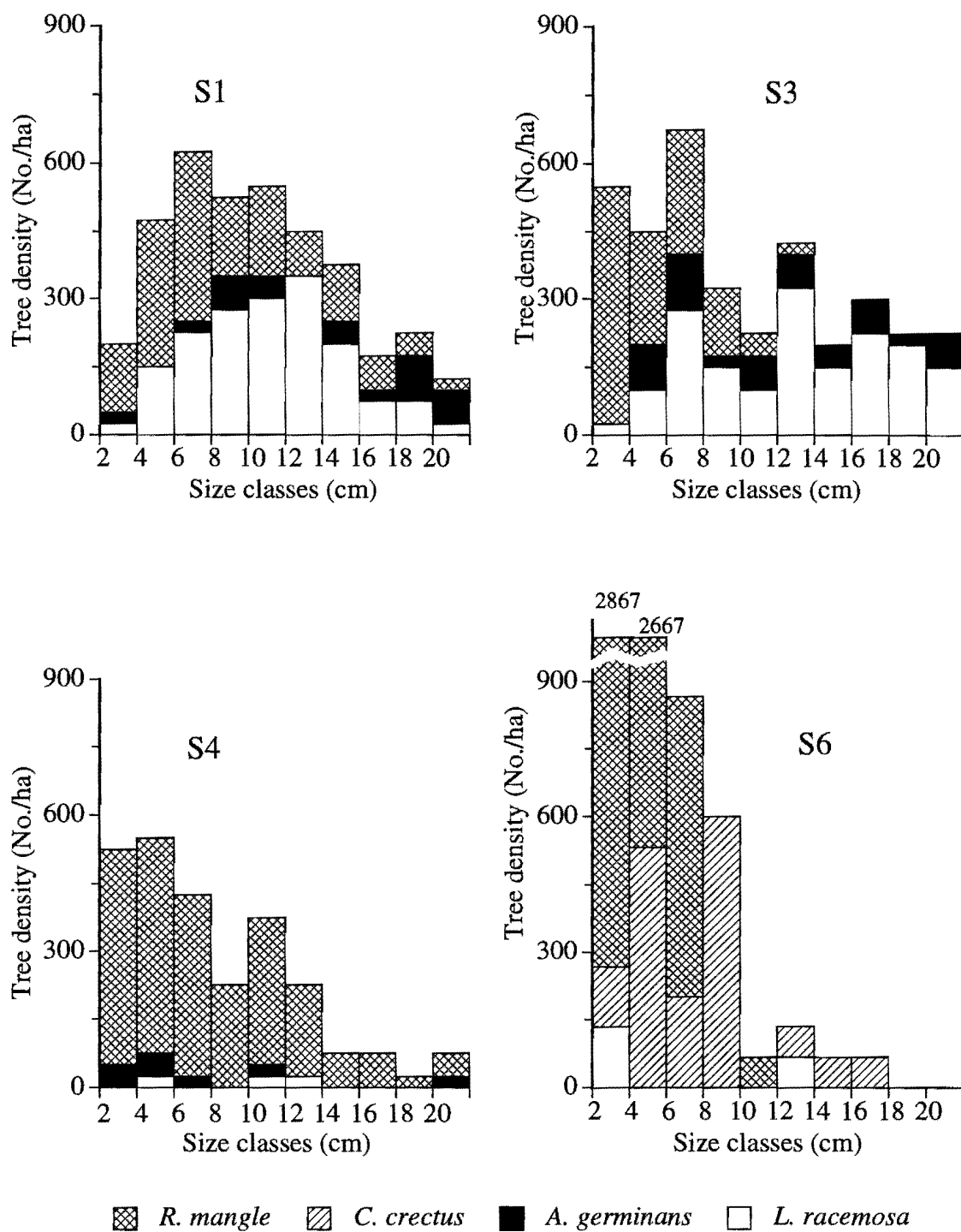


Figure 4.2 Size class distribution of mangroves by species along the Shark River estuary from the downstream location (S1) to the upstream location (S6).

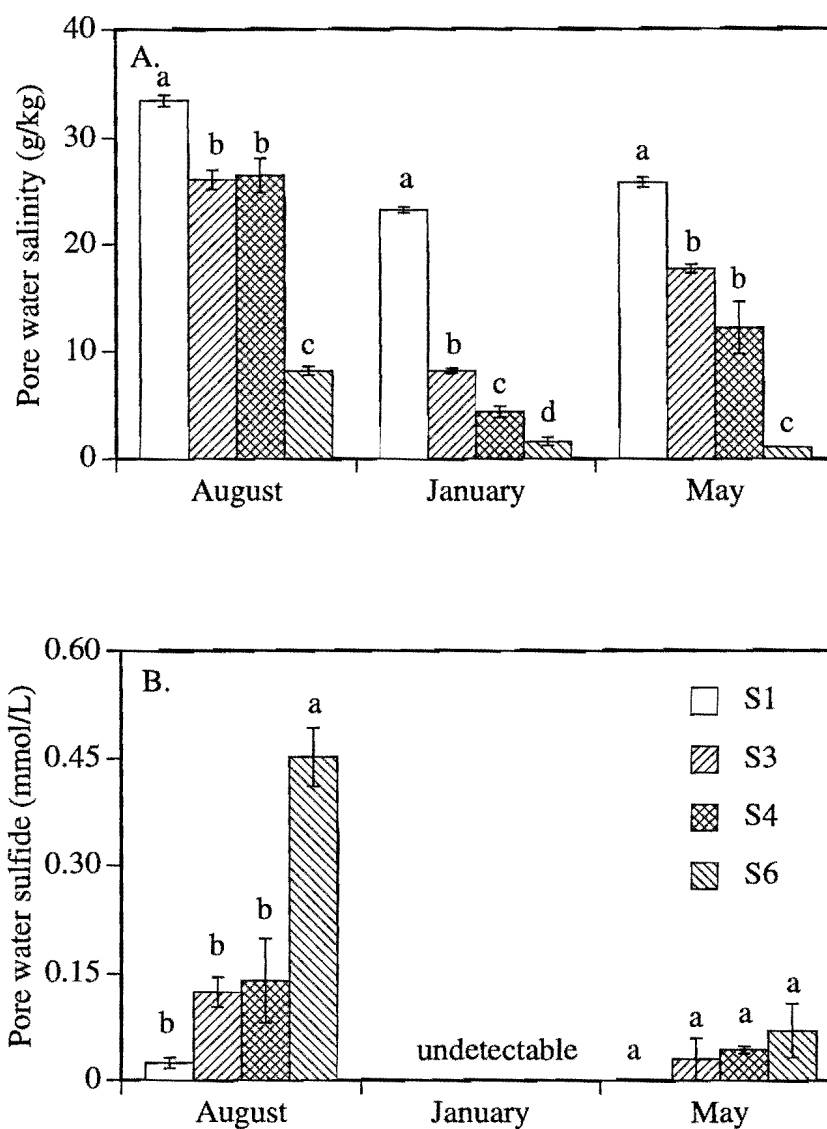


Figure 4.3 Spatial and temporal variation in pore water stressors including salinity (A) and sulfide (B) measured along the Shark River estuary during August 1994, January and May 1995. The values at each sampling date with the same letter are not significantly different ($P > 0.05$; Tukey's test). Values are mean $\pm$ SE ($n=3$).

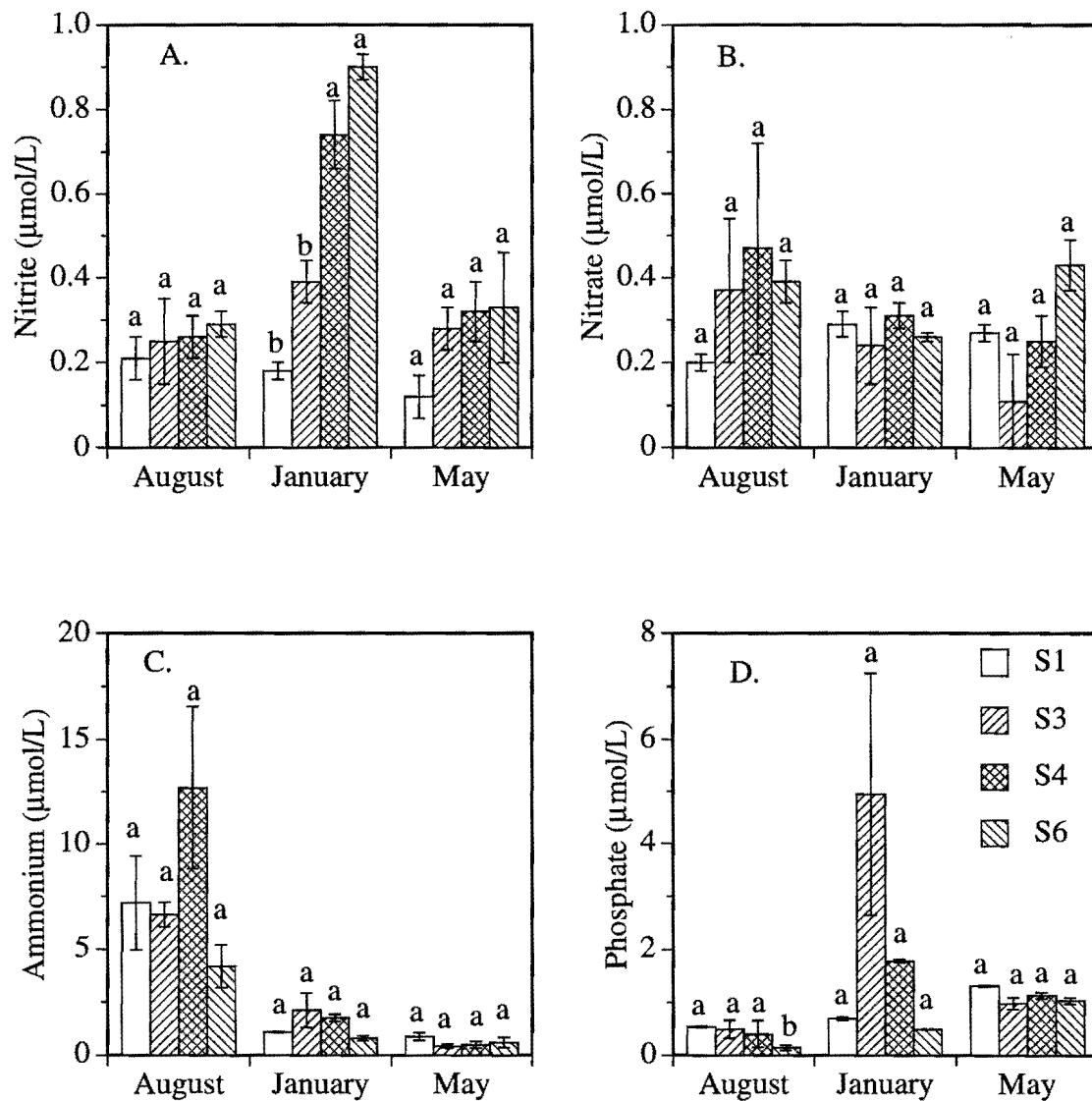


Figure 4.4 Spatial and temporal variation in pore water nutrients including nitrite (A), nitrate (B), ammonium (C) and phosphate (D) measured along the Shark River estuary during August 1994, January and May 1995. The values at each sampling date with the same letter are not significantly different ($P > 0.05$; Tukey's test). Values are mean $\pm$ SE ($n=3$).

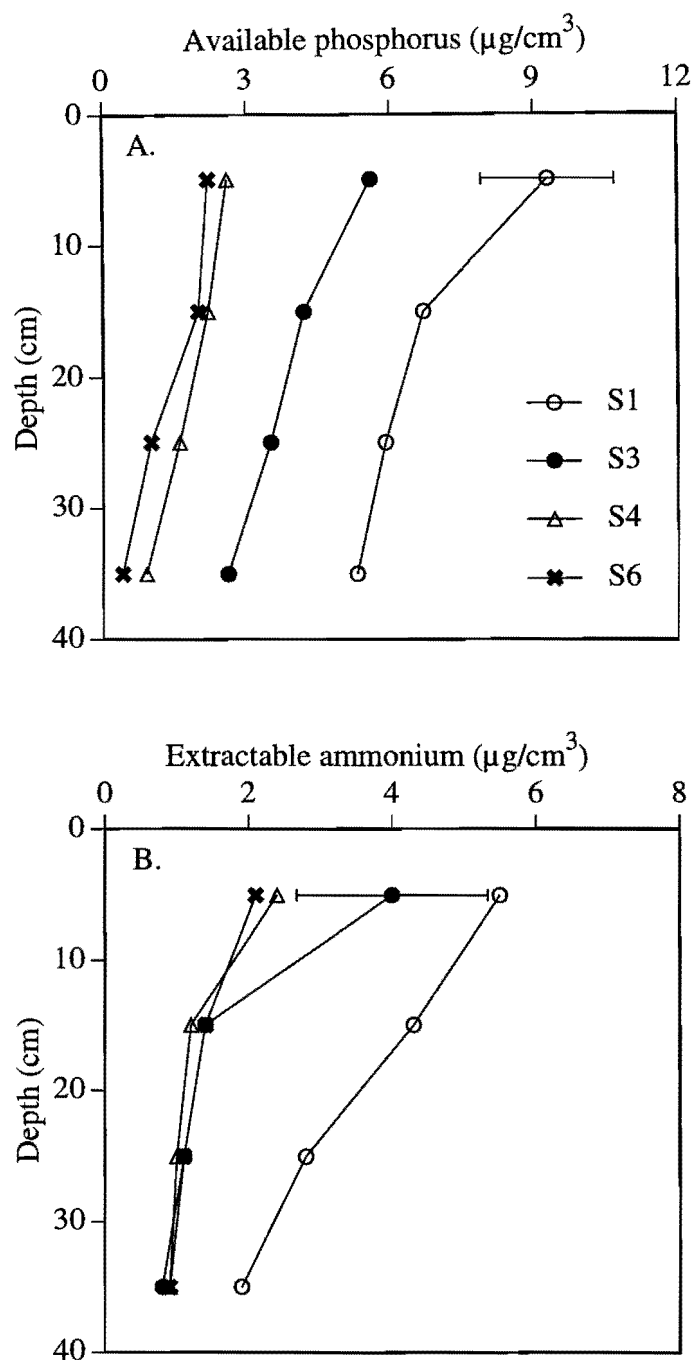


Figure 4.5 Vertical profiles of available phosphorus and extractable ammonium in mangrove soils along the Shark River estuary. Values are expressed as mean of three sampling seasons. Error bars represent the largest standard error of the mean in the data.

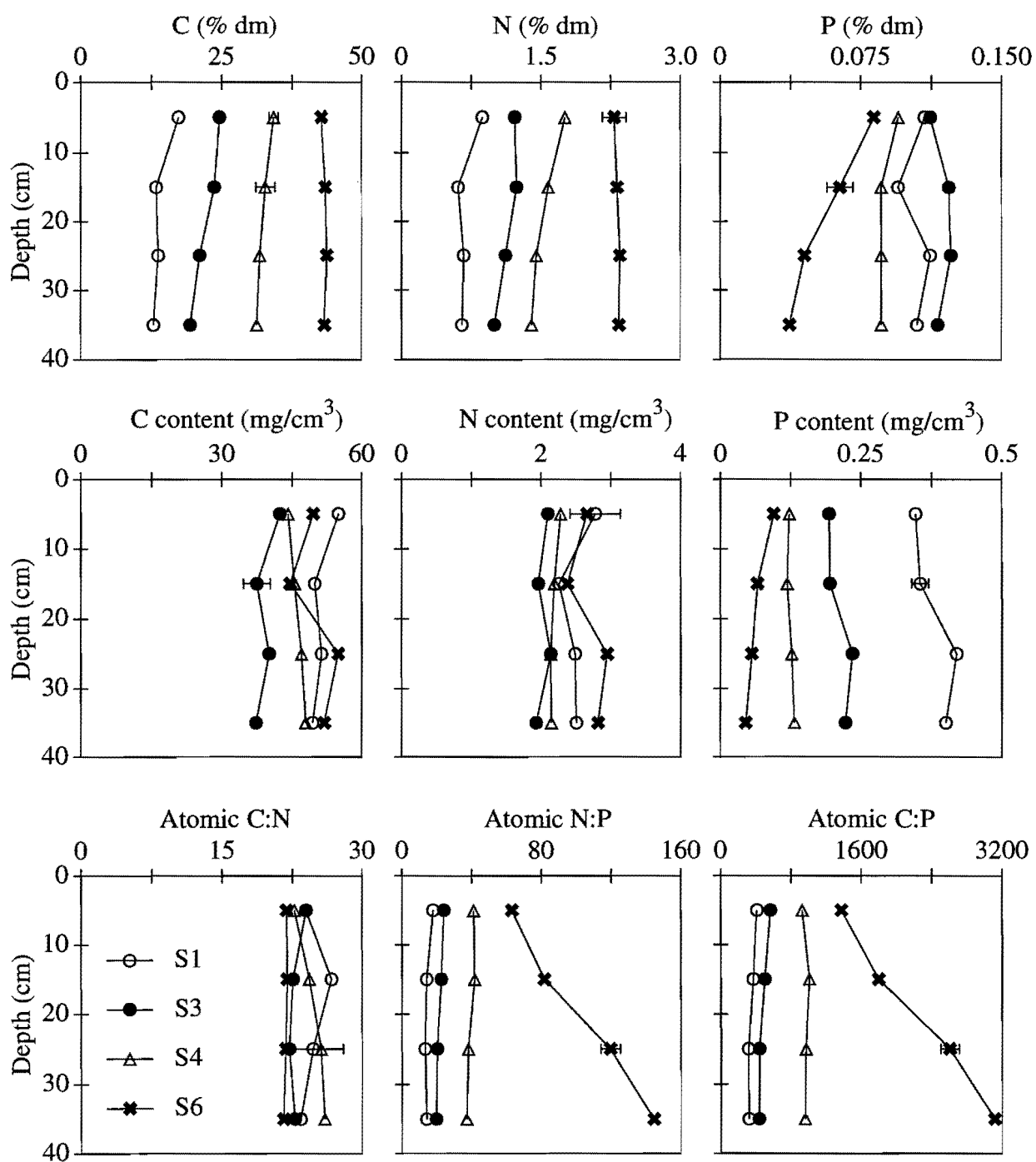


Figure 4.6 Vertical profiles of C, N and P in mangrove soils along the Shark River estuary expressed as percent dry mass (% dm), contents per unit volume of soil (mg/cm³) and atomic ratios of nutrients. Values are expressed as mean of three sampling seasons. Error bars represent the largest standard error of the mean in the data set.

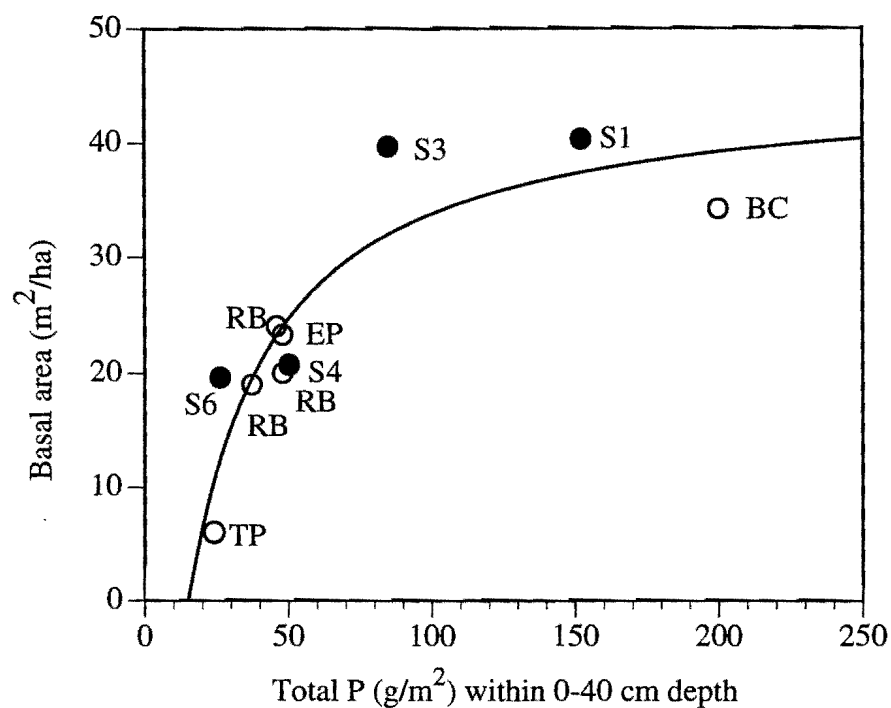


Figure 4.7 Basal area of mangrove forests relative to total phosphorus in mangrove soils. Line is prediction from Monod model (see text).

RB= Basin mangroves, Rookery Bay, Southwest Florida (Warner 1990, Lynch 1989); TP= Dwarf mangroves, Turkey Point, Southeast Florida (Pool et al. 1977, Snedaker and Brown 1981); BC= Riverine mangrove, Boca Chico, Laguna de Términos, Mexico (Day et al. 1987, Lynch 1989); EP= Fringe mangrove, Esterno Pargo, Laguna de Términos, Mexico (Day et al. 1987, Lynch 1989).

