

Patterns of Mangrove Forest Structure and Soil Nutrient Dynamics Along the Shark River Estuary, Florida

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ABSTRACT: The basal area and productivity of mangrove wetlands are described in relation to selected soil properties to understand the general pattern of optimum forest stature at the mouth of estuaries in the Everglades, such as the Shark River Slough, Florida (U.S.). The basal area of mangroves decreases from 40.4 m² ha⁻¹ and 39.7 m² ha⁻¹ at two stations 1.8 km and 4.1 km from the estuary mouth to 20.7 m² ha⁻¹ and 19.6 m² ha⁻¹ at two sites 9.9 km and 18.2 km from the mouth, respectively. The gradient in basal area at these four sites is mostly the result of approximately 34 yr of growth since Hurricane Donna. Wood productivity is higher in the lower estuary (10.7 Mg ha⁻¹ yr⁻¹ and 12.0 Mg ha⁻¹ yr⁻¹) than in the upper estuary (3.2 Mg ha⁻¹ yr⁻¹ and 4.2 Mg ha⁻¹ yr⁻¹). Porewater salinity among these four mangrove sites during seasonal sampling in 1994 and 1995 ranged from 1.6 g kg⁻¹ to 33.5 g kg⁻¹, while sulfide was generally < 0.15 mM at all sites. These soil values indicate that abiotic stress cannot explain the decrease in forest structure along this estuarine gradient. Concentrations of nitrogen (N) and phosphorus (P) are more closely related to patterns of forest development, with higher soil fertility at the mouth of the estuary as indicated by higher concentrations of extractable ammonium, total soil P, and available P, along with higher ammonium production rates. The more fertile sites of the lower estuary are dominated by *Laguncularia racemosa*, whereas the less fertile sites in the intermediate and upper estuary are dominated by *Rhizophora mangle*. Relative N mineralization per unit of total N is higher in the lower estuary and is related positively to concentrations of available P, indicating the importance of turnover rates and nutrient interactions to soil fertility. Concentrations of Ca-bound P per volume soil in the lower estuary is 40-fold higher than in the upper estuary, and along with an increase in residual P in the upper estuary, indicate a shift from mineral to organic P along the estuarine gradient. Mineral inputs to the mouth of Shark River estuary from the Gulf of Mexico (rather than upland inputs) apparently control the patterns of mangrove structure and productivity.

Introduction

Mangrove wetlands are the dominant intertidal community type of marine to fresh water ecotones along tropical estuaries (Tomlinson 1986). An ecogeomorphic classification describes the diverse patterns of mangrove forest structure and function based on the combination of geophysical, geomorphological, and ecological processes within coastal environmental settings (Twilley 1995, 1997). Environmental settings are determined by the nature of circulation, sediment transport, regional topography, physical processes, and climate (Thom 1982, 1984; Blasco 1984; Woodroffe 1992). The ecogeomorphic classification scheme proposes a gradient in the geophysical energies of a coastal life-zone will result in variation in the ecological properties of mangrove wetlands, including productivity, nutrient cycling, litter dynamics, succession, and sedimentation (Twilley 1995, 1997). Mangrove wetlands occur in diverse environmental

settings, including deltas, lagoons, and estuaries in wet, humid, or dry climates, all of which vary in specific patterns of biodiversity, energy flow, and material cycling. We propose that the ecological significance of the ecogeomorphic classification system can be verified by comparing patterns of soil nutrient biogeochemistry and mangrove structure among environmental settings as a function of past and present geomorphic and geophysical processes (Twilley 1995). Mangrove ecotones in the southwest Everglades of Florida (U.S.) offer an interesting comparison of coastal settings influenced by carbonate lagoons and estuaries with significant freshwater discharge.

The properties of mangrove communities vary within an environmental setting depending on the location of mangroves along the salinity gradient of an estuary and with distance inland from shore along the intertidal zone. Intertidal soils can be quite heterogeneous because many edaphic characteristics depend on depositional and erosional patterns and on the influence of plant communities, which add organic matter, cycle nutrients, and

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modify soil salinity and redox conditions (Thom 1967). Inputs from terrestrial runoff (terrigenous sediments) generally are considered the major nutrient source that supports mangrove forest development (Carter et al. 1973; Odum et al. 1982; McIvor et al. 1994). This hypothesis of terrestrial control predicts that nutrient availability in mangrove soils will decrease from the landward zone to the seaward zone along the estuarine gradient of a tropical estuary. Local patterns of tidal inundation will also influence soil characteristics that control species zonation of mangrove wetlands (Watson 1928; Chapman 1944, 1976; Walsh 1974). Patches and zones of forest composition result from complex gradients of hydroperiod and soil conditions, such as nutrient limitation (e.g., nitrogen and phosphorus; Boto and Wellington 1984; Feller 1995) and abiotic stressors (e.g., salinity and sulfide; Cintrón et al. 1978; Lugo 1978; Nickerson and Thibodeau 1985; McKee et al. 1988; McKee 1993). Mangrove forest structure in the Caribbean region is also influenced particularly by the frequency of hurricane disturbance, emphasizing the importance of temporal variation in forcing functions to mangrove development (Lugo 1997).