CHAPTER 5

MODELING THE VERTICAL DISTRIBUTIONS OF ORGANIC MATTER, NITROGEN AND PHOSPHORUS IN MANGROVE SOILS

ABSTRACT

The vertical distributions of organic matter, nitrogen and phosphorus in mangrove soils were investigated with a mechanistic and process-based model. The nutrient mangrove model (NUMAN) was developed from the SEMIDEC and CENTURY soil organic matter models and parameterized with data from four mangrove sites along the Shark River estuary. The soil characteristics in the four mangrove sites varied greatly in both concentrations and profiles of soil C, N and P. Organic matter, expressed as percentage of ash free dry weight, decreased from 82% in the upstream locations to 30% in the marine sites. Comparisons of the simulated and observed results demonstrated that the landscape gradient of soil characteristics can be adequately modeled by accounting for plant production, litter decomposition and export, and allochthonous input of inorganic materials. The results illustrated that the increase in organic matter content and decrease in soil bulk density from mangrove sites at the mouth of the estuary to those at upstream locations was controlled mainly by variation in allochthonous inputs of inorganic material and mangrove root production. Model simulations showed that the greatest change in organic matter, N, and P occurred in the soil surface, but changes were also evident at depths ranging from 1 cm to 5 cm at some of the sites. The rapid decomposition of labile organic matter was responsible for this decrease in organic matter. Simulated mineralization rates of nitrogen decreased quickly with depth, which corresponded with the decrease of labile organic matter. Fitting the simulation results of the model to observed nutrient profiles indicated that N and P dynamics are tightly linked to organic matter retention. In the future, NUMAN will be modified and linked to a mangrove forest gap model to simulate the feedback mechanisms of soil nutrient recycling, which controls development of the mangrove wetlands.

INTRODUCTION

Long-term geomorphic and hydrologic processes along with primary plant production largely control the formation, physical properties and chemical compositions of mangrove soils (Thom 1982). These soil characteristics have been suggested as significant controls of mangrove productivity (Boto and Wellington 1984), and soil formation has also been considered an important process contributing to biogenic carbon sinks and vertical accretion (Twilley et al. 1992, Parkinston et al. 1994). Soil formation in mangrove wetlands, as in other intertidal wetlands, is the combination of several ecological processes including organic matter production (above and belowground components), export, decomposition, and burial; as well as sedimentation of allochthonous inorganic materials. Organic matter dynamics are also tightly coupled to the biogeochemical cycles of nitrogen (N) and phosphorus (P) by the processes of decomposition, mineralization and plant uptake. Quantifying these processes can provide insights into the biogeochemistry of mangrove soils and the feedback of nutrient recycling on mangrove forest development. However, the temporal scale of soil formation in mangrove wetlands is at hundreds to thousands of years (Scholl 1964a, b). Therefore, biogeochemical models that reconstruct sediment profiles can be used to estimate the relative significance of these processes to the accumulation of organic matter and nutrients in wetland soils.

The biogeochemistry of mangrove soils was studied by modifying the SEMIDEC simulation model developed for soils in tidal marsh wetlands (Morris and Bowden 1986) and the CENTURY model developed for grasslands (Parton et al. 1987). The SEMIDEC model integrates the effects of both aboveground and belowground production, decomposition of organic matter

and mineralization, and sedimentation of allochthonous inorganic materials. A specific combination of these processes successfully predicts the profiles of organic matter, N, P and rates of N mineralization in a tidal marsh wetland.

The objectives of this study were to: (1) modify the SEMIDEC model to examine the effects of forest production, exportation, decomposition and sedimentation on C, N and P distribution in mangrove soils; (2) validate the model with measurements of spatially explicit variables along the Shark River estuary of the Everglades National Park; (3) identify key ecological processes from model simulations that account for the spatial differences among mangrove soils within this geomorphic setting; and (4) provide a soil nutrient model linked to a mangrove forest gap model, to simulate the feedback mechanisms of soil nutrient recycling.

MATERIALS AND METHODS

Soil cores were collected along the Shark River estuary in Everglades National Park in June 1994. Coring consisted of driving 15.2 cm diameter polyvinyl chloride tubing to a depth of 60 cm, compaction was minimized because of the wide diameter core. One core was taken from each site at S1, S3, S4 and S6 (Fig. 5.1). Each core was sectioned at 2 cm intervals, dried at 65°C to constant weight, and weighed for dry bulk density. Each section was ground in a grinding mill and sieved through a 20 mesh screen. Organic content, total N, and total P concentrations were determined on each section. Organic content (% ash free dry weight, AFDW) was determined by combusting each sample at 480°C for 6 h. Three randomly chosen stations in each site were marked for repeated measures of soil mineralization rates in August 1994, January and May 1995 (Chapter 3). Besides measures of mineralization rates in the 0-10 and 10-20 cm depth described in Chapter 3, I also sampled soils from 20-30 and 30-40 cm intervals. Determinations of total N, P and N mineralization rates were described in Chapter 3.

MODEL DESCRIPTION

Soil organic matter dynamics

A mangrove soil nutrient model (NUMAN) was adapted from a mechanistic and process-based model, SEMIDEC (Morris and Bowden 1986), which simulates the vertical distribution of organic matter, N, P, and mineralization in marsh sediments. The SEMIDEC model partitions soil organic matter into pools based on resistance to decomposition, assuming that each pool decomposes simultaneously and independently. Models using multiple compartments of soil organic matter have been used for terrestrial forests (LINKAGE, Pastor and Post 1986; VEGIE, Aber et al. 1991) and grasslands (CENTURY, Parton et al. 1987, Parton et al. 1988). Two pools of soil organic matter in a marsh are distinguished in the SEMIDEC model. One is the labile organic matter (LOM), with relatively rapid decay, which is analogous to the 'active' fraction of soil organic matter in the CENTURY model (Parton et al. 1987). The other pool is refractory organic matter (ROM), with slow decay, which is conceptually similar to the 'passive' fraction of soil organic matter in the CENTURY model.

A unique characteristic of the SEMIDEC model compared to other soil organic models is the calculation of the vertical profile of organic matter and nutrients. The SEMIDEC uses a life-history approach to describe the dynamics of soil organic matter and treats soil horizons as year-class cohorts, which are modified by root production and decomposition of organic matter over time as they are buried. A successful feature of the SEMIDEC model is the simulation of diagenesis for a single year cohort of sediment within a specific unit surface area, including calculations of organic matter, N and P contents in the year-class cohort. The input rates of organic and inorganic matter to the sediment are assumed to be constant.

Modifications of the SEMIDEC model were required to include some of the biogeochemical processes that are unique to coastal forested wetlands including forest production and

decomposition (Fig. 5.1). Litter fall production can be the major input of organic matter to the soil surface. Annual litter production (LP) is expressed as a direct function of forest basal area (BA):

$$LP(\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1})=a+b\cdot\text{BA}(\text{m}^2/\text{ha}); \quad [5.1]$$

where a and b are constants and were obtained by regressively fitting data collected from 17 mangrove forests in Florida, Puerto Rico and Mexico (data from Pool et al. 1975, Pool et al. 1977, Heald et al. 1979, Twilley et al. 1986, Day et al. 1987). Besides litter fall, dead trees also contribute organic matter to the forest floor (Robertson and Daniel 1989, Gong and Ong 1990). Not all of this organic matter can enter the soil, some of it is exported by tides and runoff, or consumed by animals (Heald 1969, Boto and Bunt 1981, Twilley 1985). The net accumulation of litter into mangrove soil surface was calculated as:

$$\text{NLP}=f_l\cdot\text{LP}\cdot(1.0-k_e); \quad [5.2]$$

$$\text{NTP}=(1.0-f_l)\cdot\text{LP}\cdot(1.0-k_e); \quad [5.3]$$

$$\text{NWP}=k_m\cdot\text{AMASS}\cdot(1.0-k_e); \quad [5.4]$$

where NLP, NTP, NWP are annual net accumulation of leaf litter, twigs and dead wood in mangrove soil surface, respectively. LP is expressed as $\text{g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$, f_l is a ratio of leaf litter to total litter, and other parts of litter were treated as twigs. k_e is a site specific constant related to disappearance of standing litter, which is a function of hydrology, topography, activity and frequency of consumers. k_m is the turnover rate of wood biomass and AMASS is aboveground biomass (g/cm^2).

Net deposition of leaf litter is partitioned directly into pools corresponding to labile and refractory soil organic matter, which is based on the lignin content (lc) of leaf litter. The lignin fraction in leaf litter flows into the refractory pool, and the other fraction flows into the labile pool. The compartments of standing dead wood and twigs have a specific decay constant, k_w and k_t , respectively. Losses of dead wood and twig litter are separated between microbial respiration and transfer to refractory organic matter. The first stage of decay for both dead wood and twig litter is respiration that represents a mass loss of 45% (k_0), which is similar to that in the CENTURY model for decomposition of structural organic matter. The contribution of aboveground litter to LOM and ROM at the surface ($t=0$) was calculated as:

$$\text{LOM}(0)=\text{NLP}\cdot(1.0-lc)(1.0-k_5); \quad [5.5]$$

$$\text{ROM}(0)=\{\text{NLP}\cdot lc + (1-k_0)[k_t\cdot\text{NTP}+k_w\cdot\text{NWP}]\}(1.0-k_5); \quad [5.6]$$

where k_5 is ash content of litter.

The distribution of mangrove roots is an exponential function with depth (Komiyama et al. 1989) as follows:

$$R=R_0\cdot\exp(-k_1\cdot D); \quad [5.7]$$

where R is root mass (g/cm^2) at depth D (cm) and R_0 is root mass at the surface (g/cm^2), k_1 is attenuation rate of root mass with increasing depth (D) from the surface. Root biomass within a soil cohort was calculated as in the SEMIDEC model:

$$R(t) = R_0 \int_{D_b}^{D_t} \exp(-k_1 D) dD = R_0 [\exp(-k_1 D_b) - \exp(-k_1 D_t)] / -k_1 \quad [5.8]$$

where D_b and D_t are the upper and lower depths (cm) of the soil cohort, respectively. Lacking direct information for the study sites along the Shark River estuary, I estimated annual fine root production (FRP) ($\text{g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$) and large root production (LRP) ($\text{g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$) in the soil cohort from aboveground litter production and from aboveground wood turnover rate (k_m), respectively:

$$\text{FRP}(t) = \text{LP} \cdot R(t) / \text{RMAS}; \quad [5.9]$$

$$\text{LRP}(t) = k_m \cdot R(t); \quad [5.10]$$

where RMAS is total belowground biomass (g/cm^2). Upon their death, roots also contribute to the labile and refractory organic matter pools of the soil. Organic matter input and decomposition in each year cohort of soil were modified from Morris and Bowden (1986). The mass of labile organic matter in a soil cohort is:

$$\text{LOM}(t+1) = \text{LOM}(t) - k \cdot \text{LOM}(t) + [(1 - fc_1) \cdot \text{FRP}(t) + (1 - fc_2) \cdot \text{LRP}(t)](1.0 - k_5) + \text{ROM}(t) \cdot k_2 \cdot (1 - k_0); \quad [5.11]$$

where k is the decay constant of labile organic matter, fc_1 and fc_2 are fractions of fine roots and large roots that are refractory organic matter, respectively. k_2 is the decay constant of refractory organic matter.

Inputs of refractory organic matter include the refractory fraction of roots and residue from the decomposition of labile organic matter. This pool of ROM decays at a slow rate described by the equation:

$$\text{ROM}(t+1) = \text{ROM}(t) - k_2 \cdot \text{ROM}(t) + [fc_1 \cdot \text{FRP}(t) + fc_2 \cdot \text{LRP}(t)](1.0 - k_5) + k \cdot (1.0 - k_0) \cdot k_3 \cdot \text{LOM}(t); \quad [5.12]$$

where k_3 is a proportion of decomposing LOM that enters ROM. Total soil organic matter (TOM) in a soil cohort is equal to the sum of two organic pools and root organic matter expressed as:

$$\text{TOM}(t) = \text{LOM}(t) + \text{ROM}(t) + R(t) \cdot (1.0 - k_5). \quad [5.13]$$

Inputs of inorganic material to soil surface include allochthonous inorganic material and release of minerals from decomposing litter. I assumed that root uptake of inorganic material is restricted to the soil surface, because this is where most of the fine absorbing roots in mangroves soils are found (Clough 1992). The model also assumed that the uptake of inorganic material for root growth is balanced by release of inorganic material from dead roots. Annual amounts of inorganic material absorbed by roots to support aboveground growth are equal to the sum of inorganic material in litter and wood production. Therefore, the amount of inorganic material within a soil cohort under the surface cohort was assumed constant with depth. The amount of inorganic material in the surface can be calculated as:

$$\text{Wi}(0) = k_4 + k_5 \cdot (\text{NLP} + \text{NTP} + \text{NWP}) - k_5 \cdot (\text{LP} + k_m \cdot \text{AMASS}); \quad [5.14]$$

where Wi is the amount of inorganic material. k_4 is the annual deposition of inorganic material ($\text{g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$) from allochthonous sources.

The volume of a soil cohort was calculated as:

$$V(t)=[LOM(t)+ROM(t)+R(t)]/b_o+Wi(t)/b_i; \quad [5.15]$$

where b_o and b_i are the bulk density of organic matter and inorganic material (g/cm^3) within the soil cohort, respectively. For organic soils, the inorganic term in the above equation [15] is eliminated in the SEMIDEC model. Each soil cohort in the model represents 1 yr of organic and inorganic matter accumulation per unit area (cm^2) of soil. The volume of a soil cohort is its vertical height (cm), therefore

$$D_b=D_t+V(t); \quad [5.16]$$

where D_b was solved numerically corresponding to the new cohort depth based on the volume of organic and inorganic matter in that cohort (for a full description of these calculations see the SEMIDEC model, Morris and Bowden 1986). Then this new depth was used to calculate root biomass within the soil cohort. The overall bulk density (BD, g/cm^3) of that soil cohort is the sum of labile and refractory organic matter, root biomass and inorganic material divided by height of the cohort using:

$$BD(t)=(LOM(t)+ROM(t)+R(t)+Wi(t))/(D_b-D_t). \quad [5.17]$$

Notice that this model does not account for the effect of compaction on soil formation.

Soil nitrogen and phosphorus

The nitrogen model was different from that used in the SEMIDEC model, because of the uncertainty in identifying several parameters. Instead I used the CENTURY model as an approach to simulate nitrogen dynamics by assuming that soil N is bonded to C. In the NUMAN model, C:N ratio of LOM is 8 and of ROM is 20, and both remain fixed during the simulations. The C:N ratio of LOM is the same as active soil organic fraction in the CENTURY model. The C:N ratio of ROM was based on C:N measurements of mangrove soils in this study. Thus, the amount of total N in LOM (NLOM) and ROM (NROM) was calculated as:

$$NLOM(t)=LOM(t)/(2 \times 8); \quad [5.18]$$

$$NROM(t)=ROM(t)/(2 \times 20); \quad [5.19]$$

$$TN(t)=NLOM(t)+NLOM(t)+k_6 \cdot R(t); \quad [5.20]$$

where the factor 2 is the ratio of organic matter to C based on measurements in this study, k_6 is the N concentration of roots, and TN is total N amount in that soil cohort. N flows were assumed to be related to organic matter flows. N mineralization occurs by the decomposition of LOM and ROM:

$$N_{\min}(t)=k \cdot NLOM(t)+k_2 \cdot NROM(t); \quad [5.21]$$

where $N_{\min}(t)$ is the gross mineralization rate within the cohort ($\text{gN}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$). Nitrogen loss from mangrove soil occurs as a result of plant uptake, immobilization, leaching, ammonia volatilization, and denitrification. The model calculated gross N mineralization, but did not trace

the loss of N. Total annual N mineralization from the soil (TN_{min} , g·cm⁻²·yr⁻¹) between the surface (at $t=0$) and a given depth for a specific time interval (n) is calculated by summing the mineralization in each soil cohort at the depth range as follows:

$$TN_{min} = \sum_{t=0}^n N_{min}(t) \quad [5.22]$$

Inputs of P into mangrove soils include organic P from decomposing litter and mineral P deposition on the surface. Losses of P were assumed to be a function of gross N mineralization from organic matter. That is:

$$P(0) = p_0 + k_7 \cdot (NLP + NTP + NWP); \quad [5.23]$$

$$P(t+1) = P(t) - m \cdot N_{min}(t+1); \quad [5.24]$$

where k_7 is the concentration of P in litter, p_0 is the annual deposition of allochthonous P (gP·cm⁻²·yr⁻¹) on the soil surface, and m is ratio of losses of N mineralization to P.

MODEL PARAMETERIZATION

Many of the parameters in the NUMAN were based on field results from the mangrove sites along the Shark River estuary, whereas others represent published data in the mangrove literature (Table 5.1). Litter bag studies of leaf degradation were used to derive decay constants as estimates for decomposition of LOM. Numerous studies have been conducted on decomposition of mangrove leaves. The average decay constant of *Rhizophora mangle* and *Avicennia germinans* leaves was 0.62 yr⁻¹ in a mangrove wetland of southwestern Florida using 1 mm mesh litter bags (Twilley et al. 1986), which is similar to a decay constant of 0.624 yr⁻¹ for *Laguncularia racemosa* leaves in a Mexican mangrove forest (Flores-Verdugo et al. 1987). Similar values of 0.54 and 0.64 yr⁻¹ were found for *Avicennia marina* in an Australian mangrove (Van der Valk and Attiwill 1984). Heald (1969) studied decomposition of *Rhizophora mangle* leaves in brackish, predominantly fresh and dry conditions, respectively, in the North River using 2 mm mesh bags. Fitting his data with a negative exponential function showed decay constants of 2.80, 1.47 and 0.93 yr⁻¹. Large mesh size allows greater losses of detritus from litter bags which are not completely decomposed. The decay of LOM in the NUMAN model occurs in the surface and sub-surface strata of mangrove soils. Therefore, estimating a decay constant from experiments using litter bags with a smaller mesh is better. Experiments that measure the decomposition of wood litter in mangrove wetlands are limited, but results show that decay constants for wood and twigs are low at 0.083 and 0.276 yr⁻¹, respectively (Robertson and Daniel 1989).

Parameters in the model including fc_1 , fc_2 , k_4 and k_e are unknown from the literature on mangrove ecology. I assumed that the fraction of fine roots contributed to the pool of ROM was the same fraction as for leaf litter ($fc_1=0.15$). However, I used $fc_2=0.3$ for the refractory fraction of other roots assuming that larger roots have a higher proportion of structural material.

Profiles of organic matter and bulk density are controlled by k_e and k_4 and these coefficients were determined by a model-tuning procedure, where the parameters were adjusted to fit observed soil profiles (Parton et al. 1987). The coefficient, k_4 , represents sediment accretion, which can be determined directly by measuring a profile of ²¹⁰Pb in sediment (Lynch et al. 1989). If this coefficient was known, then k_e could be estimated independently. A best fit of measured and simulated concentrations of organic matter content and bulk density was accomplished by adjusting k_4 and k_e . An increase of k_4 or k_e will lead to higher values of bulk density but lower

concentrations of organic matter. Heald (1969) measured organic matter export in a well-developed *Rhizophora mangle* forest in the North River, near the Shark River estuary, and found that 42% of leaf litter was exported to the estuary. I used $k_e=0.4$ as a reference parameter and adjusted k_e and k_4 to produce the best fit profile of nutrients. This model-tuning technique using field estimates for one of the parameters is a constraint that keeps k_4 and k_e within a reasonable range.

Site specific parameters, such as aboveground biomass and basal area, were based on values obtained from the field sites (Chapter 4). Distances of the four study sites from the mouth of the estuary were 1.8, 4.1, 9.9 and 18.2 km. Aboveground biomass was higher in S1 and S3 than in S4 and S6 (Table 5.2). The model assumed that forest structure at all sites was in steady state and thus no changes in biomass and basal area were calculated during the simulations. The decrease in forest stature from the marine to the oligohaline zone of the estuary has been observed for more than half a century (Davis 1940). The turnover rate for wood (k_m) was calculated as an average value for the four mangrove sites based on the relationship between woody production and aboveground biomass (Aber et al. 1991). The biomass and productivity of the belowground component of mangrove wetlands are poorly understood. Two *Rhizophora* forests in Puerto Rico and Panama have an average ratio of belowground to aboveground biomass of 0.74 (Golley et al. 1962, 1975), which was used to calculate belowground biomass. The depth of root distribution was assumed to be 150 cm from the sediment surface.

RESULTS AND MODEL CALIBRATION

The model was calibrated by simulating steady state production of the four mangrove sites along the Shark River estuary, which represent a landscape and salinity gradient from the oligohaline to marine soil conditions. Soil conditions in the downstream location (S1 and S3) were considered optimal for the growth of mangrove wetlands in Florida (Chapter 4). The observed soil profile of organic matter, bulk density, N and P varied significantly among the four study sites. Average concentrations of organic matter (% AFDW) to a depth of 60 cm decreased from the oligohaline to marine sites with values of 82%, 62%, 45% and 30% at S6, S4, S3 and S1, respectively. In contrast to AFDW, bulk density increased from S6 to S1 with a value of 0.142, 0.187, 0.221 and 0.438 g/cm³ as a result of decreased organic matter content. Like organic matter content, soil N concentrations declined from S6 (2.01%) to S1 (0.52%), whereas S4 and S3 had intermediates value of 1.40 and 1.08%, respectively. Higher P concentrations were found at S3 (0.097%) and S1 (0.085%) than at S4 (0.069%) and S6 (0.041%). Except in S1, vertical profiles of organic matter and bulk density in mangrove soils exhibited no clear differences with depth. N profiles varied with site, S1 and S4 had a relatively constant vertical distribution; whereas, N concentrations decreased to a depth of 40 cm in S3 and S6. P concentrations decreased from the surface to 40 cm in S3, S4 and S6, however, concentrations varied irregularly at the top 30 cm in S1.

The major source of freshwater to the estuary is from the Shark River Slough, and a gradient of salinity in mangrove soils along the estuary represents the relative importance of terrestrial runoff and Gulf water to the soil profile at a particular location. Tidal flooding increases and the influence of fresh water decreases from the upstream sites to those near the mouth of the Shark River estuary. Values of forest biomass at each respective site were used as initial conditions in the model to simulate soil nutrients profiles. The NUMAN model assumed that the loss of litter (parameter k_e) and allochthonous inorganic input (parameter k_4) were related to the spatial locations of the four sites along the estuary. The parameters k_e and k_4 were assumed to increase systematically from the oligohaline site (S6) to the marine site (S1) to produce a best fit profile (Table 5.2), since rates of organic matter export and sedimentation are higher in mangrove sites nearer the gulf coast.

The simulated concentrations of AFDW were within 12 percent of the observed concentrations in S3, S4 and S6 below depth 10 cm, however, measured concentrations of AFDW varied significantly with depth in S1 with a minimum AFDW of 15.8% at depth 16-18 cm (Fig. 5.2). Generally, the model predicted a quick decrease of AFDW at the surface, because of the rapid decomposition of LOM. The predicted depth of rapid organic matter decomposition varied among sites, ranging from 1 cm at S6 to 5 cm at S1. Simulations showed that AFDW at S4 and S6 increased slowly below the rapid decomposition layer, which was an excellent fit to the observed profile below the top 10 cm. In contrast, the model did not predict an increase in AFDW below the rapid decomposition layer at S1, but showed a relatively constant concentration with depth. The discrepancies in AFDW profiles among the downstream (S1), intermediate (S4) and upstream (S6) sites were due to higher deposition rates of allochthonous inorganic materials at the sites near the mouth of the estuary. The simulated profiles of bulk density showed a reverse trend as AFDW among the sites and a good fit was observed in S3, S4 and S6 (Fig. 5.3). Observed bulk density in S1 indicated a peak value of 0.622 g/cm^3 at 16-18 cm depth, with some variance through the whole core.

The simulated N concentrations were within the extreme concentrations of observed profiles at each site, except at surface soil in S1 and S3 (Fig. 5.4). The observed N profile in S1 was a S-shaped curve with depth, whereas simulated N concentrations were constant with depth at about the average value of the observed concentrations. The model predicted a slight increase in N concentrations following an initial decline in surface soils in sites S3, S4 and S6, which fits well with the observed N profile in S4. But this pattern of soil N is a poor fit of concentrations in S3 and S6, differences in slope of profiles at S3 and S6 were evident.

Daily rates of net N mineralization for each mangrove site were averaged from field measurements on three sampling dates (Chapter 3), and these average values were extrapolated to an annual rate, and compared to simulated gross mineralization rates (Fig. 5.5). Note that the observed N mineralization rates were representative of 10 cm sections (to a depth of 40 cm), however, simulated values were calculated for each soil cohort section. Both the simulated and observed N mineralization rates in each study site decreased quickly with depth, except for the observed values in S1. Also, the simulated values were generally higher than the observed values. However, the observed profile of N mineralization in S1 did not decrease quickly in the top 30 cm, and this rate exceeded the simulated value below the top 10 cm section. Simulated rates of N mineralization were higher than observed values, which may be an artifact of the difference in field methods and operational definitions of this process within the model. The laboratory incubations of mangrove soil in my study provided an index of net N mineralization during the incubation period, including the consumption by microbes during organic matter mineralization. Therefore, it is reasonable that the estimate of N mineralization by the model was higher than the net mineralization rates measured in laboratory incubations. The model calculated the integrated gross N mineralization rate within 0-40 cm and showed an increase from the upstream to downstream sites along the Shark River estuary with values of 4.8 (S6), 5.3 (S4), 8.9 (S3), and 8.9 (S1) $\text{mg N}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$.

Parameter p_0 , the annual input of allogenic inorganic and organic P through deposition of sediment particles or adsorption from flooding waters, was adjusted to fit the P profile for each site (Table 5.2, Fig. 5.6). Compared to mean observed P concentration of 0.85% in S1, the simulated P concentration slightly decreased from 0.91% at depth 3 cm to 0.84 at depth 60 cm by assuming $p_0=0.00019 \text{ g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$ or $1.9 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. The observed P profile in S1 indicated a low P concentration of 0.037% at depth of 16-18 cm corresponding to a high value of bulk density at that depth. Both observed and simulated P concentrations in S3 decreased gradually below an initial increase. Predicted P concentrations increased rapidly in the top 1 cm of soil in S4 and S6, then decreased rapidly with depth. This decrease in P concentrations in the model fit well with the observed P profile, which corresponded with a release of P from organic matter associated with N

mineralization.

Profiles of N:P ratios varied markedly among the sites, not only in the magnitude of N:P ratios, but also in the trends of N:P ratios with depth (Fig. 5.7). S1 had a relatively constant N:P ratio of 6.1 with depth. Except at depth of 22-24 cm, where a maximum N:P ratio of 17 was measured, observed values in S3 showed a slight increase from 10 at 2 cm depth to 12 below 54 cm. The observed N:P ratios in S4 decreased from 29 at the soil surface to 16 at 6-8 cm, then increased to 32 at 60 cm. The observed N:P ratios in S6 increased significantly from 23 at the surface to 66 at 36 cm, then shifted to 107 at 38 cm and decreased to 79 at 60 cm. Simulated N:P ratios were an excellent fit with the observed N:P profiles in S1 and S3, except for a difference in the top 4 cm. Both observed and simulated N:P ratios in S4 indicated a decrease in the soil surface followed by an increase below that depth. The simulations of S6 correctly forecasted the significant increase of N:P ratio with depth.

DISCUSSION

The NUMAN model of mangrove soils was modified from the SEMIDEC and CENTURY models, and parameterized with independent field measurements in mangrove soils along the Shark River estuary. Comparisons of simulated and observed results demonstrated that significant landscape gradients of soil characteristics can be adequately modeled using plant production, loss rates of standing litter, decomposition of organic matter, and allochthonous inputs of inorganic material as key ecological processes. The NUMAN model simulates vertical distributions of organic matter, and N and P concentrations in mangrove soils as a function of organic matter diagenesis in a coastal forested wetland. This model also predicts various rate processes, such as N mineralization, sedimentation and root turnover rate, based on the profiles of organic and inorganic matter.

I hypothesized that organic matter concentrations in mangrove soils would be elevated at those sites with low export rates of litter and low deposition rates of inorganic material from allochthonous sources. These processes are site-specific along the longitudinal axis of the Shark River estuary. Litter export rates used in the NUMAN model ranged from 0.4 to 0.6 for this estuary, which were based on several published data. For Florida mangroves, Heald (1969) estimated that 42% of the litter fall in a fringe mangrove was exported as leaf litter detritus in the North River, the similar result was found by Lugo and Snedaker (1975) that 41% of leaf litter fall was exported in a black mangrove forest of Rookery Bay. In Australian mangroves, Boto and Bunt (1981) calculated litter export rate was 81% of litter fall. Flores-Verdugo et al. (1987) observed 90% of the litter fall was exported to the adjacent lagoon in a white mangrove forest in Mexico.

Observed results in my study showed that soil organic matter concentrations among mangrove wetlands increased dramatically with increased distance from the estuary mouth, while bulk densities decreased, suggesting that sedimentation rates decreased along the axis of the estuary. The NUMAN model is able to simulate the spatial gradient of soil profiles by adjusting the amount of inorganic material input in a reasonable range as compared to recent studies of sediment accumulation among mangrove forests (Lynch 1989) (Table 5.3). Lynch (1989) used ^{210}Pb dating techniques to estimate the accretion rates in mangrove forests in southwest Florida and Mexico and found that accumulation of inorganic material varied significantly among ecological types of mangroves, ranging from 107 to 1404 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. The model required an input of 1500 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ of inorganic material to maintain a soil profile with a bulk density of 0.438 g/cm^3 in S1. A riverine mangrove forest in Terminos Lagoon, Mexico, where rivers contribute large amounts of sediment, had a bulk density of 0.412 g/cm^3 and required 1404 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ of inorganic material accumulation. It is interesting to note that litter production for S1 calculated

from the allometric equation in the NUMAN model was $13.1 \text{ Mg}\cdot\text{ha}^{-2}\cdot\text{yr}^{-1}$, which is close to the value of $12.5 \text{ Mg}\cdot\text{ha}^{-2}\cdot\text{yr}^{-1}$ in the riverine mangrove forest at Terminos Lagoon (Day et al. 1987). This implies that a similar rate of organic matter production contributes to comparable rates of soil formation.

Inorganic material accumulation estimated by the model for S3 was similar to the measured rate for a fringe mangrove forest in Estero Pargo. However, the organic matter content is higher in S3 than in Estero Pargo (45.3% vs 32.4%), probably reflecting higher organic production in S3 as indicated by the difference in basal area of the two forests (39.7 vs $23.3 \text{ m}^2/\text{ha}$). Organic matter, bulk density and N concentration in soils in S4 are similar to those of a basin mangrove in Rookery Bay, where there has been extensive mangrove research (Lugo and Snedaker 1975, Twilley 1985, Twilley et al. 1986). Model simulations for S4 using a litter export rate of 45% of litter fall ($k_e=0.45$) required an input of $180 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ of inorganic material to fit the soil profile of bulk density at this site. This sedimentation rate was similar to the measured rate of inorganic sediment accumulation in Rookery Bay basin forest ($107\text{-}179 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). There are no literature values of sedimentation for a mangrove wetland representative of S6, which is a site with extremely high organic matter concentrations, yet it appears that an inorganic input rate of $76 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ is reasonable for this oligohaline site. The lack of inorganic sediment input is due to the presence of low concentrations of suspended sediment from the Shark River Slough, and increased distance from the Gulf of Mexico.

Patterns of organic matter and bulk density distributions based on simulation results assume that compaction is negligible. This assumption is suitable for the study sites because observed organic matter and bulk density profiles of mangroves do not change markedly to a depth of 60 cm. However, changes in bulk density concentration with depth indicate that compaction in mangrove sediments can be significant (Lynch 1989).

Compared with P accumulation rates measured in the other mangrove forests, the model calculated a higher input of P for the downstream locations (S1 and S3), due to higher P concentrations in soils along the estuary (Table 5.3). In Water Conservation Area 2A in the freshwater Everglades, Davis (1991) estimated P retention of 1.1 to $1.4 \text{ gP}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and Reddy et al. (1993) reported P accumulation ranging from 0.11 to $1.14 \text{ gP}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ depending on distance from inflow structure. These observed rates are similar to the estimates by the NUMAN model for S3, S4 and S6 at 1.2 , 0.4 , and $0.27 \text{ gP}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, respectively.

In its present form, the model simulated N and P mineralization rates based on only the decomposition of labile organic matter which is set at a fixed rate. The model was able to produce reasonable rates of N and P mineralization, and N:P ratio profiles, compared to observed results. These simulations suggest that N and P dynamics in mangrove soils were tightly linked to C dynamics. N dynamics in mangrove soil are complex and involve microbial metabolism and chemical and physical processes, such as N fixation (Alongi et al. 1992), fluxes between overlying water (Rivera-Monroy et al. 1995a), ammonification (Chapter 3), nitrification and loss N through denitrification (Rivera-Monroy et al. 1995b, Rivera-Monroy and Twilley 1996). N mineralization rates were also related to other nutrient availabilities such as P, and varied dramatically with season (Chapter 3). Although P may exist with several minerals, organic P was the major component of this nutrient in mangrove soils among the study sites (Chapter 3). Further investigations into the effects of microbial activity on organic matter dynamics are needed for an accurate assessment of N and P mineralization.

One of the objectives of an ecosystem model is to identify those ecological processes that are poorly understood and which may play an important role in the biogeochemical properties of an ecosystem. My study suggested that the rates of root production, which lacked any direct verification, are critical processes in controlling organic matter accumulation and the vertical distribution of organic matter in mangrove soils. Mangrove peat in south Florida consists mainly of mangrove rootlets (Davis 1940, Scholl 1964a,b), suggesting that underground litter production

plays a critical role in forming peat of mangrove forest. However, direct measurements of root production in mangrove wetlands are difficult, especially in identifying dead and live roots, and the effect of depth on organic matter decomposition is also not clear. Therefore, these model simulations provide a valuable estimate of the potential contribution of these processes by fitting observed soil profiles with new parameters.

The ability of the model to simulate organic matter diagenesis in soil was limited by its assumption that driving variables are in steady state. ^{14}C dating techniques revealed that mangroves have developed in the Shark River region over the past 3000 yrs (Scholl 1964a,b). Mangrove rootlets have contributed significantly to the 1-4 m of peat that has developed during the late Holocene transgression (Davis 1940, Craighead 1971). However, hurricanes, which are one of major large scale and cyclic disturbances for mangroves in Florida (Lugo and Snedaker 1974), can destroy mangrove biomass and redistribute tremendous amount of sediments in mangrove wetlands (Smith et al. 1994). These processes can seriously influence model predictions based on steady state assumptions of ecological processes. Observed soil profiles in S1 exhibited obvious shifts in bulk density and organic matter with depth. These sharp gradients in soil profiles probably reflect different sedimentation rates in this site. Site S1 was the only site with a four cm thick layer located 15 cm below the surface soil which had a significantly higher bulk density of $0.62 \text{ g}\cdot\text{cm}^{-3}$ compared to the mean bulk density of $0.44 \text{ g}\cdot\text{cm}^{-3}$ within 0-60 cm at S1. This difference in bulk density may be related to large amounts of sedimentation caused by Hurricane Donna in 1960. It has been observed that Hurricane Andrew resuspended sediments from the Gulf of Mexico and deposited 1-10 cm thick layers of sediment in mangrove wetlands in the Everglades National Park (Smith et al. 1994). The hurricane-induced sedimentation may decrease with distance from the source of resuspended sediments at the mouth of the estuary. I did not observe a peak of bulk density at other sites along the Shark River estuary similarly to the one measured in S1.

The NUMAN model used a constant rate of mangrove litter production based on the basal area structure of the forest. However, forest production is constrained by environmental variables, such as soil nutrient availability, which is determined by nutrient mineralization from organic matter and inputs of allochthonous materials. For future applications, the model can be modified and linked to forest dynamics model as a subroutine to simulate the feedback mechanisms of nutrient cycling, which controls the development of mangrove ecosystems.

Table 5.1. Definition and values of parameters used in the NUMAN model.

Parameters	Definition	Unit	Values	Source
b_o	Bulk density of organic matter	g/cm ³	0.1154	This study
fc_1	Fraction of fine root that is refractory	g/g	0.15	estimated
fc_2	Fraction of large root that is refractory	g/g	0.3	estimated
fl	Ratio of litter leaves to total litter	g/g	0.70	Pool et al. 1975, Twilley et al. 1986
k_0	Proportion of microbial respiration during decomposition	g/g	0.45	Parton et al. 1987
k	Decay constant for labile organic matter	yr ⁻¹	0.62	See text
k_1	A distribution parameter for root biomass	cm ⁻¹	0.04	Komiyama et al. 1987
k_2	Decay constant for refractory organic matter	yr ⁻¹	0.00067	Parton et al. 1987
k_3	Proportion of labile organic matter flowing into refractory organic matter after decomposition	g/g	0.03	Parton et al. 1987
k_4	Annual deposition of inorganic material	g·cm ⁻² ·yr ⁻¹	Table 5.2	
k_5	Ash concentration in litter	g/g	0.10	Benner et al. 1990
k_6	N concentration in roots	g/g	0.005	Stanford 1976
k_7	P concentration in litter	g/g	0.0002	Stanford 1976
k_e	Disappear rate of standing litter	yr ⁻¹	Table 5.2	
k_m	Turnover rate of wood	yr ⁻¹	0.425	Chapter 4
k_t	Decay constant of litter twigs	yr ⁻¹	0.276	Robertson and Daniel 1989
k_w	Decay constant of dead root	yr ⁻¹	0.083	Robertson and Daniel 1989
lc	Lignin content in litter leaves	g/g	0.15	Benner et al. 1990
LP	Litter production	g·cm ⁻² ·yr ⁻¹	Table 5.2	
m	Ratio of N mineralization to P loss	g/g	0.00672	Morris and Bowden (1986)
R_0	Total root biomass	g/cm ²	Table 5.2	
RMASS	Total root biomass	g/cm ²	Table 5.2	
p_0	Annual allochthonous deposition of P	g·cm ⁻² ·yr ⁻¹	Table 5.2	
AMASS	Total aboveground biomass	g/cm ²	Table 5.2	

Table 5.2. Site specific parameters for simulations of the NUMAN model.

Parameter	S1	S3	S4	S6	Methods and source
Aboveground biomass (g/cm ²)	2.5	2.5	1.27	0.787	Allometric method, Chapter 4
Belowground biomass (g/cm ²)	1.85	1.85	0.94	0.582	Ratio of below/aboveground biomass
Basal area (m ² /ha)	40.36	39.67	20.72	19.61	Field survey, Chapter 4
R ₀ (g/cm ²)	0.074	0.074	0.0377	0.023	Allometric method
LP (g·cm ⁻² ·yr ⁻¹)	0.13	0.129	0.074	0.071	Regression method
k ₄ (g·cm ⁻² ·yr ⁻¹)	0.15	0.06	0.018	0.0076	Best estimate
k _e (yr ⁻¹)	0.6	0.58	0.45	0.4	Best estimate
p ₀ (g·cm ⁻² ·yr ⁻¹)	0.00019	0.00012	0.00004	0.000027	Best estimate

Table 5.3. Comparisons of mangrove forest structure and sediment characteristics.

	Rookery Bay ¹	Boca Chica ²	Estero Pargo ²	Shark River ³			
				S1	S3	S4	S6
Distance from open water (m)	10-70	10	15	20	20	20	5
Basal area (m ² /ha)	20-25	34.2	23.3	40.4	39.7	20.7	19.6
Litterfall (Mg·ha ⁻² ·yr ⁻¹)	8.1	8.3	12.5	13.1 ^a	12.9 ^a	7.4 ^a	7.1 ^a
Bulk density (g/cm ³)	0.188-0.221	0.412	0.288	0.438	0.221	0.187	0.142
AFDW (%)	52.3-64.3	22.5	32.4	30.3	45.3	62.3	82.2
N (%DM)	1.4-1.73	0.32	0.57	0.52	1.08	1.40	2.01
P(%DM)	0.05-0.058	0.043	0.058	0.085	0.097	0.069	0.041
Accumulation rate of inorganic matter (g·m ⁻² ·yr ⁻¹)	107-179 ^b	1404 ^b	566 ^b	1500 ^c	600 ^c	180 ^c	76 ^c
Accumulation rate of P (g·m ⁻² ·yr ⁻¹)	0.15-0.20 ^b	0.78 ^b	0.48 ^b	1.9 ^c	1.2 ^c	0.4 ^c	0.27 ^c

1. Data source: basal area from Warner (1990), litterfall from Steyer (1988), other data from Lynch (1989);

2. Data source: basal area and litterfall from Day (1987), other data from Lynch (1989);

3. Data source: this study;

a. Based on allometric method;

b. based on ²¹⁰Pb dating techniques;

c. model best estimates.

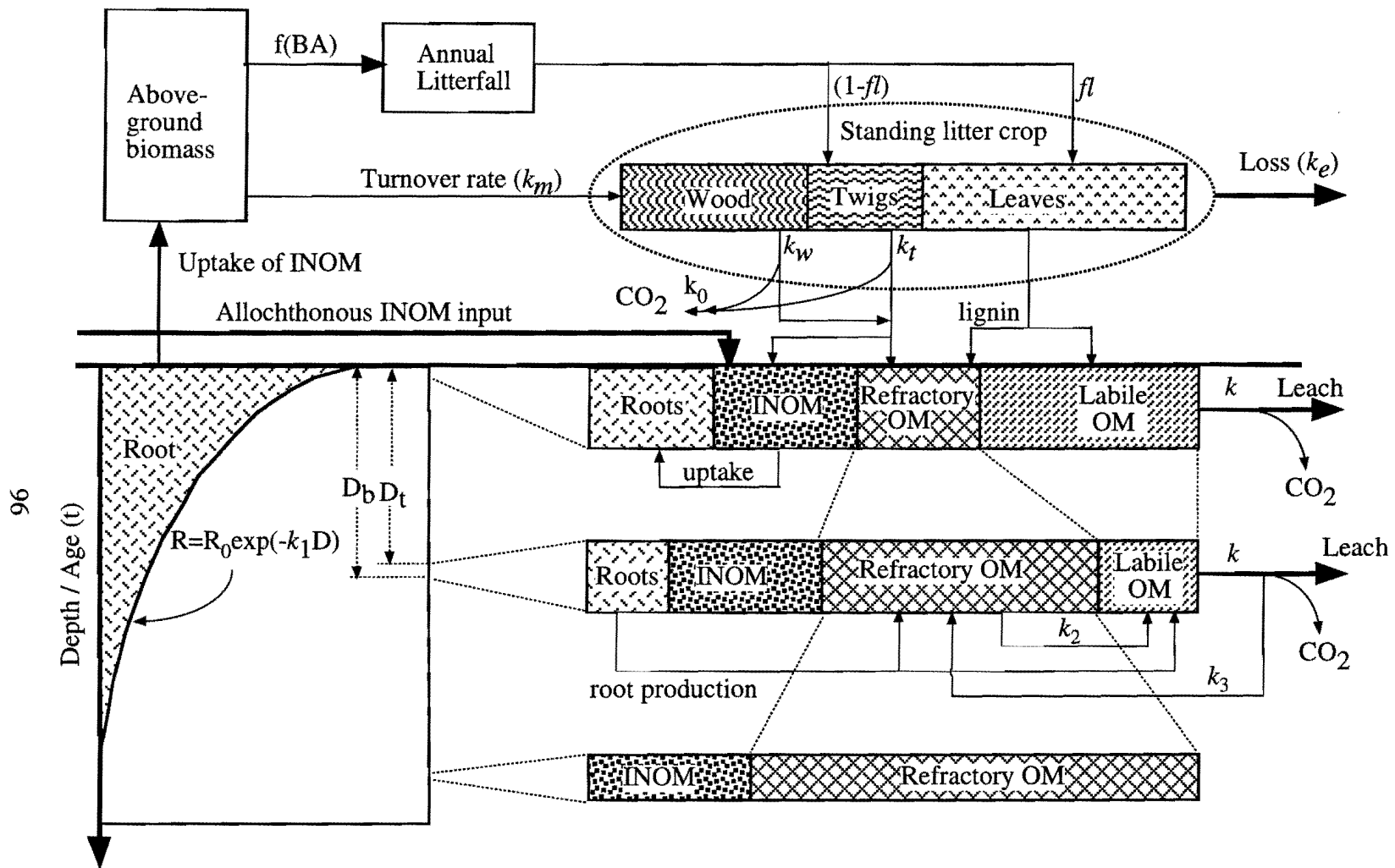


Figure 5.1. Conceptual diagram of the NUMAN model that simulates the biogeochemistry of sediment cohorts changing with depth in a mangrove ecosystem. (OM: organic matter; INOM: inorganic material).