The coastal forested wetlands in the southwestern Everglades of Florida extend from Whitewater Bay to Ten Thousand Islands and include one of the largest mangrove areas in the Gulf of Mexico (Davis 1940; Smith et al. 1994). The stature of mangrove forests along the more marine zones of estuaries in this region is about 25 m; tree height decreases inland toward a mangrove-marsh ecotone inhabited by "dwarf" mangroves (Davis 1940; Lugo and Snedaker 1974; Smith et al. 1994). More than 50 yr ago, Davis (1940 p. 334) noted that the lower estuaries of this region contain "probably the optimum growth of mangroves in the Americas", in contrast to conditions limiting mangrove growth just a few km inland as indicated by the presence of "dwarf" mangrove zones. There have been no synoptic surveys of soil conditions and plant structure to test what specific environmental conditions control the productivity of mangrove wetlands in this land-margin ecosystem. Mangrove wetlands along the Shark River estuary in the southwestern Everglades provide a natural trajectory experiment to investigate the relative association between soil nutrient biogeochemistry and mangrove development in response to a whole-scale disturbance (Diamond 1986). Hurricane Donna swept through the Shark River region in 1960 causing mortality of nearly 80% of the trees (Craighead and Gilbert 1962). We document the spatial pattern of mangrove forest regeneration correlated with selected soil properties following 34 yr of development. We tested the hypothesis

that reductions in forest structure along the estuarine gradient are associated with variations in soil fertility and stressors along one of the major sources of fresh water to this coastal region, the Shark River estuary.

Study Area

The Shark River estuary is on the west coastal plain of Everglades National Park, one of the largest estuaries of the southwest Florida coast. The study area is located where water is transported from the Shark River Slough to the Gulf of Mexico (Fig. 1). Mean annual air temperature in the Everglades National Park is 24°C, with a seasonal range from 19°C in January to 28°C in August (Thomas 1974). Average annual precipitation in the Everglades National Park is 1,320 mm, with distinct wet (60% annual rainfall from June to September) and dry (25% annual rainfall from November to April) seasons (Duever et al. 1994). Discharge of fresh water from Shark River Slough to the estuary follows patterns of seasonal and inter-annual rainfall; historically, changes have occurred in these flows (Light and Dineen 1994). Tides within the Everglades National Park are predominantly diurnal and have a mean amplitude of 1.1 m (Provost 1973). Seasonally higher sea levels from May to November along the Gulf Coast of Florida (Provost 1973) result in more frequent tides in mangrove wetlands from August to October (Twilley 1985; Twilley and Chen 1998).

Mangrove forests consisting of three mangrove species, *Rhizophora mangle* L. (red mangroves), *Avicennia germinans* (L.) Stearn (black mangroves), and *Laguncularia racemosa* (L.) Gaertn. (white mangroves), form a continuous band extending 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 restricted where the salinity does not exceed 10 g kg⁻¹. Four sites were located along a salinity gradient of the Shark River estuary, approximately 1.8 km, 4.1 km, 9.9 km, and 18.2 km inland from the estuary mouth (Fig. 1) (25°19'30"N, 81°09'W to 25°25'N, 80°58'W). These sites represent a hydrologic gradient from tide-dominated inundation near the estuary mouth to freshwater runoff from the Shark River Slough in the upstream region. Sites S1.8 and S4.1 (distances from the mouth are used as nomenclature for the individual sites) were in the marine zone of Shark River estuary, S9.9 was in the mesohaline zone, and S18.2 was in the oligohaline zone (Odum et al. 1984; Duke 1992). In June 1994, we established four adjacent 10 m × 10 m plots (in a 20 m × 20 m block) about 10–20 m inland from the shore at sites S1.8, S4.1, and S9.9. Three smaller (5 m × 10 m) plots about 5 m from shore were established at