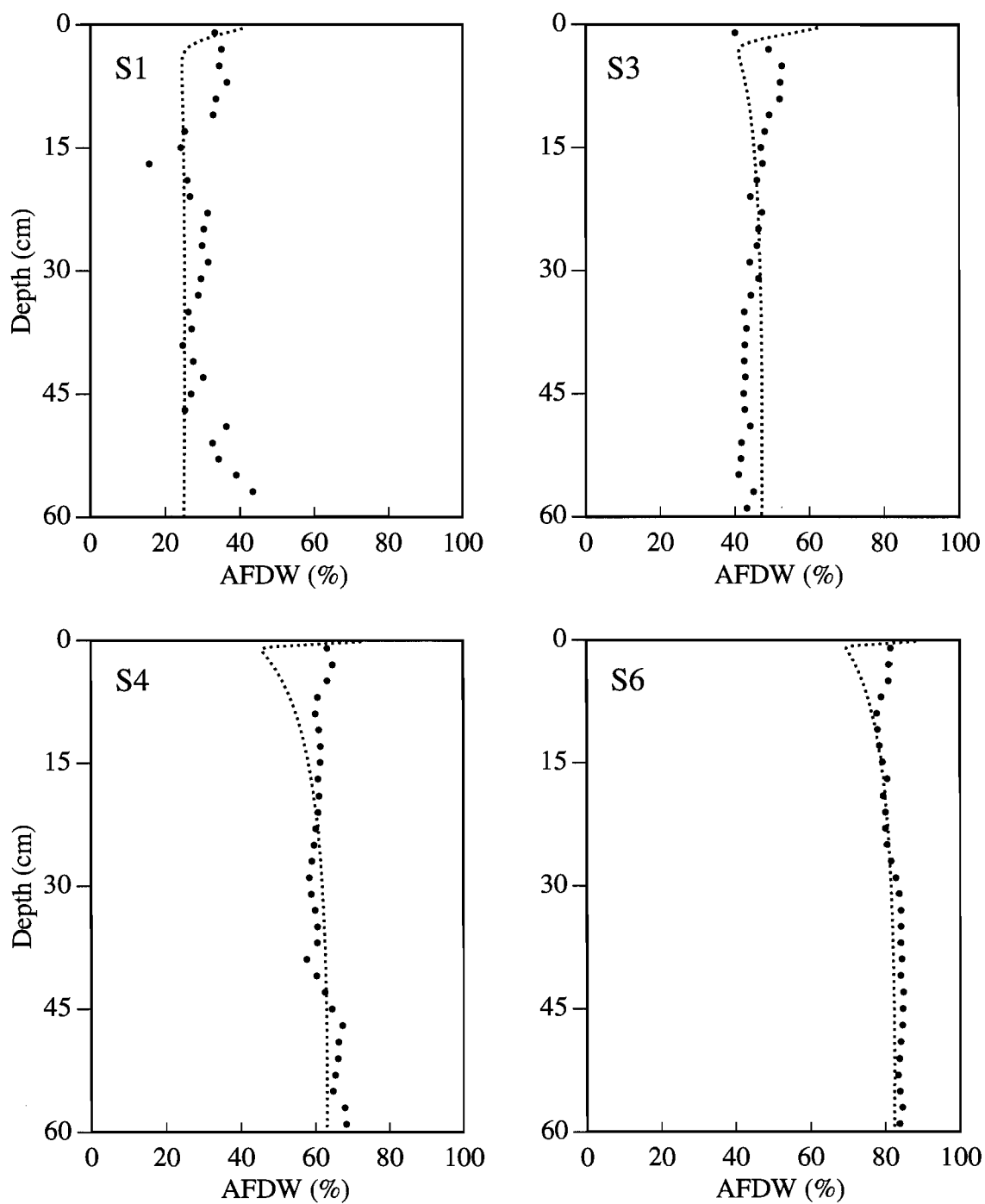


Figure 5.2. Comparison of observed concentrations of organic matter (AFDW %) (solid dot) and simulated concentrations (dashed line) in mangrove soils for the downstream (S1 and S3), intermediate (S4) and upstream (S6) sites along the Shark River estuary.

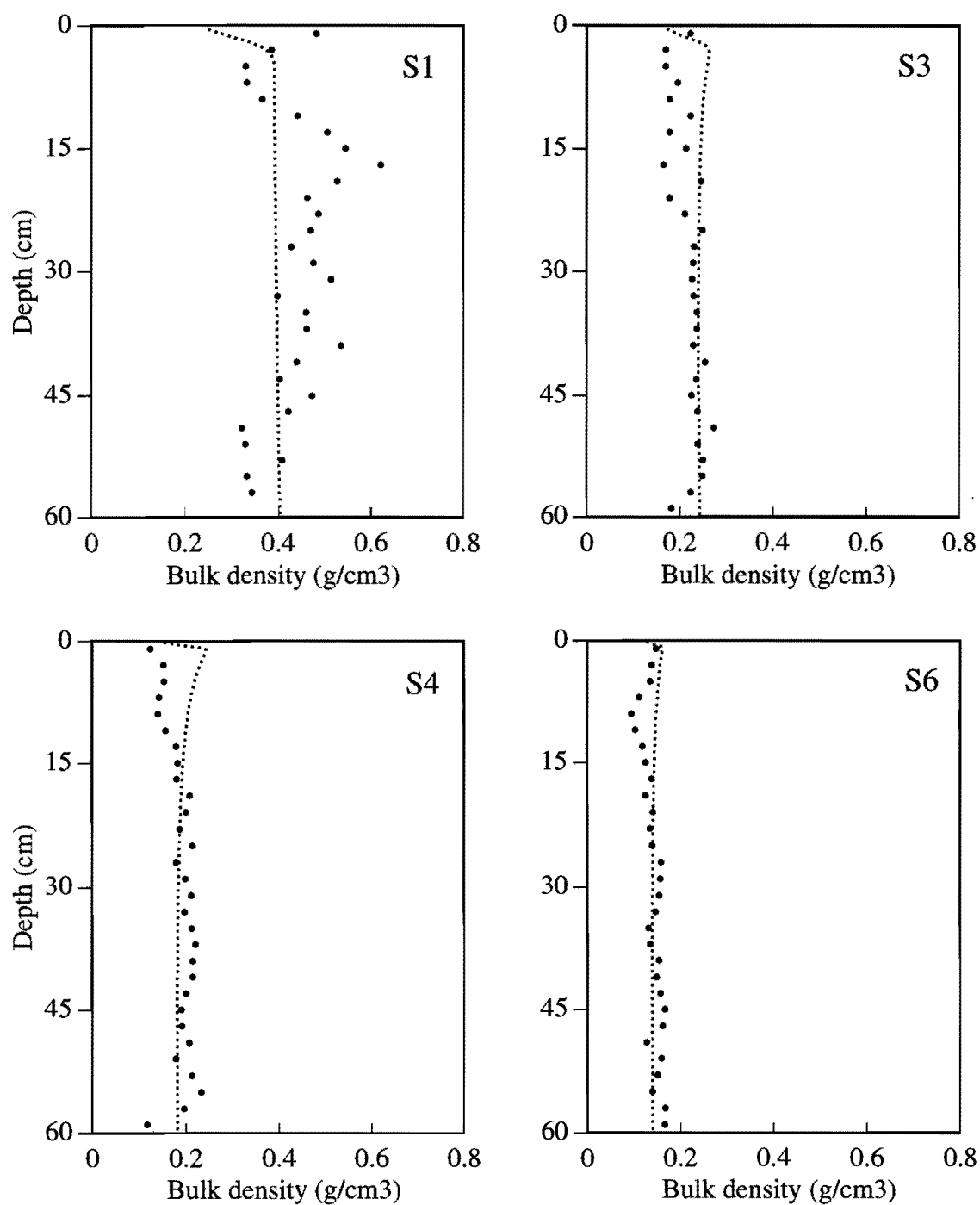


Figure 5.3. Comparison of observed (solid dot) and simulated (dashed line) bulk density in mangrove soils for the downstream (S1 and S3), intermediate (S4) and upstream (S6) sites along the Shark River estuary.

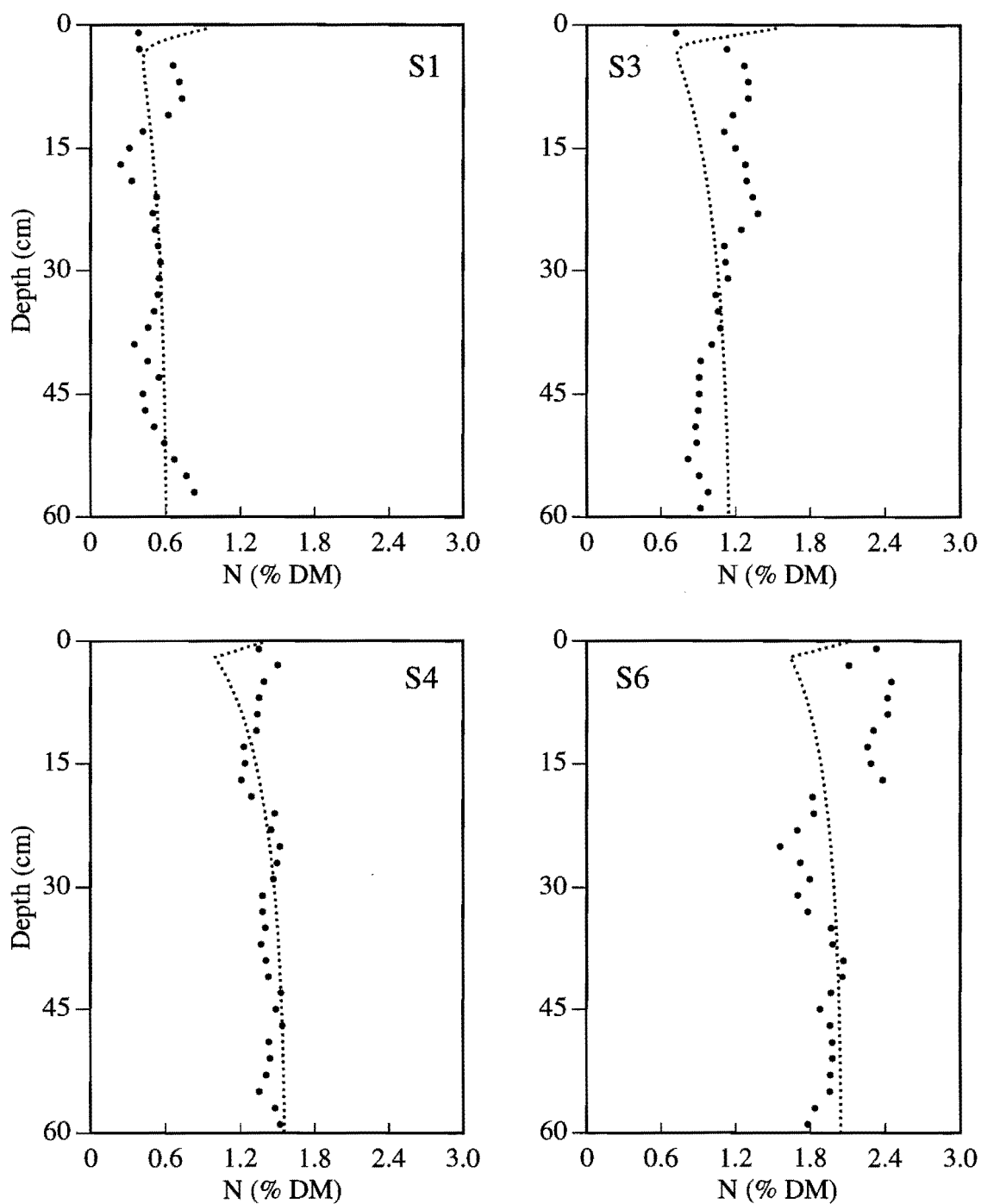


Figure 5.4. Comparison of observed concentrations of total nitrogen (solid dot) and simulated concentrations (dashed line) in mangrove soils for the downstream (S1 and S3), intermediate (S4) and upstream (S6) sites along the Shark River estuary.

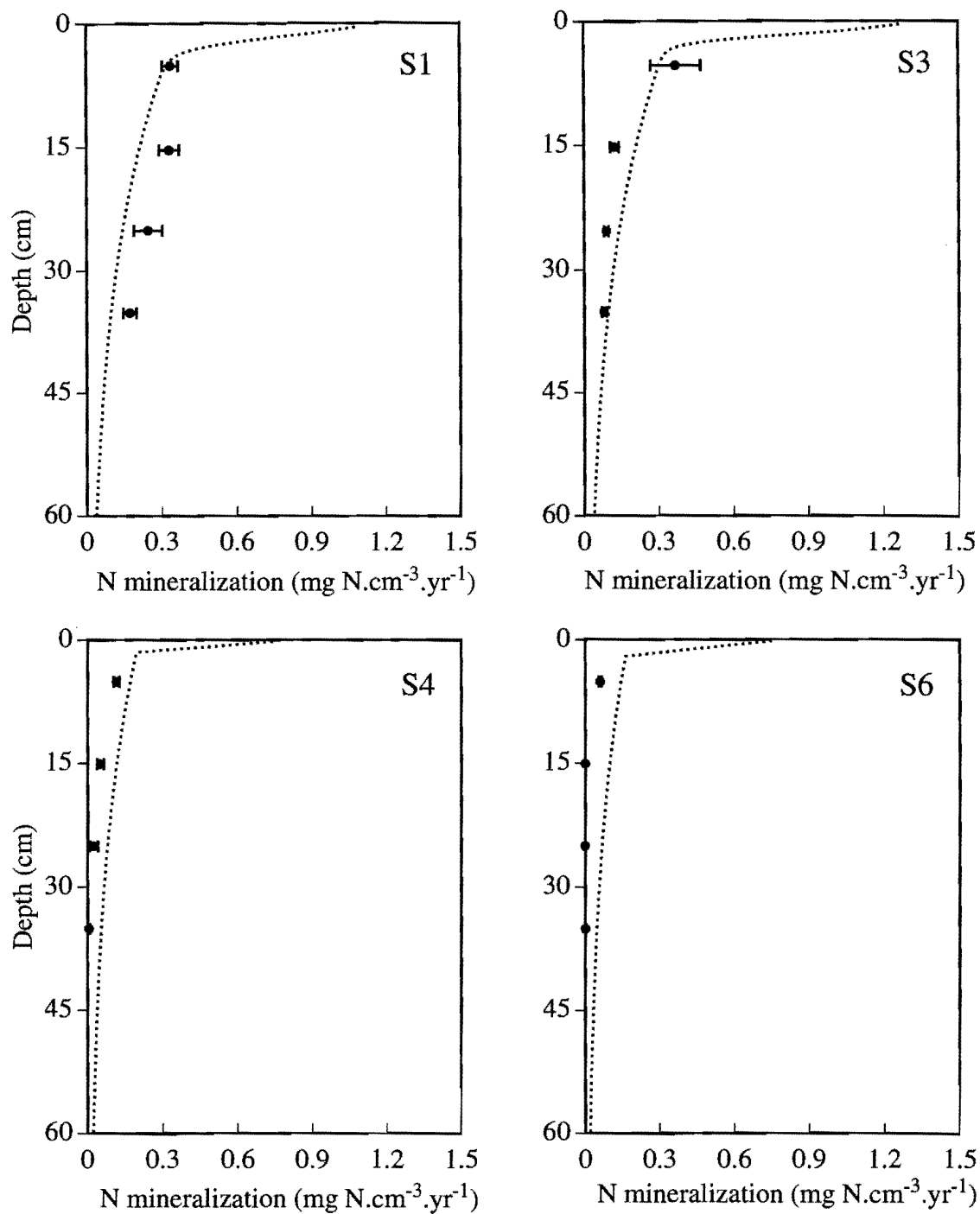


Figure 5.5. Comparison of observed (solid dot) and simulated (dashed line) nitrogen mineralization in mangrove soils for the downstream (S1 and S3), intermediate (S4) and upstream (S6) sites along the Shark River estuary. Observed values are mean $\pm$ SE (n=3).

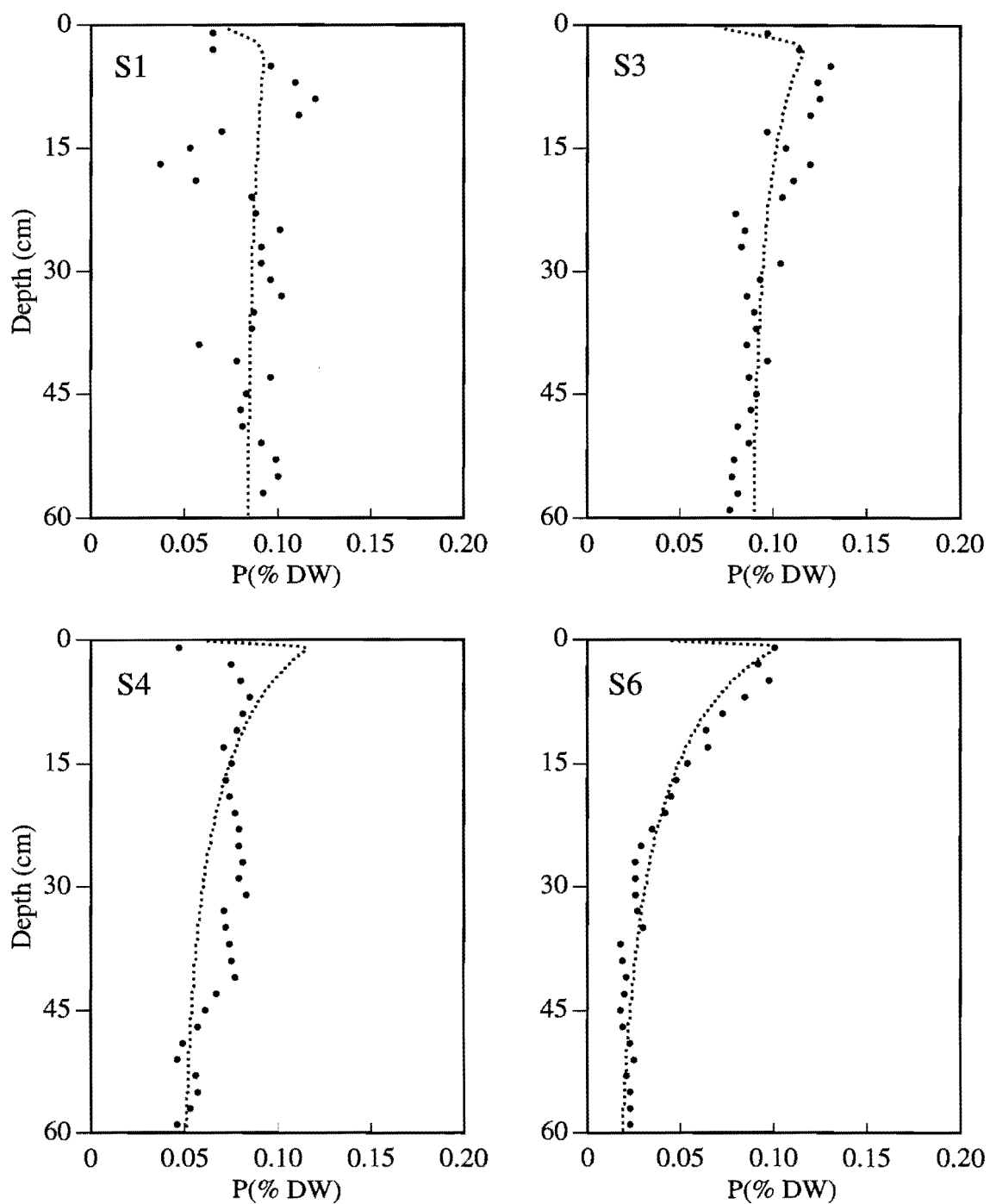


Figure 5.6. Comparison of observed concentrations of total phosphorus (solid dot) and simulated concentrations (dashed line) in mangrove soils for the downstream (S1 and S3), intermediate (S4) and upstream (S6) sites along the Shark River estuary.