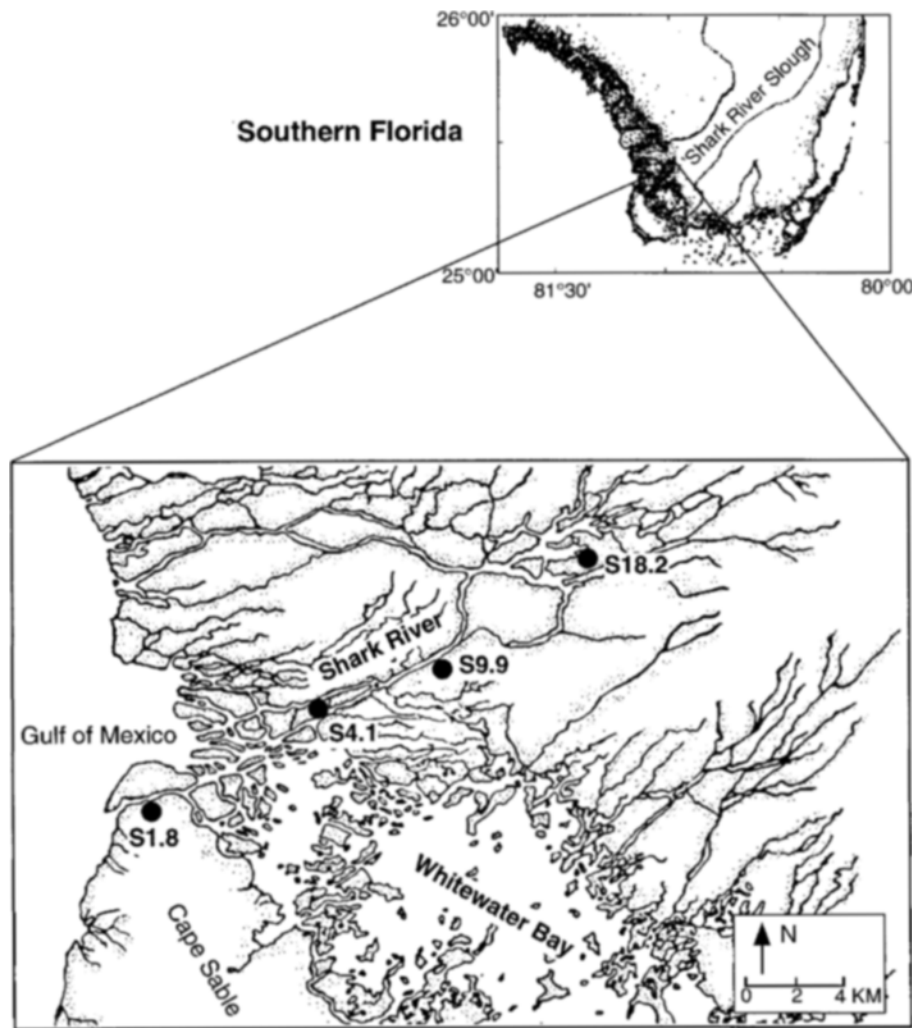


Fig. 1. Study site locations along the Shark River estuary in the Everglades National Park.

S18.2; the smaller size was due to the restricted zone of mangroves at this upstream region. Mangrove forest structure and soil properties were measured at the four sites. Three randomly chosen stations within each block were fixed for repeated measures of interstitial porewater, soil nutrient concentrations, and mineralization rates in August 1994 and January and May 1995. Plots are the experimental units for basal area and density of forests, while the individual stations are sampling units tested for differences in soil characteristics.

Materials and Methods

FOREST STRUCTURE AND GROWTH

In January 1995 we tagged and measured all trees in each plot having a diameter at breast height (dbh) > 2.5 cm and re-measured them in February 1996. Twenty to 30 trees were chosen randomly in each block at all four sites to measure tree height (using

a range finder), which was used to develop a regression between dbh and tree height for each species (Chen 1996). Forest structure is defined as density and basal area of trees using equations of Cintrón and Schaeffer-Novelli (1984b), including the calculation of relative importance values. Total above-ground biomass was calculated using published allometric equations from Cintrón and Schaeffer-Novelli (1984a) for *R. mangle* and *L. racemosa*, and from Day et al. (1987) for *A. germinans*. The annual net increase in biomass was estimated as the difference between the initial and final biomass of each individual tree using species-specific equations. We used the sum of these differences to estimate biomass production for each site. There is no allometric equation for *C. erecta*, so the allometric equations for *L. racemosa* were used to estimate the biomass of *C. erecta* because of the similarity in growth forms of these two species.

SOIL PROPERTY DETERMINATION

Interstitial Porewater Analyses

Using a plastic siphon and syringe (McKee et al. 1988), porewater samples were collected from three soil stations in each block at 20 cm depth in August 1994 and May 1995, and at 40–50 cm depth in January 1995 (due to lower water levels). One aliquot of porewater 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 sample was filtered to reduce error associated with suspended sediments; the first 10 ml of each sample was discarded to avoid oxidation. The next 5 ml of sample was immediately added to an equal volume of antioxidant buffer and brought to the laboratory where it was analyzed for sulfide concentrations with a LAZAR Model IS-156 sulfide sensing electrode (McKee et al. 1988). A third aliquot of porewater was passed through a GF/F filter and stored frozen until assayed for inorganic nutrients. Ammonium (NH_4^+) concentrations were measured by a colorimetric method (Parsons et al. 1984); and nitrite (NO_2^-), nitrate (NO_3^-), and phosphate (PO_4^{3-}) were determined by ALPKEM Autoanalyzer using standard techniques (Strickland and Parson 1972).

Soil Sampling

We sampled soils, using a 5.0-cm diam core, to 40 cm depth at three stations within each block. Soil samples were divided into 10-cm intervals 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 at 60°C to a constant weight and ground with a Wiley Mill to pass through a 250- μm mesh. Cores with a 15.2 cm diam were used to estimate soil bulk density because the wider diameter reduced compaction. Carbon (C) and nitrogen (N) contents were determined on two replicates of each sample with a LECO CHN analyzer using standard protocols. Total P (TP) was extracted from soils with 1 N HCl after ignition at 550°C (Aspila et al. 1976) and inorganic PO_4^{3-} was determined on filtered samples (Parsons et al. 1984). Available PO_4^{3-} was determined by dilute acid-fluoride extraction of fresh soil samples (Olsen and Sommers 1982). Amount of P extracted by this method is generally used as the available P index in plant ecology (Binkley and Vitousek 1989).

P Fractionation

We used a sequential extraction scheme developed by Hieltjes and Lijklema (1980), with modifications for wetland soils (Koch and Reddy 1992; Gale et al. 1994) and estuarine sediments (Zwols-

man 1994). Soil samples for P fractionation were collected from each station in August 1994. Fresh soil samples were extracted sequentially with 1 M KCl (1:10 m/v), 0.1 M NaOH, and 0.5 M HCl by shaking (250 rpm) samples for 2 h, 16 h, and 24 h with each extractant, respectively. After each step, the suspensions were centrifuged and the supernatants were analyzed colorimetrically for inorganic PO_4^{3-} according to Parsons et al. (1984). A subsample of the NaOH extract was digested by the Kjeldahl procedure to determine TP in the extract. Phosphorus concentrations in extracts of KCl, NaOH, and HCl solution are defined as labile P, Fe-Al bound P, and Ca-bound P, respectively (Gale et al. 1994). Organic P was determined as the difference between TP and inorganic P in the NaOH-extract and is defined as hydrolyzable organic P. Residual P is defined as the difference between the TP, which was determined by the ignition-acid extraction method (Aspila et al. 1976), and the sum of all extracted forms of P.

N and P Mineralization

Since no single method provides accurate estimates of N and P mineralization, all methods should be considered an index of nutrient availability for comparative purposes (Binkley and Vitousek 1989). We used anaerobic incubations of soil cores in the laboratory to determine net N and P mineralization rates, which were used to compare soil quality among the four mangrove sites along the estuary. Glass tubes (2.5 cm diam and 10 cm length) were used to recover intact soil samples. 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 cm and 10–20 cm intervals were collected at each sampling station and maintained at 4°C until incubations began. One tube from each pair was extracted with 1 M KCl (1:10 m/v) soon after samples were transported to the laboratory; the other tube was incubated anaerobically in the dark in an environmentally controlled chamber at 25°C for 15 d, followed by the same extraction. The extract was centrifuged and analyzed for NH_4^+ , $\text{NO}_2^- + \text{NO}_3^-$, and PO_4^{3-} using standard techniques described above. Rates of net nitrification, ammonification, and P mineralization for each soil depth were determined by subtracting the initial concentration of exchangeable $\text{NO}_2^- + \text{NO}_3^-$, NH_4^+ , and PO_4^{3-} from extracted concentrations at the end of the incubation period. Mineralization rates were converted to a soil area basis using respective bulk density values. Denitrification was not measured but was assumed to be minimal given the NH_4^+ and NO_3^- concentrations measured in the porewater at

all sites (Rivera-Monroy et al. 1995; Rivera-Monroy and Twilley 1996)

STATISTICAL ANALYSES

A repeated-measures ANOVA was used to analyze the effects of site and sampling date on porewater variables (salinity, sulfide, and inorganic nutrients) and soil variables (acid fluoride P, exchangeable NH_4^+ , exchangeable $\text{NO}_2^- + \text{NO}_3^-$, N mineralization, and P mineralization). We also used linear contrasts to evaluate the differences in selected variables among sites on each sampling date. The differences among sites for components of the P fraction and forest basal area were tested using one-way ANOVA. All statistical tests were done using either original data or log-transformed data to meet assumptions of parametric analysis.