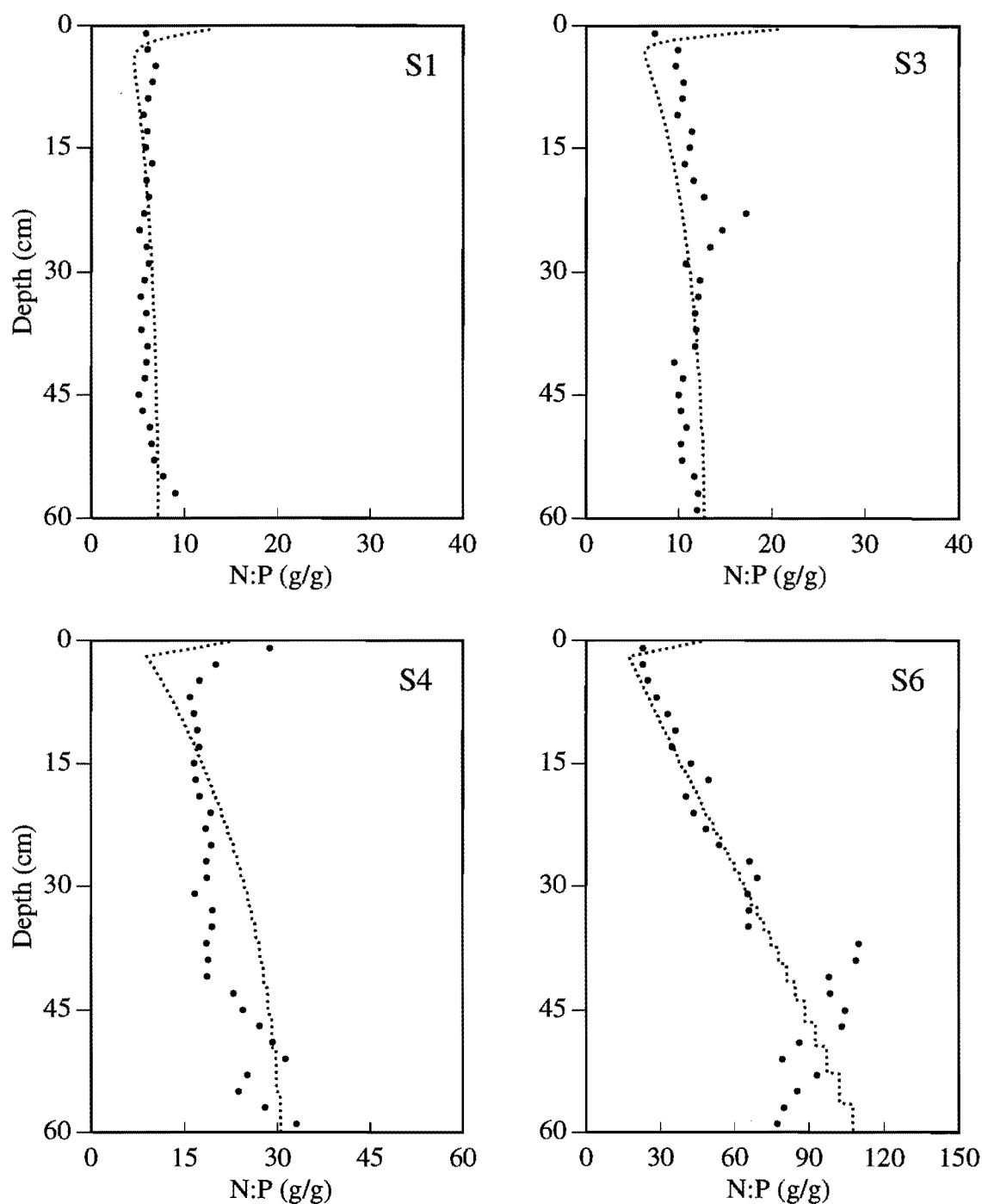


Figure 5.7. Comparison of observed ratios of N:P (solid dot) and simulated ratios (dashed line) in mangrove soils for the downstream (S1 and S3), intermediate (S4) and upstream (S6) sites along the Shark River estuary. Note that the scale for S1 and S3 is different from S4 and S6.

CHAPTER 6

MODELING THE DEVELOPMENT OF MANGROVE FORESTS ALONG SPATIAL GRADIENTS OF SOIL RESOURCE AVAILABILITY AND TOXIC STRESS

ABSTRACT

A computer model (MANGAL) derived from an individual-based gap model (FORMAN) and a soil organic matter model (NUMAN) was developed to investigate mangrove forest dynamics in relation to soil characteristics. Simulated forest structure was compared to that of three mangrove forests along the Shark River estuary, Florida, with a known disturbance history. Simulations of total and species-specific basal area of each mangrove site fit well with data from field surveys of the forests. Low nutrient availability in the intermediate site of the estuary limited the forest development. The measured size-class distribution of *Rhizophora mangle* showed higher frequencies for the smaller size classes, however, that of *Laguncularia racemosa* was bell-shaped. The model accurately tracked this pattern for each species. Mangrove succession was projected using the present stand condition of the downstream marine site in the estuary. Without disturbance, dominance of *L. racemosa* was eventually replaced by *R. mangle* or *Avicennia germinans*, depending on the recruitment rate of *A. germinans*. Simulated basal area of the three mangrove species along gradients of soil nutrient resource and salinity illustrated a change in competitive balance among the three species over time. *L. racemosa* dominated in fertile soils with low stress at early stages of recovery, but its abundance decreased while *A. germinans* increased in this region. The dominance of *R. mangle* was limited to regions with low nutrient availability and low salinity.

INTRODUCTION

A central question in mangrove ecology is the role that climatic, geomorphologic, hydrologic, edaphic, and biological factors play in the temporal and spatial patterns of abundance, distribution and species composition and zonation of coastal forested wetlands (Lugo and Snedaker 1974, Chapman 1976, Lugo 1980, Snedaker 1982, Woodroffe 1983, Thom 1982, Thom 1984, Twilley 1995). On broad geographical scales, the major variable governing the distribution of mangrove species is climate (Blasco 1984, Woodroffe and Grindrod 1991). On a regional scale, climate is much less variable, while soil can be quite heterogeneous because many edaphic characteristics depend on geomorphologic setting and hydrology (Thom 1982). The effect of hydrologic condition is primarily on the chemical and physical aspects of soil condition, which, in turn, affect the structure and function of a mangrove ecosystem (Lugo and Snedaker 1974).

Soil factors that exhibit resource and toxic stress gradients have repeatedly been shown to affect the structure and function of mangroves. Nutrient limitation (Onuf et al. 1977, Boto and Wellington 1984, Feller 1995, Twilley 1995) and hypersalinity (Lugo and Snedaker 1974, Cintrón et al. 1978) are among soil factors that have been suggested to be the most important mediators of the structure of mangrove wetlands. Quantifying the spatial and temporal variation in structure and composition of forest communities as a result of complex interactions among biotic populations and their soil environment can provide insights into how landscape patterns of forest will develop under different environmental settings and disturbance events. Simulation models are necessary for landscape analysis of patterns because it is difficult for experiments to be conducted across multiple scales in time and space (Turner 1989). In these circumstances, models provide a useful tool to describe, quantify and project forest dynamics.

Compared with modeling of other wetland ecosystems, ecological modeling of mangroves is very primitive to nonexistent (Mitsch et al. 1988), although these wetlands dominate most of the tropical and subtropical intertidal regions of the world. Several process-based models have been

developed using different approaches and different objectives in mind. Miller (1972) developed a model with a series of equations that predict primary productivity and transpiration of the mangrove forest canopy at an hourly time scale. The model predicted net and gross primary productivity, respiration, and transpiration, and was tested on data from a *Rhizophora* mangrove in Florida. Lugo et al. (1976) applied the concepts of energy and material flows to simulate the effects of upland runoff and tidal flushing on production and biomass in an overwash mangrove ecosystem. They found the time required to reach steady state levels of mangrove biomass was similar to the average time between tropical hurricanes, about 20 yrs. Their model also predicted that reductions in upland runoff caused a decrease in the productivity of mangrove wetlands. The impacts of tropical storms, herbicides and nutrient enrichment on mangrove ecosystems were simulated by Sell (1977) using a model similar to the model used by Lugo et al. (1976). The model suggested that complete mangrove recolonization of areas sprayed with herbicides may take 55 yrs to more than 100 yrs.

With the introduction of computer simulation techniques and better information about the growth and reproduction of different tree species, an individual-based simulation model can provide more realistic assessments of forest development (Huston et al. 1988). Individual-based gap models track the growth of each tree on a plot of defined size on the basis of species-specific life history traits and limitations of resource availability on the individual (Shugart 1984, Botkin 1993). This approach has been used to model various types of forests and has become a major means to simulate terrestrial forest dynamics (Shugart et al. 1992, DeAngelis and Gross 1992, Liu and Ashton 1995, Pacala et al. 1996). Although the individual-based gap model originated from studies on temperate forests (Botkin et al. 1972), it has been successfully applied to simulate the dynamics of forested wetlands (Phipps 1979, Pearlstine et al. 1985) and tropical rain forests (Shugart et al. 1980, Doyle 1981). The individual-based model has been extended to include selected ecosystem-level processes, such as dynamics of edaphic nutrient availability in forest succession. Feedback effects of nutrient resource distribution, especially nitrogen, through decomposition of litter have been linked within the design of gap models (Aber et al. 1982, Weinstein et al. 1982, Pastor and Post 1986).

The primary objective of this study was to quantify the effects of spatial gradients in soil characteristics on the growth and development of mangrove wetlands. The JABOWA-FORET (Botkin et al. 1972, Shugart 1984) individual gap model was used as a basic design to develop a model to simulate mangrove forest development with links to soil nutrient dynamics. Nutrient cycling in open mangrove ecosystems is more complex than in terrestrial ecosystems, because it is controlled by both nutrient cycling within the mangrove, and net exchange of materials between the wetland and coastal waters. The model was first tested against field survey data on mangrove forests with a known hurricane-disturbance history along a defined nutrient gradient. The model was then used to project the general trajectory of forest structure development under specific initial conditions. Finally, the model explored the effects of edaphic conditions on mangrove structure by simulating mangrove forest dynamics along the spatial gradient of soil nutrient availability and salinity.

METHODS

Model description

The basic structure of the mangrove wetland model, MANGAL, includes a model that simulates demographic dynamics of mangroves (FORMAN) and another model that tracks nutrient resources in soil (NUMAN). The FORMAN model, which is a modification of the JABOWA and FORET models, was used to calculate rates of recruitment, growth and mortality for mangrove tree species in a 0.05 ha plot. The model used a gap size of 500 m², which was typical for lightning gap sizes among the study sites (Chapter 3). The NUMAN model (Chapter 5), which simulates

soil organic matter dynamics in a mangrove wetland, was used to link soil fertility with tree growth. Fig. 6.1 is a conceptual model of the MANGAL model. The linkage of both the FORMAN and NUMAN models into an integrated MANGAL model represents the initial efforts to develop an ecosystem-based approach to simulating the properties of mangrove wetlands.

In general, the FORMAN model represents tree growth on an annual basis for individual trees in a forest gap. The species-specific optimal growth rate of a mangrove is decreased by taking into account the effects of resource availability (light and nutrients), toxic stress (soil salinity) and average climate as measured by the number of growing degree days. A set of parameters for each species is given in Table 6.1. The structure of the JABOWA and FORET models has been well documented (Shugart 1984, Botkin 1993), so only specific modifications from JABOWA and FORET that were used to develop the FORMAN model will be discussed in detail.

The optimal growth of trees: The FORET model assumes that the growth equation for a tree under optimal conditions is:

$$\frac{dD}{dt} = \frac{G \cdot D \cdot (1-D \cdot H) / (D_{\max} \cdot H_{\max})}{(274+3b_2 D-4b_3 D^2)} \quad [6.1]$$

in which D is the DBH (diameter at breast height) of the tree (cm), H is tree height (cm), $D_{\max}$ and $H_{\max}$ are maximum values of diameters and heights for a given tree species. G , b_2 and b_3 are species-specific growth parameters. The optimal growth is constrained by life history traits. However, the realized growth is limited by shading, temperature, nutrient availability and soil salinity in the FORMAN model.

Light effect: The light that reaches a given tree is a function of total leaf area in the canopy above the tree. Leaf area was assumed proportional to leaf weight, which is in turn proportional to tree diameter:

$$LW = a \cdot D^b; \quad [6.2]$$

$$LA = c \cdot LW; \quad [6.3]$$

where LW and LA are leaf weight (g) and leaf area (m^2); a and b are species-specific constants (Cintrón and Schaeffer-Novelli 1984); c is the specific ratio of leaf area to leaf weight. The light extinction through the canopy is calculated as:

$$Q(h) = Q_0 \exp(-k \int_h^\infty LA(h') dh') \quad [6.4]$$

where $Q(h)=Q_0$ is the available light at a height (h); Q_0 is incident light; $LA(h')$ is the cumulative leaf area above height h . A typical attenuation constant (k) for the canopy of a mangrove forest is 0.5 (Clough 1992).

Botkin et al. (1972) used two expressions to calculate the reduction of growth by shading effect, r :

$$r_s(AL) = 1 - \exp[-4.64 \cdot (AL - 0.05)] \quad [6.5]$$

$$r_i(AL) = 2.24 \cdot \{1 - \exp[-1.136 \cdot (AL - 0.08)]\} \quad [6.6]$$

where r_s and r_i are the reduction of photosynthesis rates for shade-tolerant and shade-intolerant trees, respectively. AL is available light on the tree, which is equal to $Q(h)$. Field observations indicate that *R. mangle* and *A. germinans* are more tolerant of shading than *L. racemosa* (Wadsworth 1959, Ball 1980, Roth 1992). Based on comparisons of potential growth and partition of biomass among these three species in two manipulated light levels, McKee (1995b) found that *L. racemosa* was more competitive at high levels of light. In FORMAN, $r_s(AL)$ was calculated using equation [5] for *R. mangle* and *A. germinans*, while $r=(r_s(AL)+r_i(AL))/2$ was used for *L. racemosa* (Fig. 6.2).

Temperature effect: Botkin et al. (1972) assumed that the effect of temperature on growth was a response to an annual accrued number of degree days above some threshold temperature. They calculated the number of growing degree-days as follows:
DEGD =

$$\frac{365}{2\pi} (T_{July} - T_{Jan}) - \frac{365}{2} (T_{base} - \frac{T_{July} + T_{Jan}}{2}) + \frac{365}{\pi} \left[\frac{(T_{base} - \frac{T_{July} + T_{Jan}}{2})^2}{(T_{July} - T_{Jan})} \right] \quad [6.7]$$

where T_{July} , T_{Jan} and T_{base} are average temperature in January, July and base temperature, respectively, in which all temperatures are in degrees Fahrenheit. FORMAN followed the same equation except using 47 °F (mean temperature of the coldest month at the northern limit of the mangrove distribution) as the base temperature instead of 40 °F. Mangroves are tropical plants, which have an optimal tree growth in the lower tropical latitudes where peak biomass occurs (Twilley et al. 1992, Saenger and Snedaker 1993). The temperature multiplier T(DEGD) was modified for the FORMAN model. JABOWA and FORET models used a parabolic function to represent the degree day effect, which is not suitable for tropical mangroves. Instead, equation [8] was used to describe the effect of climate (global temperatures) on mangrove growth (Fig. 6.2):

$$T(DEGD) = 1 - (DEGD_{min}/DEGD)^2; \quad [6.8]$$

where $DEGD_{min}$ is the extreme low value of DEGD within the range of species distribution. *A. germinans* has the most northern distribution in the northern hemisphere (Sherrod and McMillan 1985). The growth multiplier approached 1.0 with an increase in growing degree days. There was no maximum degree day limitation in the FORMAN model.

Salinity stress: The abundance of salt is the single most important factor in the mangrove environment that regulates growth, height, survival and zonation of mangroves (Lugo and Snedaker 1974). Mangroves are facultative halophytes since they do not require salt water for growth but are able to tolerate high salinity (Tomlinson 1986). McMillan (1974) compared the response of three mangrove species to short term hypersaline exposure and found that *R. mangle* and *L. racemosa* has a narrower salt-tolerance than *A. germinans*. The relative tolerance of three mangrove species under greenhouse conditions was found to be similar among the three mangrove species within a salinity range of 0-45 g/kg (McKee 1995b). The interspecific differential response of mangroves to salinity occurred at salinities from 45- 60 g/kg, which inhibited the growth of *R. mangle* and *L. racemosa* significantly more than that of *Avicennia germinans*. The growth multiplier of salinity was sigmoid and calculated as follows (Rastetter 1990):

$$S(SALT) = 1 / \{ 1 + \exp[d \cdot (U_i - U)] \} \quad [6.9]$$

where $S(SALT)$ is the multiplier, U is the salinity, U_i is the value of U where the multiplier is 0.5, and d is a constant. Salinity has no effect on the growth of all three species of mangrove from 0 to

about 35 g/kg (Fig. 6.2). At salinity >50 g/kg the level of tolerance to salinity occurs at the following rank: *A. germinans* > *L. racemosa* > *R. mangle*. The upper tolerance of salinity for *R. mangle* is about 70 g/kg, compared to 85 g/kg for *L. racemosa* and 100 g/kg for *A. germinans*, which are similar to field observations by Odum et al. (1982).

Nutrient resource: The pool of available nutrients in mangrove soils is a product of several processes that proceed on different time scales including plant production (aboveground and belowground), decomposition of litter fall, mineralization of organic matter, input by rainfall, sedimentation by tide and runoff, and uptake by plants. The NUMAN model (Chapter 5) was developed to simulate the availabilities of nitrogen and P in mangrove soils by coupling the simultaneous effect of these processes. In brief, the NUMAN model was modified from the SEMIDEC (Morris and Bowden 1986) and CENTURY (Parton et al. 1987) models of soil organic matter for marshes and grasslands, respectively. NUMAN was calibrated with field measurements in the Shark River estuary and estimated rates of several processes including nitrogen mineralization, P accumulation from exogenous sources, and export of organic detritus from mangrove wetlands to coastal waters. The NUMAN model was modified and linked to the demographic FORMAN model to form the MANGAL model. The only modification of the NUMAN in the MANGAL model was that soil was treated as a single depth without considering vertical distribution of C, nitrogen and P. Soil depth in MANGAL was established relative to the vertical distribution of the root system, which was estimated at 150 cm in the present version. The change in soil elevation due to organic matter production and decomposition, and input of allochthonous inorganic material was calculated as an accretion rate. Leaf and twig litter, and fine root production were calculated based on forest basal area as simulated by FORMAN. Dead wood and large root production were calculated based on the biomass of individual dead trees that occurred during the simulation. Litter from the canopy was added to the forest floor at the end of each year.

Nutrient availabilities expressed as a rate of nitrogen mineralization and concentration of total P from NUMAN were constraints on mangrove growth. The classification of tree species into three types of nutrient tolerance has been commonly applied in forest gap models (Weinstein 1982, Aber et al. 1982, Pastor and Post 1986). The following function is used to limit growth of plants in responses to nutrient availability (Weinstein et al. 1982):

$$S(NUT) = c_1 + c_2 \cdot RNA + c_3 \cdot RNA^2 \quad [6.10]$$

where $S(NUT)$ is a growth modification factor; c_1 , c_2 and c_3 are coefficients; RNA is relative nutrient availability with a value from 0 to 1.0. Based on the differential responses of the three mangrove species to nutrient levels in a greenhouse study (McKee 1995b), the responses of three mangrove species to availability of nutrient resource were differentiated (Fig. 6.2).

RNA based on nitrogen was calculated as a ratio of net nitrogen mineralization to nitrogen required in plant uptake. If the rate of nitrogen mineralization was greater than uptake, RNA had a value of 1.0. However, if uptake exceeded the mineralization rate, RNA equalled the ratio of net mineralization to uptake. Total P concentrations in mangrove soil were used to calculate RNA because they represent the net effect of plant uptake and exogenous inputs. Plants can absorb P from soil by excreting phosphatase without the microbial oxidation of organic matter and associated nitrogen (McGill and Cole 1981). The soil P-availability index, based on extractions with dilute acid among my study sites, was related to total soil P (Chapter 3). In the present version of MANGAL, RNA based on total P (per unit area soil) was calculated using a Monod equation that describes the function of total soil P vs mangrove forest basal area (Chapter 4):

$$PR = \frac{(R_{ac} - R_{min})PR_{max}}{R_{ac} - R_{min} + \alpha} \quad [6.11]$$

where PR is production, $PR_{\max}$ is the maximum production, R_{ac} is the amount of resource acquired, $R_{\min}$ is nutrient availability at zero production and α is half-saturation constant with respect to R_{ac} (see Bridgham et al. 1995 for details). The fit of the Monod model with data from 10 mangrove forests was significant ($r^2=0.80$), and $R_{\min}$ was positive (15.2 g P/m^2) with a half-saturation constant of soil P of 29.3 g P/m^2 to a depth of 40 cm (Chapter 4). The ratio of $PR/PR_{\max}$ was used as an index of the relative availability of P. Tree growth was only constrained by the most limiting element in any one year. The smaller RNA value of either nitrogen or P was used as the nutrient multiplier for plant growth.

Realized growth: Equation [6.1] was multiplied by equations [6.8], [6.9], [6.10], and by either equation [6.5] or [6.6], to produce the growth equation used in the FORMAN model:

$$dD/dt = \frac{G \cdot D \cdot (1 - D \cdot H/D_{\max} \cdot H_{\max})}{(274 + 3b_2 D - 4b_3 D^2)} \cdot T(DEGD) \cdot r(AL) \cdot S(NUT) \cdot S(SALT). \quad [6.12]$$

Sapling establishment: The number of saplings added annually to a simulated plot (gap) was a function of the maximum number of saplings, the amount of light, and site condition (Botkin 1993):

$$E = \xi \cdot f(AL) \cdot S \cdot Q \quad [6.13]$$

where E is the number of saplings that enter a simulated plot in a year, ξ is a uniformly chosen random number (0 to 1.0), $f(AL)$ is a function of available light, S is the species-specific annual maximum number of saplings that can be added to a plot, and Q is the site specific condition for recruitment of each species. In the current version of FORMAN, S was set at 30 for each species, and the number of saplings added to a plot for each species was as follows for *R. mangle* and *A. germinans*:

$$E = \xi \cdot AL^2 \cdot 30 \cdot Q. \quad [6.14]$$

For *L. racemosa* the equation was:

$$E = \xi \cdot AL^{2.5} \cdot 30 \cdot Q. \quad [6.15]$$

These functions assumed that mangrove saplings enter a plot at the maximum rate if the canopy is open. However, the sapling recruitment rate decreased rapidly as the canopy closed, as indicated by an increase in leaf area index. Saplings of *L. racemosa* were less shade-tolerant than *R. mangle* and *A. germinans* (Wadsworth 1959, Ball 1980, Roth 1992). Saplings entered the plot at a size (DBH) of 1.27 cm. Q depended on the condition of the site for recruitment.