Results

FOREST STRUCTURE AND GROWTH

The landscape patterns of mangrove forest structure along the Shark River estuary exhibited differential recovery from disturbance by Hurricane Donna in 1960. Mean tree heights in the four sites decreased from 10.1 m in the lower estuary to 5.4 m in the upper estuary (Fig. 2A). *R. mangle*, *A. germinans*, and *L. racemosa* were found in the lower estuary (S1.8, S4.1, and S9.9). *A. germinans* did not occur in the upper estuary site, which was the only location where *C. erecta* was observed (S18.2; Fig. 2B-D). *R. mangle* was found in all sites and this species represented 35% to 90% of total tree density among the study sites (based on > 2.5 cm dbh). Mangrove forests were mixed-species communities at S1.8 and S4.1, where *L. racemosa* had the highest importance value and *A. germinans* the least (Fig. 2D). Further up the estuary, *R. mangle* was dominant at S9.9 and co-dominant with *C. erecta* at S18.2 (Fig. 2C,D). Mean basal areas were similar in the two lower estuary sites at about $40 \text{ m}^2 \text{ ha}^{-1}$, but the upper estuary sites at about $20 \text{ m}^2 \text{ ha}^{-1}$ (Fig. 2C) were significantly lower (Tukey's test, $p < 0.05$).

The density of larger trees (dbh > 10 cm) was $1,900 \text{ trees ha}^{-1}$ in the lower estuary and only $334 \text{ trees ha}^{-1}$ in the upper estuary (Fig. 3). However, the mean density of all trees with dbh > 2.5 cm was lower at the mouth of the estuary compared to the upper estuary (Fig. 2B). There was a higher density ($5,534 \text{ trees ha}^{-1}$) of smaller trees (< 6 cm dbh) in the upper estuary, and tree density decreased exponentially with an increase in dbh at S18.2 (Fig. 3). There also was a decrease in tree density with increase in size class at sites S4.1 and S9.9. The frequency distribution of size classes was bell-shaped in the lower estuary at S1.8 (Fig. 3).

Mean total aboveground biomass in 1994 was approximately $2\times$ higher in the lower estuary (about

250 Mg ha^{-1}) compared with the upper estuary (Fig. 2E). Rates of wood productivity ($\text{kg tree}^{-1} \text{ yr}^{-1}$) were highest for *L. racemosa* and *A. germinans* at S4.1 and decreased along the estuary in the upstream location (Table 1). Growth rates of *R. mangle* varied by only a factor of 3 among the four sites and its peak rate also occurred in the lower estuary. The annual increments in total basal area also decreased from the lower to upper estuary (Table 1). *R. mangle* contributed 78% (S9.9) and 86% (S18.2) of total wood productivity in the upper estuary, due to the higher density of *R. mangle* in these sites. *L. racemosa* dominated total wood productivity in the lower estuary. Wood productivity was higher in the lower estuary, approximately twice that of the upper estuary (Table 1).

SOIL CHARACTERISTICS

Salinity decreased from the lower to the upper estuary on all sampling dates; peak salinity concentrations at each station occurred during August (Fig. 4A). Salinities ranged from 33.5 g kg^{-1} (S1.8 in August) to 1.6 g kg^{-1} (S18.2 in January). The sites with the greatest temporal change in salinity were S4.1 and S9.9 (Fig. 4A). Porewater sulfide concentrations were significantly different among the sites in August, with the highest concentration (mean of 0.46 mM) in the upper estuary at S18.2 and the lowest concentrations ($< 0.15 \text{ mM}$) in the lower estuary at S1.8 (Fig. 4B). No sulfide concentrations could be detected in porewaters at any of the sites in January when the ground water level was 40 cm below the surface. Porewater pH was near neutral at all sites, with mean values ranging from 6.6 to 6.9.

Mean porewater NO_2^- and NO_3^- concentrations were $< 1 \text{ }\mu\text{M}$ and $< 0.5 \text{ }\mu\text{M}$, respectively, at all sites during the three sampling dates (Fig. 4C,D). In January, concentrations of NO_2^- were significantly higher at S18.2 and S9.9 than at S1.8 and S4.1 (Fig. 4C). There were no significant site and date effects on NO_3^- (Table 2). Porewater NH_4^+ concentrations were significantly different among sampling dates, with the highest mean in August (Fig. 4E); there were no significant site effects on NH_4^+ concentrations (Table 2). Mean porewater PO_4^{3-} concentrations were $< 2 \text{ }\mu\text{M}$ at all sites during the three sampling dates, except at S4.1 in January (Fig. 4F). There was a significant effect of date and a significant interaction between site and sampling date, but there was no site effect on PO_4^{3-} concentrations (Table 2).

The highest exchangeable $\text{NO}_2^- + \text{NO}_3^-$ in all four sites was 0.06 g N m^{-2} (data are not shown), which indicated that most of the inorganic N in these mangrove soils was dominated by NH_4^+ (Fig. 5A). Mean exchangeable NH_4^+ pools within the 0–

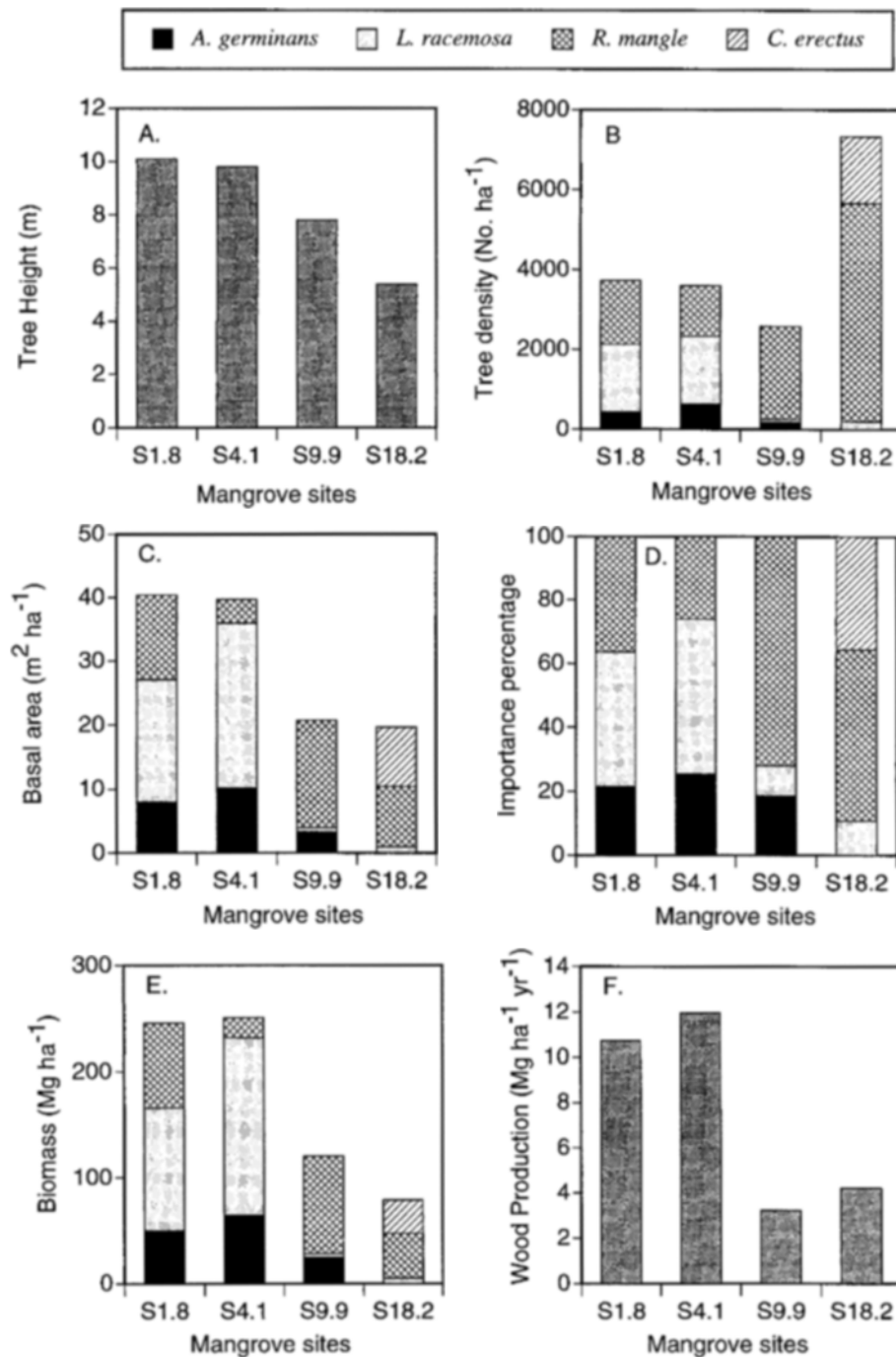


Fig. 2. Mangrove forest structure by species at sites along the Shark River estuary from the downstream location (S1.8) to the upstream location (S18.2) including: A) mean tree height, B) density of trees >2.5 cm diameter at breast height, C) basal area, D) importance values, E) biomass, and F) wood production. Data are expressed as mean value of plots in A, B, C, and E.

20 cm soil interval decreased significantly along the estuary for three sampling dates (Fig. 5A). The extractable PO_4^{3-} pool was significantly greater at the mouth of the estuary for all sampling dates but was not significantly different between S9.9 and S18.2 in August and May (Fig. 5B).