Mortality: Two sources of mortality were included in the model: age-dependent mortality and mortality caused by suppressed growth. The probability of mortality for each tree was handled as in other gap models (Botkin et al. 1972, Shugart 1984) and increased with age. Trees whose rate of DBH growth was $< 0.01 \text{ cm}$ for two consecutive yrs were subjected to additional mortality (Solomon et al. 1986, Pastor and Post 1986).

The study forest

The study sites are located along the Shark River estuary on the west coastal plain of

Everglades National Park (Fig. 3.1). Davis (1940) suggested that mangrove forests in the downstream region of the estuaries in southwestern Everglades are "probably the optimum growth of mangroves in the Americas". Coastal forested wetlands in the southwestern Everglades of south Florida extending from the Whitewater Bay region to Ten Thousand Islands include one of the greatest mangrove areas in the Gulf of Mexico (Davis 1940, Smith et al. 1994). Mangroves have developed in this region for more than 3000 yrs (Scholl 1964a,b). Three mangrove species, *R. mangle* L., *A. germinans* (L.) Stearn and *L. racemosa* (L.) Gaertn., form a continuous band of forested wetlands that extend from the Gulf of Mexico to the inland limit of periodic salt water influence. Mangrove wetlands in this region recovered by natural succession after the disturbance of Hurricane Donna in 1960, with an instant mortality of mangroves reported at 50 to 70%, but the eventual tree mortality was higher (Craighead and Gilbert 1962).

Model simulations

The first step in this modeling exercise was to simulate the regeneration of three mangrove forests (S1, S3 and S4) after disturbance by Hurricane Donna along the Shark River estuary (Fig. 3.1). MANGAL was used for this comparison. Detailed descriptions of the forest structure and soil characteristics along the Shark River estuary were presented in Chapters 3, 4 and 5. To compare simulation results of mangrove forest development after 34 yrs of regeneration with field observations, the initial conditions of the stands were needed. Although tree mortality of mangroves was extreme high following Hurricane Donna, the presence of a few large trees presently in the study sites indicates that there was some survival following the disturbance (Chapter 4). Survivors were identified by DBH in 1995 and a reasonable mean growth rate of DBH for each species. Tree mean growth rates were estimated based on measurements of DBH between 1995 and 1996 along the Shark River estuary and in a mangrove forest recovering from Hurricane Andrew (1992) near the mouth of Broad River. The mean DBH growth rates in the last 34 yrs were estimated as 0.5, 0.4 and 0.2 cm/yr for *L. racemosa*, *A. germinans* and *R. mangle*. Therefore, trees presently found at each site with DBH > 34 times the mean DBH growth rate for the respective species are considered survivors of the 1960 disturbance. Initial DBH of survivors in 1960 was hindcasted as difference between DBH in 1995 minus 34 x mean DBH growth rate. For species that have a high sprout ability after the loss of a trunk, such as *L. racemosa* (Wadsworth 1959), multiple stems were treated as sprouts from the disturbance by Hurricane Donna in 1960. In the model, new sprouts were the same as a sapling. The model used this reconstructed data set as initial stand conditions and simulated 50 times. Because of the stochastic properties of the model, the model was run 50 times and output was averaged over 50 simulated plots.

Site-specific initial conditions included initial trees described above, soil fertility, salinity, and recruitment. The initial soil concentrations of organic matter, nitrogen, and P, along with pore water salinity, among the three sites were based on field measurements (Chapters 4, 5). Several site-specific rates of soil processes, such as inorganic matter accumulation, export, and P accumulation, were estimated with the NUMAN model as described in Chapter 5. Q (the site condition for sapling recruitment in a specific site) was user-defined based on parent tree density and model calibration. For *L. racemosa*, *R. mangle*, and *A. germinans*, Q was 1: 1: 0.27 in S1; 1: 0.83: 0.27 in S3; 0.1: 0.83: 0.1 in S4, respectively.

The second model exercise was to project mangrove succession in the downstream site (S1) of the Shark River estuary. MANGAL used the measured data in the plots in 1994 as initial vegetation condition and run for 500 yrs. The sensitivity of model to recruitment was tested. One projection assumed the same sapling recruitment as run for the first 34 yrs as noted above, the other assumed the equal sapling recruitment for all three species.

In the model, the growth of each tree was constrained by four environmental variables including light, temperature, nutrient availability and salinity, in which nutrient availability and salinity were related to soil characteristics and hydrologic regime. I assumed that soil fertility and

salinity were relatively constant as a function of location in an environmental setting. Results of simulations using the FORMAN model compared the response of three mangrove species to the axes of soil nutrient resource and salinity stress. The spatial gradient in relative nutrient availability (RNA) in the model was basically the concentration of total P among the study sites (Chapter 5). These response surfaces can be used to investigate the potential landscape distribution of species and relative competitive success (Botkin 1993). In this model exercise, I assumed that the maximum number of saplings that entered all simulated plots annually was equal for all three mangroves, and there was no effect of site conditions on sapling recruitment ($Q=1$).

The program was written in ANSI C. Data structure of the linked lists was used as to connect each individual tree in the simulated plot. Linked lists are dynamic, the length of the list can increase or decrease as necessary when trees are added or deleted in the simulated plot, respectively.

RESULTS

Regeneration following disturbance

The first test of the MANGAL model was to compare field measurements obtained from 400 m² plots in three mangrove sites along the Shark River estuary with simulations of forest regeneration from 1960 to 1994 in response to the disturbance by Hurricane Donna (Chapter 4). The simulated results of total basal area were similar to observed values in each respective mangrove site (Fig. 6.3). The differences in basal area at the downstream locations (S1 and S3) and intermediate location (S4) were due to soil nutrient availability and species composition. Concentrations of soil total P in S1 and S3 were significantly greater than in S4 (Chapter 4). The model also predicted that the percentage of total basal area by species was very close to the observed values in all three sites (Fig. 6.4). In the downstream sites, *L. racemosa* made the largest contribution to total basal area; however, *R. mangle* was dominate at the intermediate site.

One merit of using the individual-based approach to develop ecosystem models is the ability to simulate specific information at several hierarchical levels. For example, not only can the total metrics of a forest be described in the simulations, such as basal area, but also species-specific size class distributions can be analyzed. A comparison of size-class distribution in forest structure between simulation results and field observations can provide insights into the performance of MANGAL. The model captured the shapes of the *R. mangle* size-class distribution, indicating high densities in small size-classes (<8 cm DBH) in all three sites (Fig. 6.5). The model predicted a decline in density of size-classes <6-8 cm, which was a good fit with observed results in S1, but not in S3. A decline in density of these size classes was not observed in either field or simulated results in S4. This may be related to the higher light levels on the forest floor, which allows the establishment of saplings. The size-class distribution of *L. racemosa* was bell shaped, which was significantly different from the patten observed for *Rhizophora* (Fig. 6.5, 6.6). Although there were differences between simulated and field results among some size-classes, the model generally followed the pattern with low stem frequencies in larger and smaller size-classes. *L. racemosa* was a minor component in S4, saplings that entered the simulated plot were reduced, which was probably due to a lack of parent trees in this site and poor soil fertility. *L. racemosa* dominated in the medium to large size-classes in S1 and S3, which was an initial response to forest regeneration after a disturbance, indicating this species has pioneer qualities in this region of intertidal zone. Densities of *A. germinans* in all sites were lowest compared to the other two species; however, this species had a higher frequency in the largest size cohort (DBH>20 cm), because they represented survivors of the hurricane disturbance (Fig. 6.7). The model was able to tract the growth of these survivors, which indicated that the reconstructed data of the simulations were reasonable scenarios. The model also predicted that there was a bell-shaped pattern of size class distribution, which was similar to the field data in S1.

Projection of mangrove succession

Significant changes in species dominance using basal area were observed when MANGAL was run for an additional 500 yrs to project patterns in mangrove succession at S1 (Fig. 6.8). In the downstream site of the Shark River estuary, higher soil fertility favored a quick recovery of *L. racemosa* after the forest canopy was removed by hurricane force winds. Simulations using either the same sapling recruitment as in the first 34 yrs (Fig. 6.8A) or those using the equal sapling recruitment for all three species (Fig. 6.8B) predicted that *L. racemosa* continued to dominate in total basal area for the next 30 to 40 yrs. However, long-term succession of mangroves was sensitive to recruitment for each species. The dominance of *L. racemosa* was gradually replaced by *R. mangle* if the recruitment of *A. germinans* was kept at low rates (Fig. 6.8A). However, if there was no site effect on maximum sapling recruitment for all three species, *A. germinans* was able to quickly overcome *L. racemosa* and total basal area of the plot increased significantly (Fig. 6.8B). The decline of *L. racemosa* was due to low recruitment of this species under severe shading.

Salinity and nutrient response surfaces

FORMAN was developed as a tool to investigate the dynamics of mangrove wetlands in relation to their soil characteristics. In these simulations, I was interested in examining the sensitivity of mangrove succession to spatial gradients in soil conditions. Several biological and physical factors that can have an important impact on mangrove structure, such as seedling predation and hurricanes, were not included in this analysis. However, FORMAN model is able to explore other environmental gradients by minor modifications of specific parameters. There was no limit to recruitment among the three species in these simulations.

Model simulations of forest development were adjusted by changing conditions of soil fertility and salinity, using a constant climatic condition (temperature) similar to south Florida. In this simulated landscape gradient, total basal area of mangroves increased with increased soil fertility, but decreased with increased soil salinity (Fig. 6.9). Extremely low nutrient availability severely limited mangrove development. Current mangrove wetlands in the lower Shark River estuary, approximately at 35 yrs, located in optimal soil conditions (low salinity and high fertility) achieved a high total basal area, which was close to the basal area of these forests after 100 yrs. After 200 and 300 yrs, total basal area had a higher variance compared to values in 35 and 100 yrs. This may be related to demographic stochasticity in the older forest.

The differential responses in basal area of three mangrove species were observed along temporal scales and environmental gradients. In 35 yrs, *L. racemosa* had the maximal basal area at salinities <50 g/kg and RNA >0.5 , but this species was excluded in areas with low soil fertility and high salinity. Growth of *R. mangle* was slow and this species was a small component of total basal area compared with the other two species in fertile soil. *A. germinans* dominated in areas of salinity >60 g/kg (Fig. 6.10). If the model was allowed to continue to run up to yr 100, niche differentials (associated with soil resource use and tolerance to salt) were significant along both nutrient resource and salinity gradients (Fig. 6.11). *L. racemosa* remained dominant in fertile and low salinity regions; *R. mangle* outcompeted the other two mangrove species and mainly occupied the regions of poor soil fertility. *A. germinans* flourished and achieved very high basal area in plots where both soil salinity and fertility were higher, whereas *L. racemosa* and *R. mangle* were excluded from these plots. The long-term simulations (200 to 300 yrs) indicated that *A. germinans* subsequently increased steadily in the plots with higher fertility and a wide range of salinities, whereas the basal area of *L. racemosa* declined (Fig. 6.12, 6.13). The dominance of *L. racemosa* was eventually replaced by *A. germinans*, however, *R. mangle* and *A. germinans* formed mixed associates in these plots.

DISCUSSION

Although gap phase dynamics as a natural phenomenon has been described for more than four decades (Watt 1947) and widely examined in temperate and tropical forests, the importance of gap dynamics in mangrove wetlands has only recently been discussed (Smith 1992, Smith et al, 1994). The concept of gap dynamics as a driving natural phenomenon of vegetation patterns has been applied in the development of forest dynamic models (Shugart 1984). The applications of individual-based models to describe dynamics of tropical forests were few compared with hundreds of individual-based models developed for temperate forest. This restriction has been connected with the lack of available data for diverse species in tropical forests, which limits the parameterization of these models (Botkin 1993, Liu and Ashton 1995). Data for tropical mangrove forests are also limited, but mangrove species richness in the Neotropics is much lower than in upland tropical forests. The development of the MANGAL model represents a synthesis of available data for three Caribbean mangrove species as applied to individual gap models to explore the long-term dynamics of mangrove forest development.

MANGAL simulates mangrove forest development by integrating demographic processes and soil nutrient dynamics. Tests of the model against data measured from three 34 yr mangrove forests along the Shark River estuary provide strong support for the successional dynamics predicted by MANGAL. The model tracked well total basal area, and species-specific contributions to total basal area. The model also appeared to predict the frequency of species-specific size-class distributions. These comparisons between simulation results and field observations provide confidence that MANGAL can project mangrove forest dynamics.

MANGAL predicted that *L. racemosa* dominates in the early stages of forest development because of its fast growth potential in fertile soil conditions, along with its ability to sprout. *L. racemosa* sprouts more vigorously than *A. germinans* after the loss of the tree trunk, however *R. mangle* does not have this potential (Wadsworth 1959). Also *L. racemosa* had a high growth rate under high light and soil nutrient availability under greenhouse conditions (McKee 1995b). A high growth rate of *L. racemosa* was observed in the Everglades National Park after disturbance by Hurricane Andrew in 1992 (Smith 1995, Twilley et al. unpublished data). The model predicted that the high light conditions required for *L. racemosa* to regenerate restricts its development to early stages of gap dynamics. Once the canopy of a gap closes, *L. racemosa* regeneration is severely limited and it becomes a minor component of mangrove communities as the pioneer trees of this species die. Wadsworth (1959) observed that there were *A. germinans* and *R. mangle* seedlings but no *L. racemosa* under a *L. racemosa* forest and implied that *L. racemosa* was relatively intolerant to shading. Differential shade-tolerance has been proposed as an important agent of interspecific competition during mangrove succession. Ball (1980) found that seedlings of *R. mangle* tend to persist for a longer period than those of *L. racemosa* under the forest canopy, based on historical aerial photographs, measurements of seedling and sapling densities, and frequency of live and dead trees in south Florida. She suggested that *L. racemosa* was being replaced by *R. mangle* because of their difference in shade-tolerance. Putz and Chan (1986) synthesized long-term observations from permanent plots in a Malaysian mangrove forest. They also demonstrated that shade-tolerant species, such as *Bruguiera gymnorhiza*, steadily increased in abundance in the mangrove forest dominated by *Rhizophora apiculata*.

Several authors have drawn attention to the importance of gaps in the forest canopy on the establishment and growth of mangroves (Macnae 1968, Putz and Chan 1986, Smith 1987a,b). Smith et al. (1994) further proposed that gaps are an important seedling source for mangrove regeneration after formation of large disturbed areas such as hurricanes. They compared the survivorship of mangroves between areas of forests that had formed gaps and reference areas with canopy after Hurricane Andrew. They found that mangroves in the gap areas had lower mortality than those under the canopy.

Field observations indicated the low density of *A. germinans* saplings, suggesting a low

recruitment of *A. germinans* in my study sites. One possible explanation is the differential predation on mangrove seedlings. In south Florida, Smith et al. (1989) demonstrated that grapsid crabs and snails had a potential to consume more than 80% of *A. germinans* propagules in a 4 d experiment. However, their experiment showed there was no consumption on *R. mangle*. Seed predation has been proposed as a key factor influencing mangrove structure and zonation in Australia (Smith 1987a, Smith et al. 1989). Except seed predation, the establishment of mangrove seedlings has been proposed to be controlled by the light, water level, tidal frequency, salinity, temperature, presence of a seedling source, and herbivory (Rabinowitz 1978, Smith 1987a, Smith et al. 1989, Robertson et al. 1990, Jiménez and Sauter 1991, Clarke 1993, Clarke and Allaway 1993, Ellison and Farnsworth 1993, McKee 1995a). The JABOWA/FORET models assume isometric spatial interaction among plots with regard to seed dispersal. Seed dispersal and seedling growth are not explicitly simulated in these former gap models. Further modification of the MANGAL model is needed to include seedling dispersal and the site specific establishment of saplings in mangrove forests.

Without exogenous disturbances, such as hurricanes, the model predicted that *A. germinans* increased in dominance if saplings of the three species have the equal possibility to enter a plot. Hurricanes occur several times during the life span of a mangrove tree in south Florida. Direct comparisons of simulation results with field measurements are difficult because of the immature stage of mangrove forest development in this region. One exception is a black mangrove forest near Flamingo in south western Florida described by Craighead (1971). That forest was about 250 yrs and dominated by *A. germinans* tree with mean DBH of about 1 m. Unfortunately, this forest was destroyed by the Labor Day storm in 1935.

Soil nutrient resources in mangroves vary with location in the horizontal intertidal zone (Boto and Wellington 1984, McKee 1995a) and longitudinal axis of an estuary (Chapter 3). The resource ratio hypothesis of plant succession predicts that spatial heterogeneity of resources favor different plant species in different locations (Tilman 1982). However, physical and chemical stress factors in mangroves such as high salinity might also lead to changes in species composition due to species-specific tolerances to these stressors. The model simulations with varying soil nutrient availability and salinities illustrate how the competitive balance among species is altered by the environment. A continuum of species response surfaces to gradients of nutrients and salinity can be used to investigate the potential landscape distribution of these three mangrove species. The results of these simulations project the dominant influence of autogenic processes such as plant competition without impacts of disturbance. They therefore represent the realized niche of each species for the selected dimensions of soil nutrient resource and salinity stress (Botkin 1993). Because the model's sensitivity to spatial gradients of soil nutrient and salinity was emphasized here, other allogenic processes, such as hurricane disturbance which is an important factor to set back Caribbean mangroves (Roth 1992, Smith et al. 1994, Doyle et al. 1995), are not included in current simulations. However, MANGAL can be modified to explore and investigate the responses of mangroves to natural and human disturbance.

Table 6.1. Species-specific parameters used in the MANGAL model.

Parameters	<i>Avicennia germinans</i>	<i>Laguncularia racemosa</i>	<i>Rhizophora mangle</i>
G	243	162	267
D _{max} (cm)	140	80	100
H _{max} (cm)	3000	3500	4000
AGE _{max} (yr)	200	300	250
b ₂	71.58	48.04	77.26
b ₃	0.447	0.172	0.396
a	38.9033	38.9033	27.551
b	1.6205	1.6205	1.7914
DEGD _{min}	5782	7636	7636
U _i (g/kg)	72.0	65.0	58.0
d	-0.18	-0.30	-0.25
c ₁	-0.5	-1.0	0
c ₂	2.87963	4.42437	1.33469
c ₃	-1.6554	-2.50	-0.72425
S	30	30	30

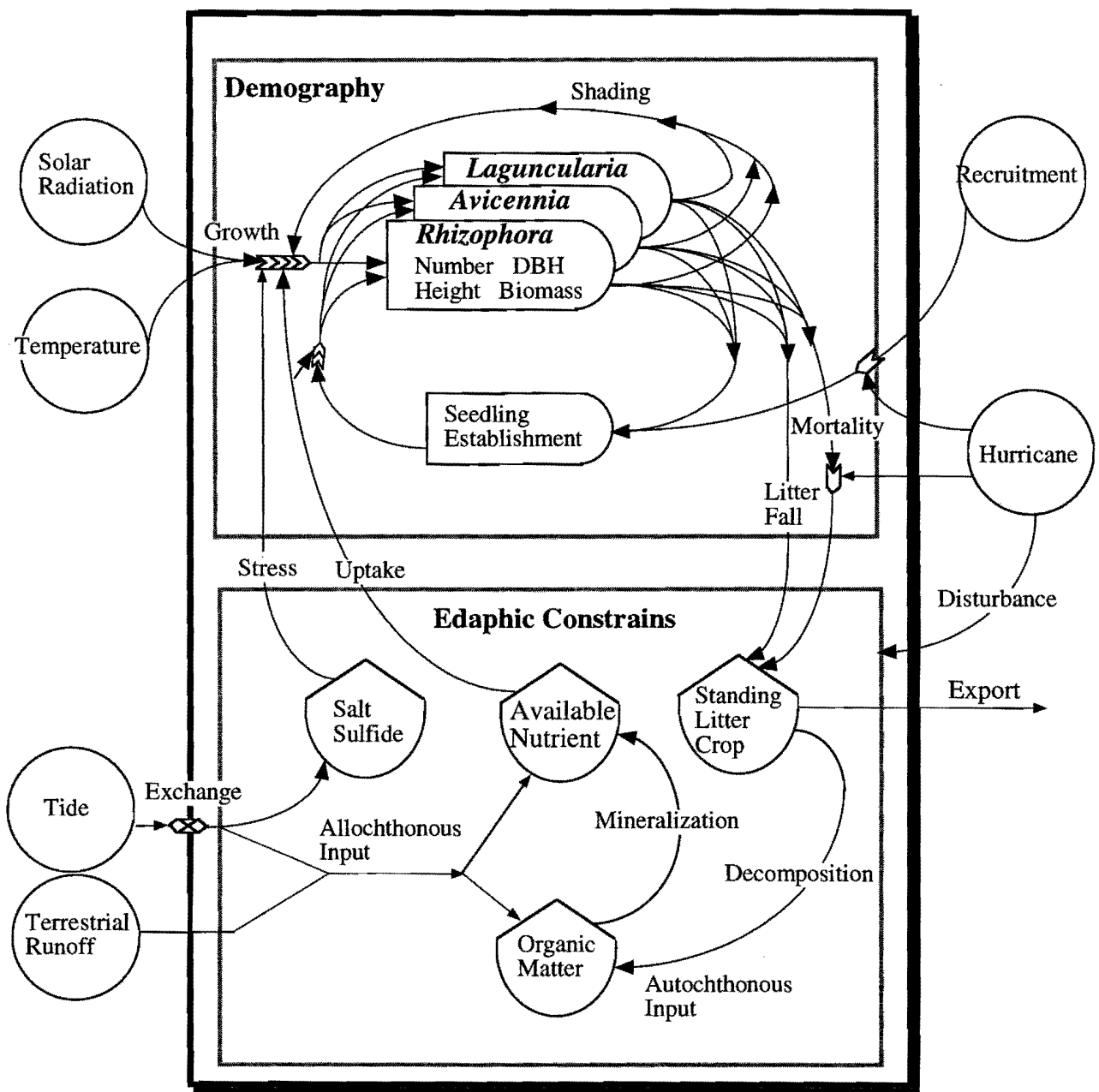


Figure 6.1. Conceptual model of mangrove forest development including edaphic constraints.