The production of NO_3^- from the remineralized NH_4^+ in the soil incubations was negligible for all sites and dates (data are not shown). In January net NH_4^+ production was significantly higher at S1.8 and S4.1 than at S9.9 and S18.2 (Fig. 5C). For all sites, no net NH_4^+ mineralization was measured

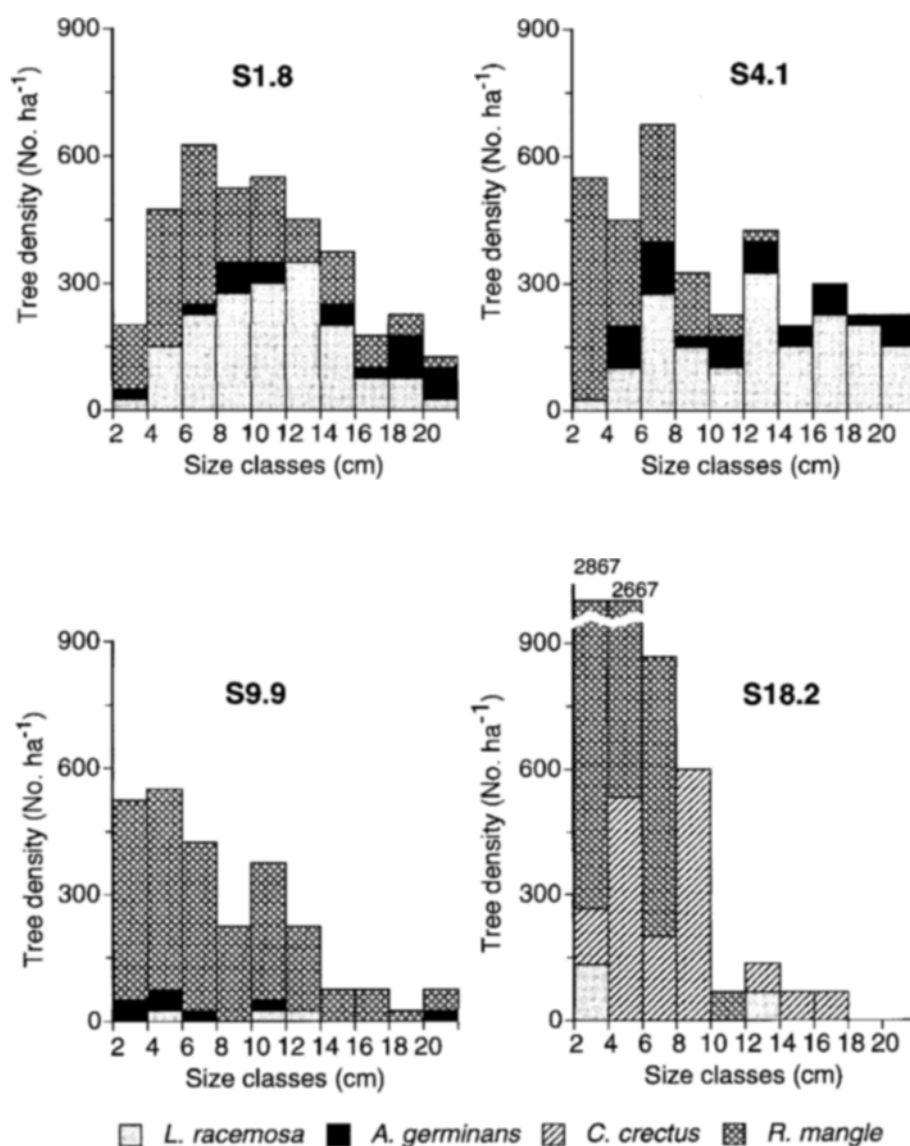


Fig. 3. Size class distribution of mangroves by species along the Shark River estuary from the downstream location (S1.8) to the upstream location (S18.2). Data are means of plots for each site.

in August. Mean daily net ammonification rates within the 0–20 cm depth for three sampling dates decreased from the marine to oligohaline sites: 182 mg N m⁻² d⁻¹, 135 mg N m⁻² d⁻¹, 46 mg N m⁻² d⁻¹, and 17 mg N m⁻² d⁻¹. Net P mineralization rates were more variable than N mineralization (Fig. 5D). In January net P mineralization was significantly higher in the upper estuary than lower estuary. Mean daily rates of net P mineralization over the three sampling dates within the 0–20 cm soil were positive at S9.9 and S18.2, compared to negative values reflecting immobilization at S1.8 and S4.1 (Fig. 5D).