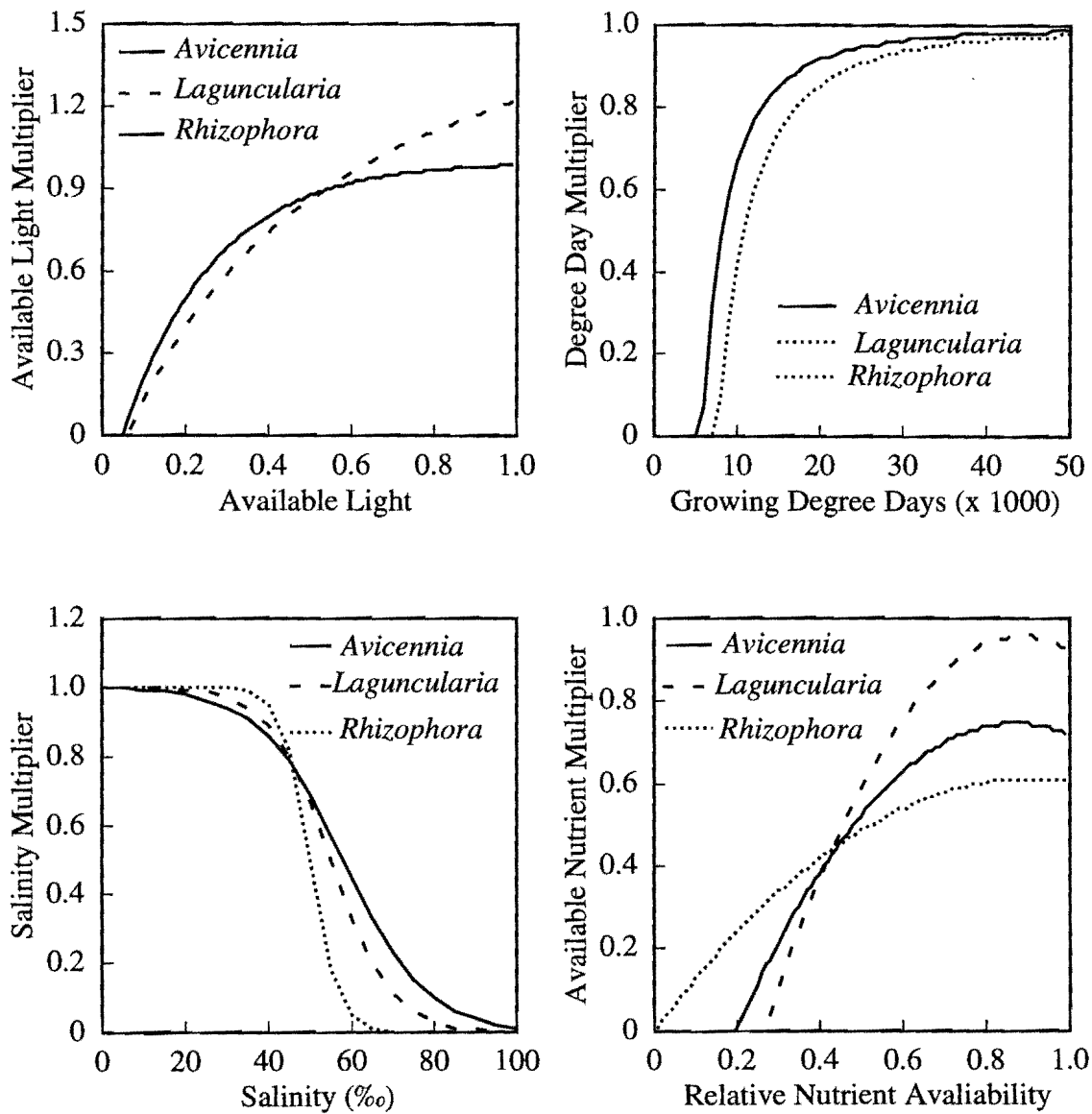


Figure 6.2. Growth multiplier curves for three mangrove species.

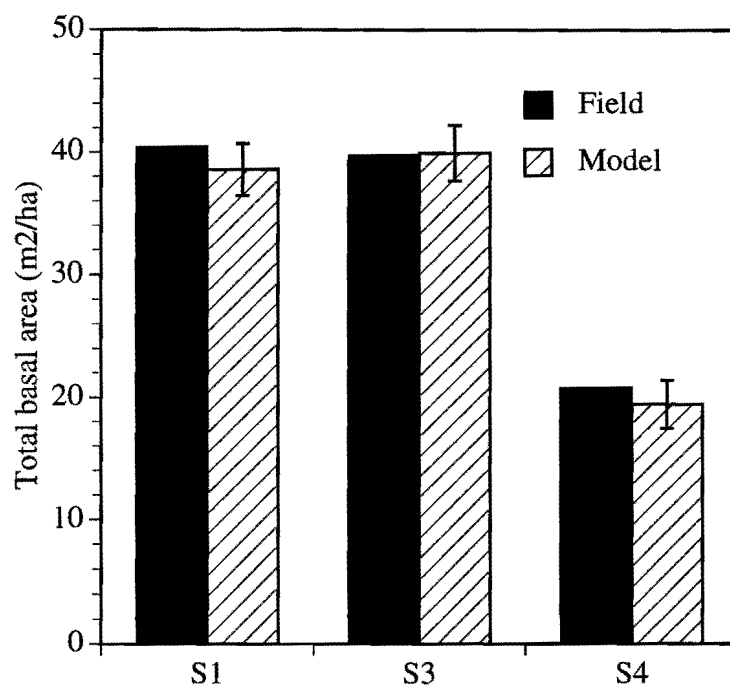


Figure 6.3. Comparison of simulated and measured total basal area of three mangrove forests along the Shark River estuary. Simulation results were expressed as average $\pm$ S.D. of 50 runs by MANGAL.

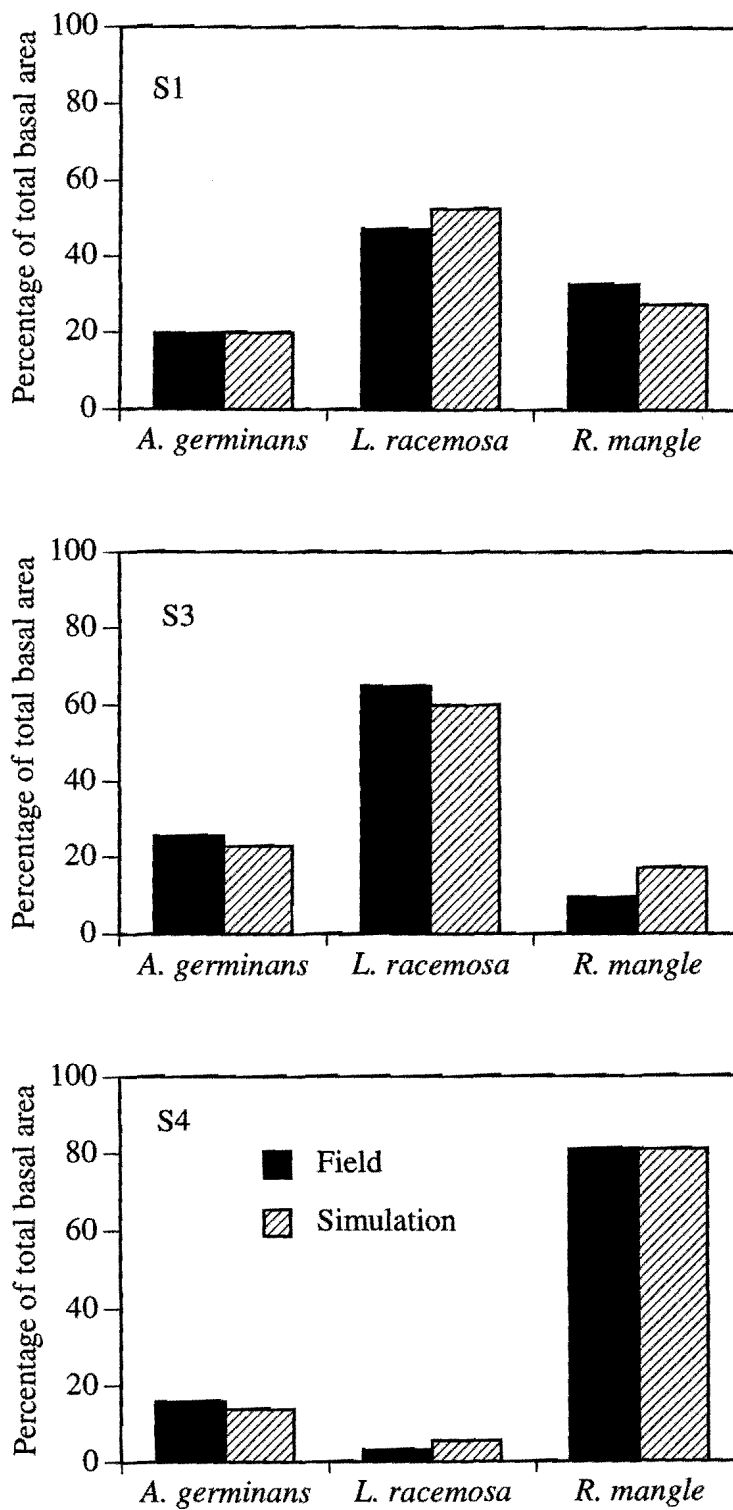


Figure 6.4. Comparison of relative dominance for three mangrove species using basal area between field surveys and simulations of the MANGAL model.

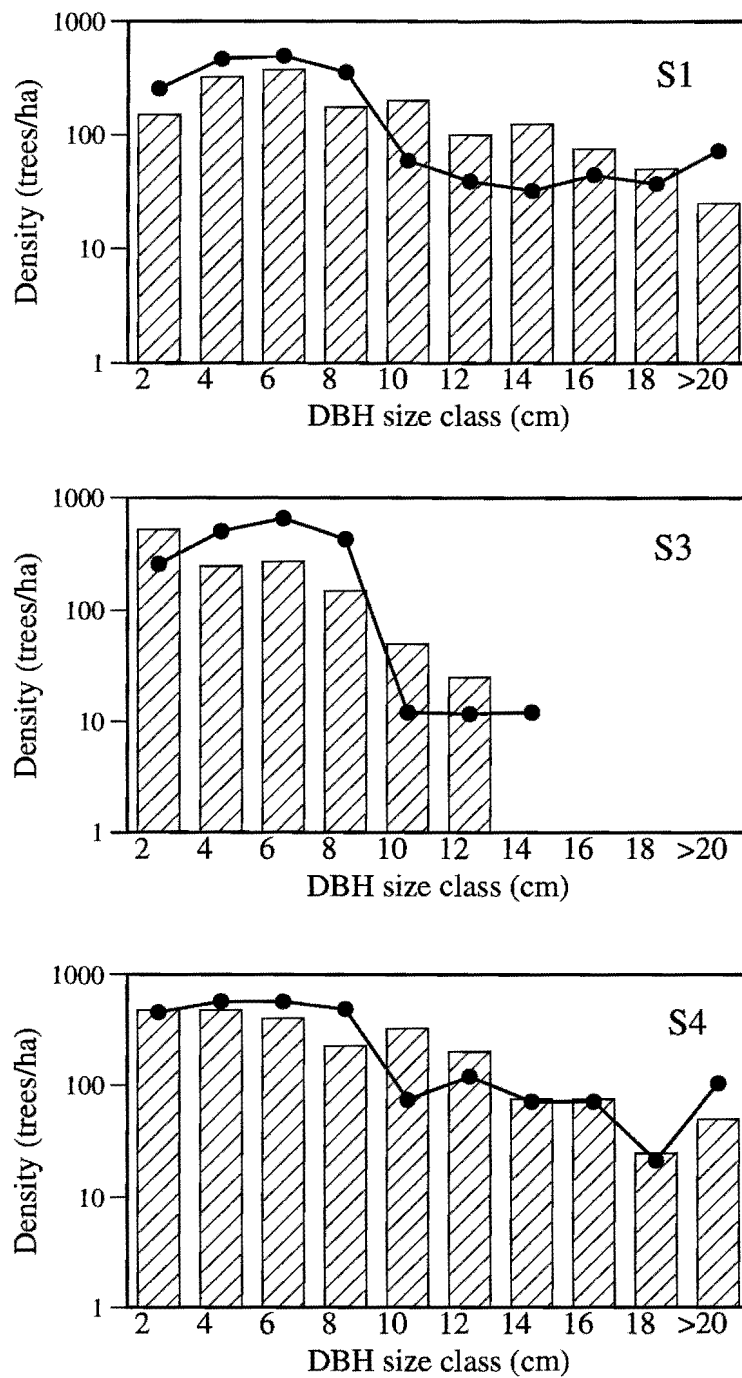


Figure 6.5. Size-class distribution of *Rhizophora mangle* for three mangrove sites. Solid line is the average of 50 simulations of the MANGAL model. Bar represents the field surveys.

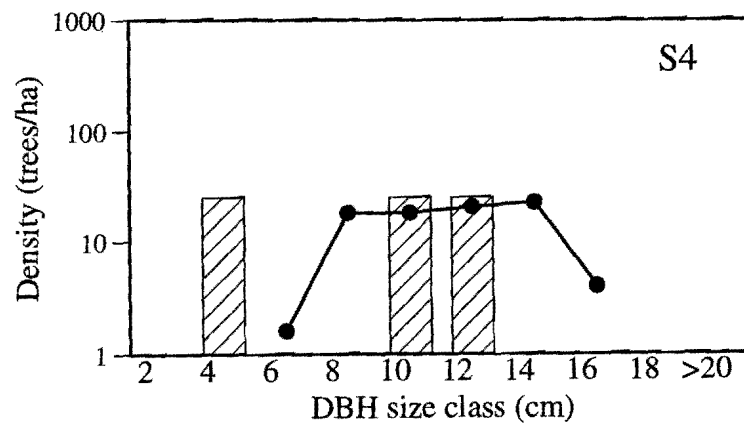
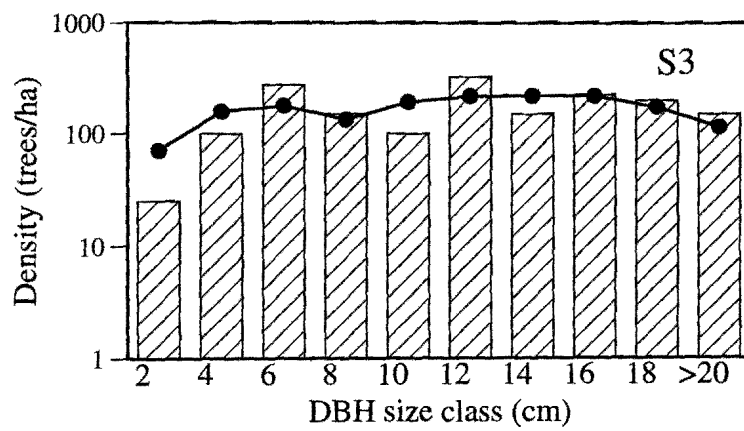
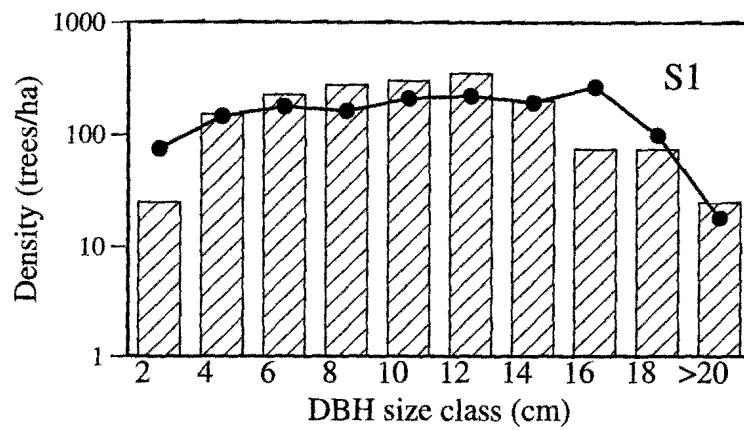


Figure 6.6. Size-class distribution of *Laguncularia racemosa* for three mangrove sites. Solid line is the average of 50 simulations of the MANGAL model. Bar represents the field surveys.

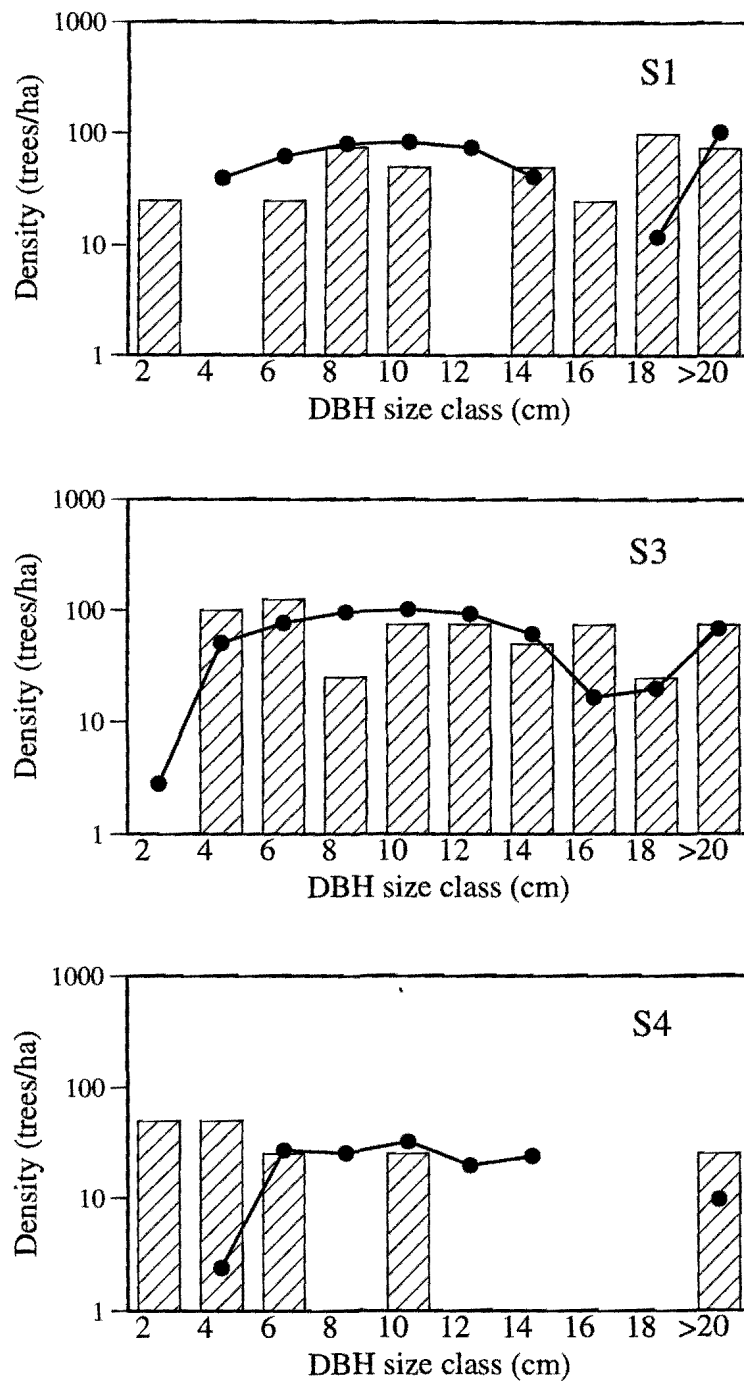


Figure 6.7. Size-class distribution of *Avicennia germinans* for three mangrove sites. Solid line is the average of 50 simulations of the MANGAL model. Bar represents the field surveys.

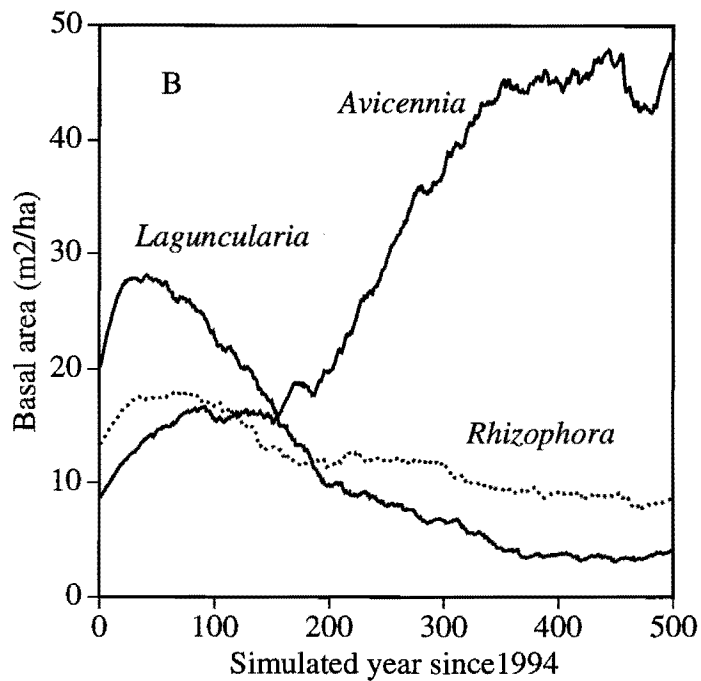
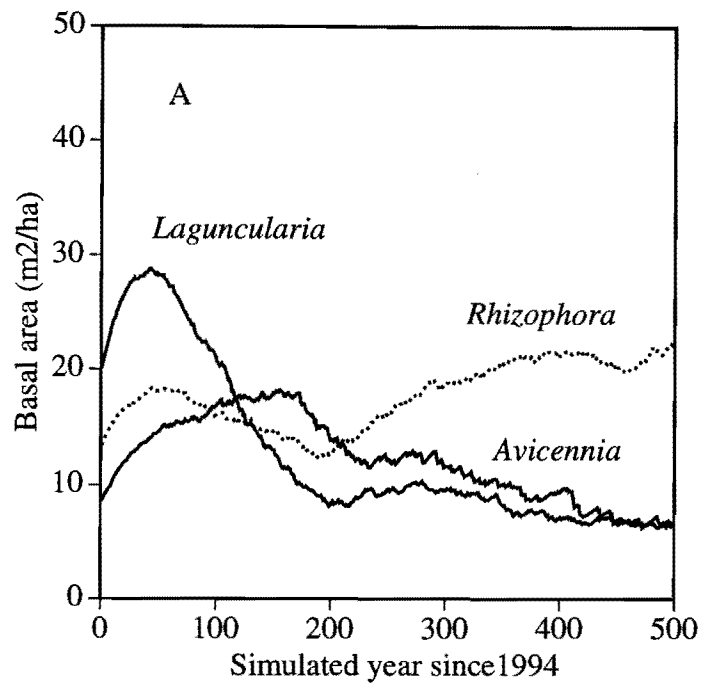


Figure 6. 8. Projected basal area of three mangrove species at the marine site (S1) of the Shark River estuary by the MANGAL model. A: represents low *Avicennia germinans* recruitment. B: represents the equal recruitment for three species.

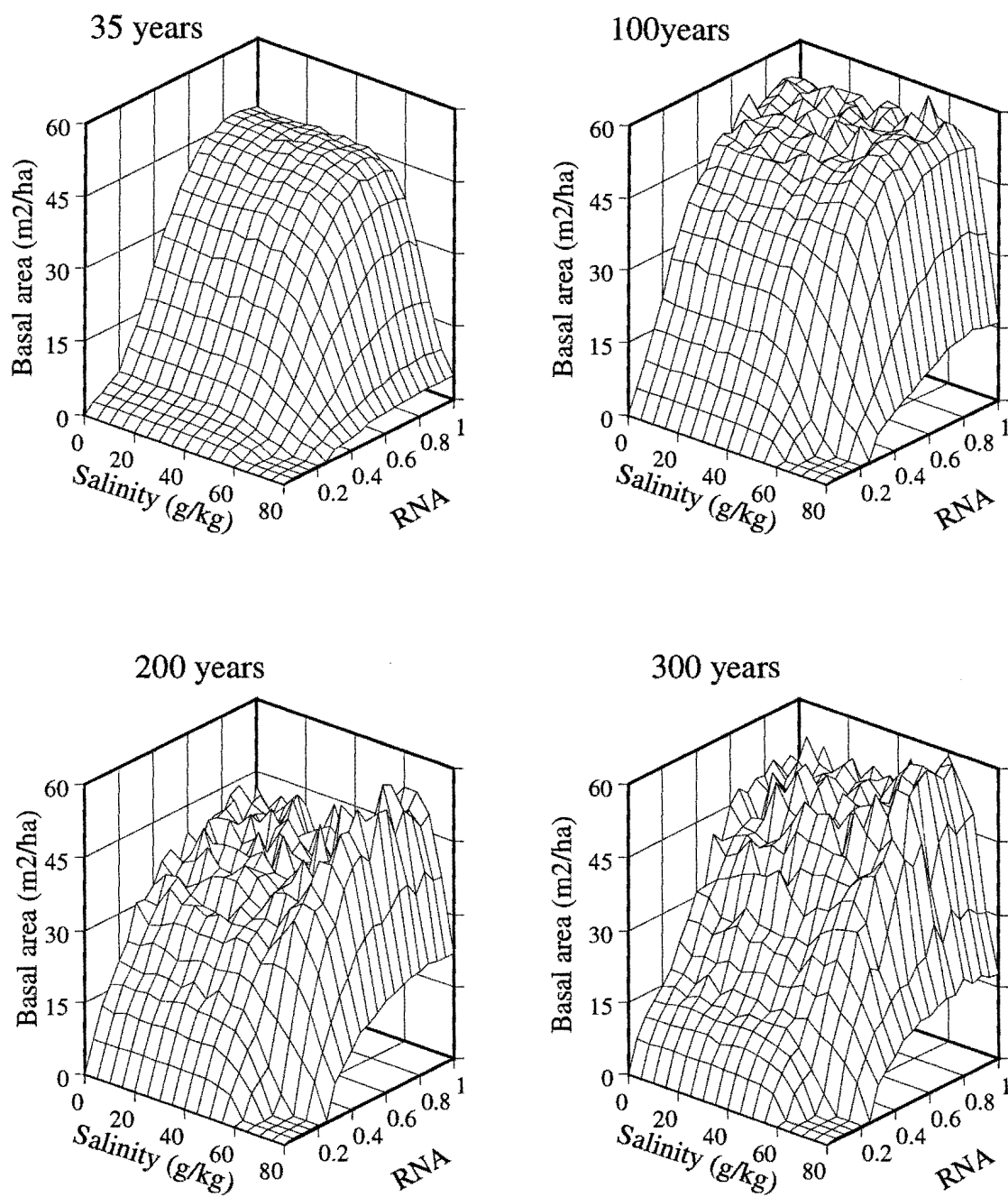
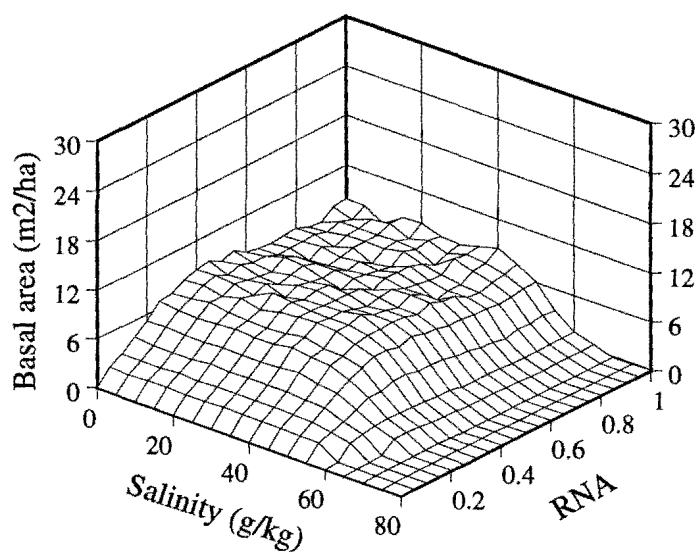
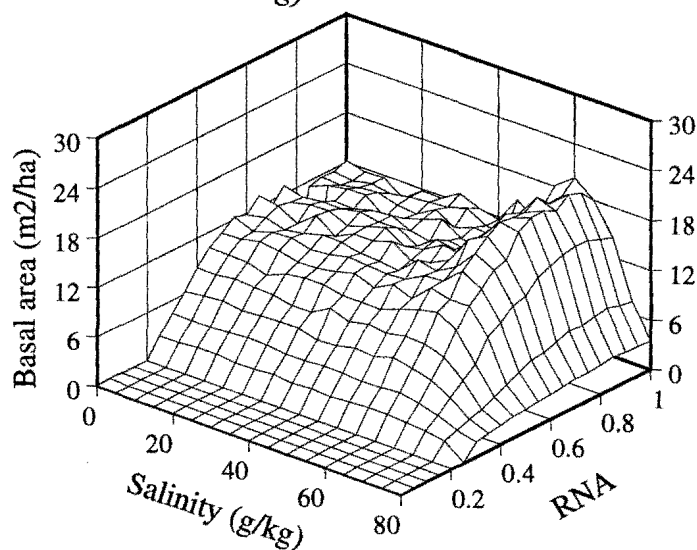


Figure 6.9. Simulated total basal area of mangrove forests along gradients of soil nutrient availability and salinity by FORMAN model.

Rhizophora
mangle



Avicennia
germinans



Laguncularia
racemosa

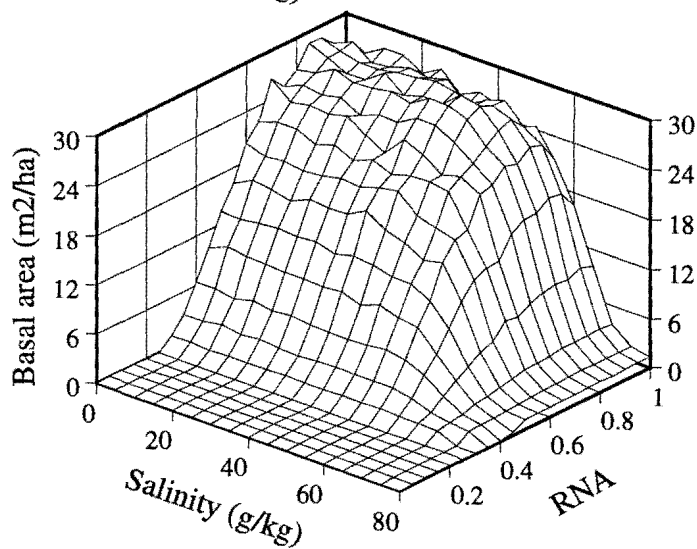
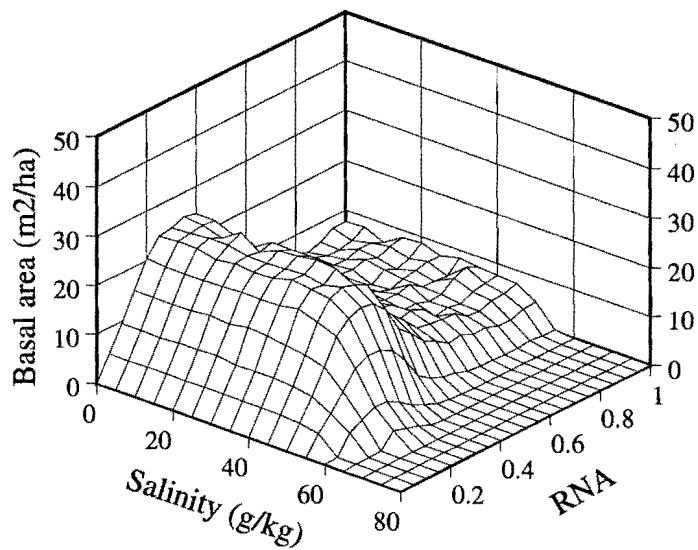
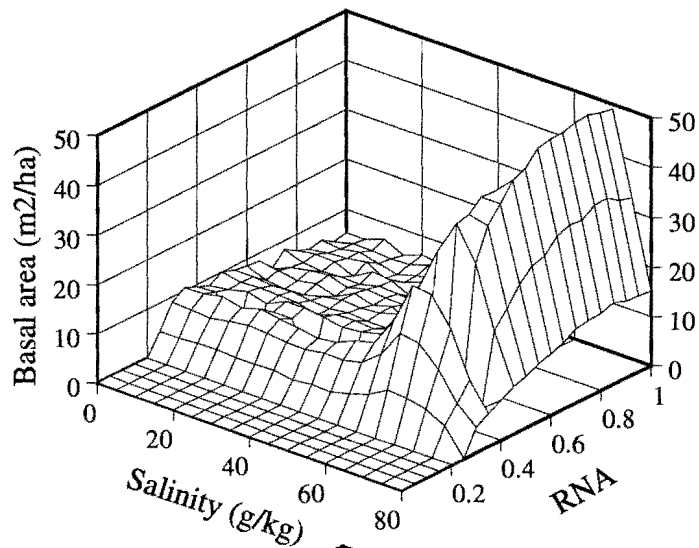


Figure 6.10. Simulated succession of mangrove forest gaps after 35 years of development along gradients of soil nutrient availability and salinity stress by the FORMAN model.

Rhizophora
mangle



Avicennia
germinans



Laguncularia
racemosa

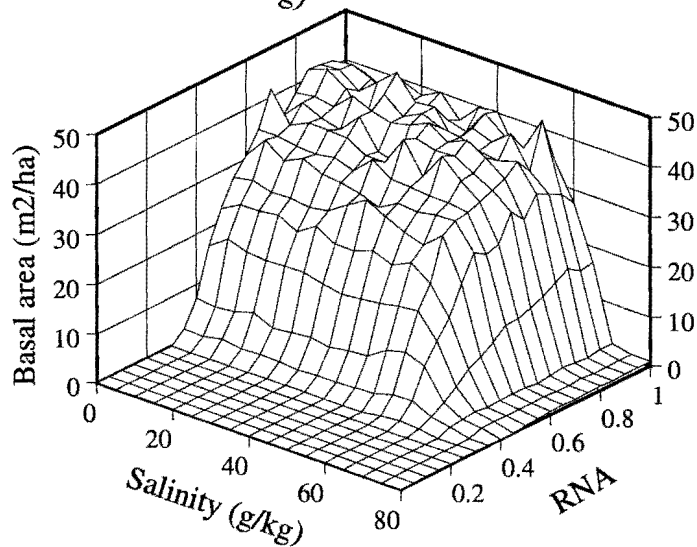
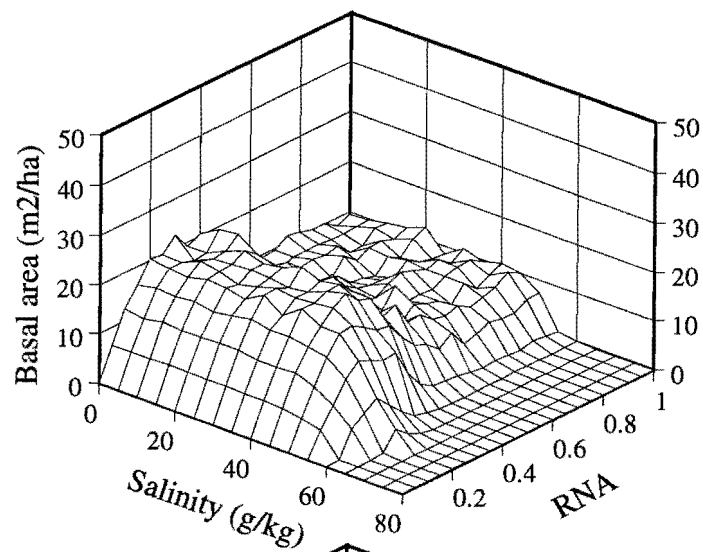
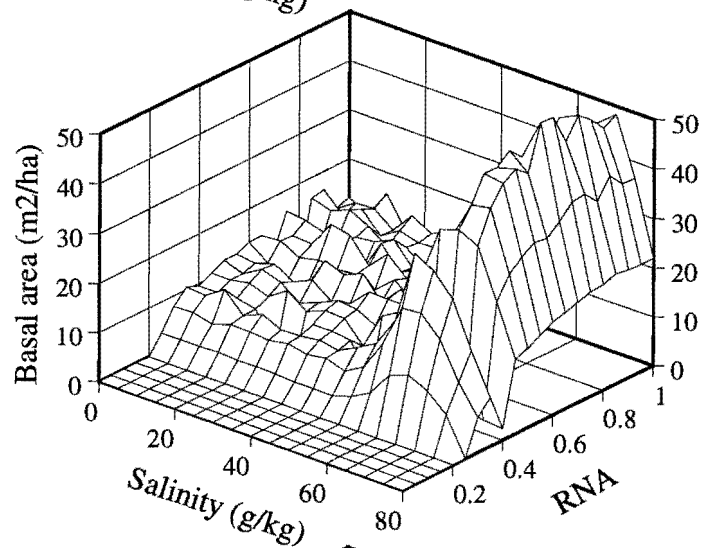


Figure 6.11. Simulated succession of mangrove forest gaps after 100 years of development along gradients of soil nutrient availability and salinity stress by the FORMAN model.

Rhizophora
mangle



Avicennia
germinans



Laguncularia
racemosa

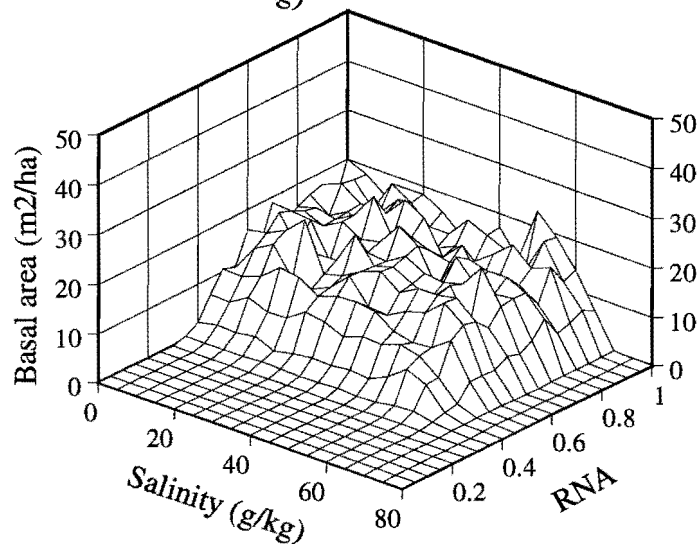
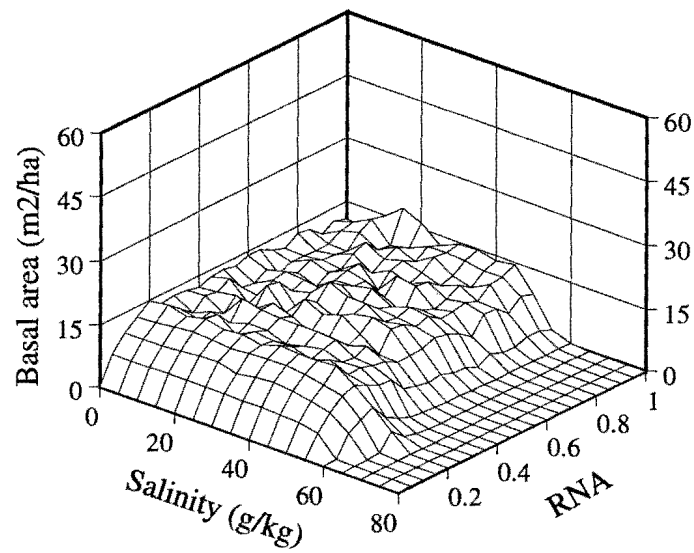
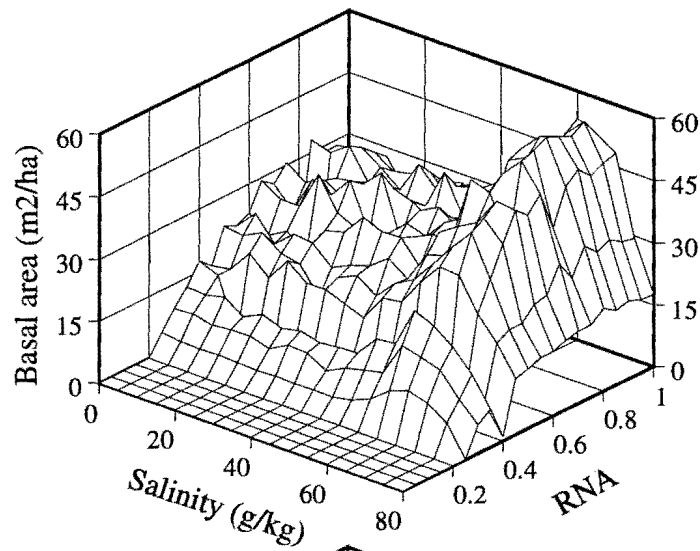


Figure 6.12. Simulated succession of mangrove forest gaps after 200 years of development along gradients of soil nutrient availability and salinity stress by the FORMAN model.

Rhizophora
mangle



Avicennia
germinans



Laguncularia
racemosa

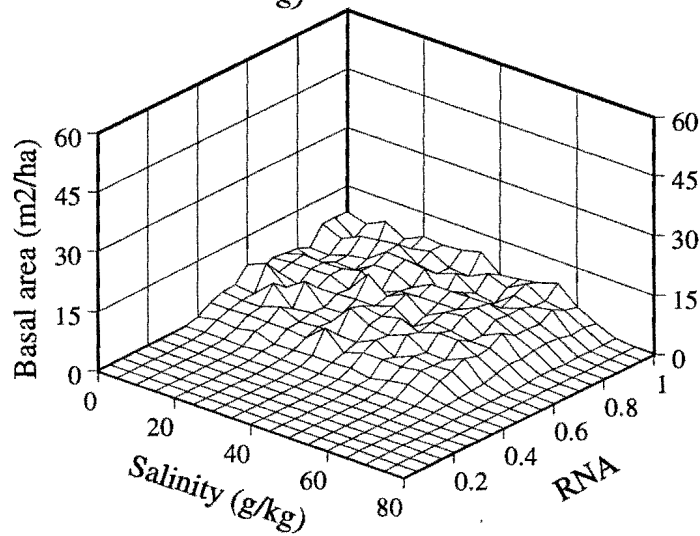


Figure 6.13. Simulated succession of mangrove forest gaps after 300 years of development along gradients of soil nutrient availability and salinity stress by the FORMAN model.

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