Both total C and N concentrations in the top 40

cm of mangrove soils increased linearly with distance along the Shark River estuary from S1.8 to S18.2 (Table 3). P concentrations showed an inverse relationship with distance from the estuary mouth. Bulk density also decreased with increasing distance from the mouth of the estuary (Table 3). When nutrient pools were expressed as mass per unit area, C and N pools were not correlated with distance along the estuary (Fig. 6A,B). The consistent relation between C and N concentrations in these mangrove soils was reflected in atomic C:N, which were between 22:1 and 25:1 along the salinity gradient of the estuary (Fig. 6D). However, P content decreased exponentially from 152.2 g m⁻²

TABLE 1. Average wood production per tree, total annual basal area increment, and wood productivity per unit area of mangroves along the Shark River estuary, the Everglades National Park.

	Station			
	S1.8	S4.1	S9.9	S18.2
Average Wood Production (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
Basal Area 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 wood productivity	1.40	1.29	0.46	0.83

at S1.8 to 26.3 g m⁻² at S18.2 (to depth of 40 cm) (Fig. 6C). Accordingly, atomic N:P increased exponentially with distance from the estuary mouth, from 15:1 at S1.8 to 102:1 at S18.2 (Fig. 6E).

The amount of labile P was significantly higher at S1.8 than other sites but was not significantly different among S4.1, S9.9, and S18.2 (Table 4). The contribution of labile P to the pool of TP never exceeded 2% among all sites within the 0–20 cm depth (Fig. 7). Concentrations of the Fe/Al-bound P pools also decreased from S1.8 to S18.2 (Table 4). The contribution of Fe/Al-bound P to TP ranged from 8.2% to 10.5% and did not exhibit a significant trend along the estuary (Fig. 7). The amount of hydrolyzable-organic-P ranged from 2.39 g m⁻² to 7.64 g m⁻² and was significantly higher in the lower estuary than the upper estuary (Table 4). Except at S1.8, the hydrolyzable-organic-P fraction was the second largest pool of TP among sites along the estuary. The concentrations of Ca-bound P exhibited a 40-fold decrease from the lower to the upper estuary (Table 4). The percentage of TP that was Ca-bound P also decreased significantly from 32.6% at S1.8 to 3.3% at S18.2 (Fig. 7). The Ca-bound P pool was greater than the Fe/Al-bound P pool in S1.8 and S4.1, while Fe/Al-bound P concentrations were greater than Ca-bound P concentrations in S9.9 and S18.2. Residual P was the largest P fraction at all sites, with a significant increase along the estuary from 45% of TP at S1.8 to 70% at S18.2 (Fig. 7). The amount of residual P, in g m⁻², decreased significantly along the estuary (Table 4).

Discussion

The Shark River estuary provides an opportunity to evaluate mangrove development along an estuarine gradient of soil fertility on a decadal time

scale (30–40 yr) using a specific starting point from a known disturbance, Hurricane Donna in 1960. There is a distinct change in community composition and productivity of mangroves along the estuary, particularly between 5 km and 10 km from the mouth of the estuary. Basal area, biomass, and wood production declined by nearly half in this region of the estuary and dominance shifted from mixed species dominated by *L. racemosa* to nearly monospecific forests dominated by *R. mangle*. In the upper estuary, the size class distribution is dominated by a higher density of smaller trees, indicative of young regenerating forests. The basal area and biomass of the two sites in the lower estuary are representative of more mature forest stands. If we assume a clear forest stand following Hurricane Donna and use the average species-specific tree growth rate at each location measured in our study, the basal area would be about 45 m² ha⁻¹ at the mouth of the Shark River estuary compared with 20 m² ha⁻¹ at sites in the upper estuary following 34 yr of growth. These values are similar to values measured in the field and suggest that each area is representative of environmental conditions and not different stages of maturity. We also tested this assumption in model simulations of these sites using growth rates in this study to demonstrate that differences in initial conditions are insufficient to create the gradient in forest structure observed along the estuary (Chen and Twilley 1998).

Mangrove soils along the Shark River estuary can be characterized as only slightly reducing, with mean redox potentials of 214 mV and 117 mV at S1.8 and S9.9, respectively (Koch 1996). Sulfide concentrations can also indicate the effects of flooding and abiotic stress on mangrove development. Porewater sulfide concentrations ranging from 1.5 mM to 4.1 mM have been described as significant to patterns of forest structure in Florida (Carlson et al. 1983; McKee 1993), the Bahamas (Nickerson and Thibodeau 1985), and Belize (McKee et al. 1988; McKee 1995). Concentrations of sulfide (< 0.46 mM) were lower in our sites in the Shark River estuary compared to these reported values, indicating that this stressor is not responsible for the decreased stature of mangrove wetlands along the 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). Threshold salinities above which there is an apparent reduction in forest structure have been estimated at 65 g kg⁻¹ in Puerto Rico (Cintrón et al. 1978) and 50 g kg⁻¹ in Mexico (Day et al. 1987). Porewater salinity in mangrove wetlands along the Shark River estuary during all three sampling dates did not exceed 35 g kg⁻¹, be-

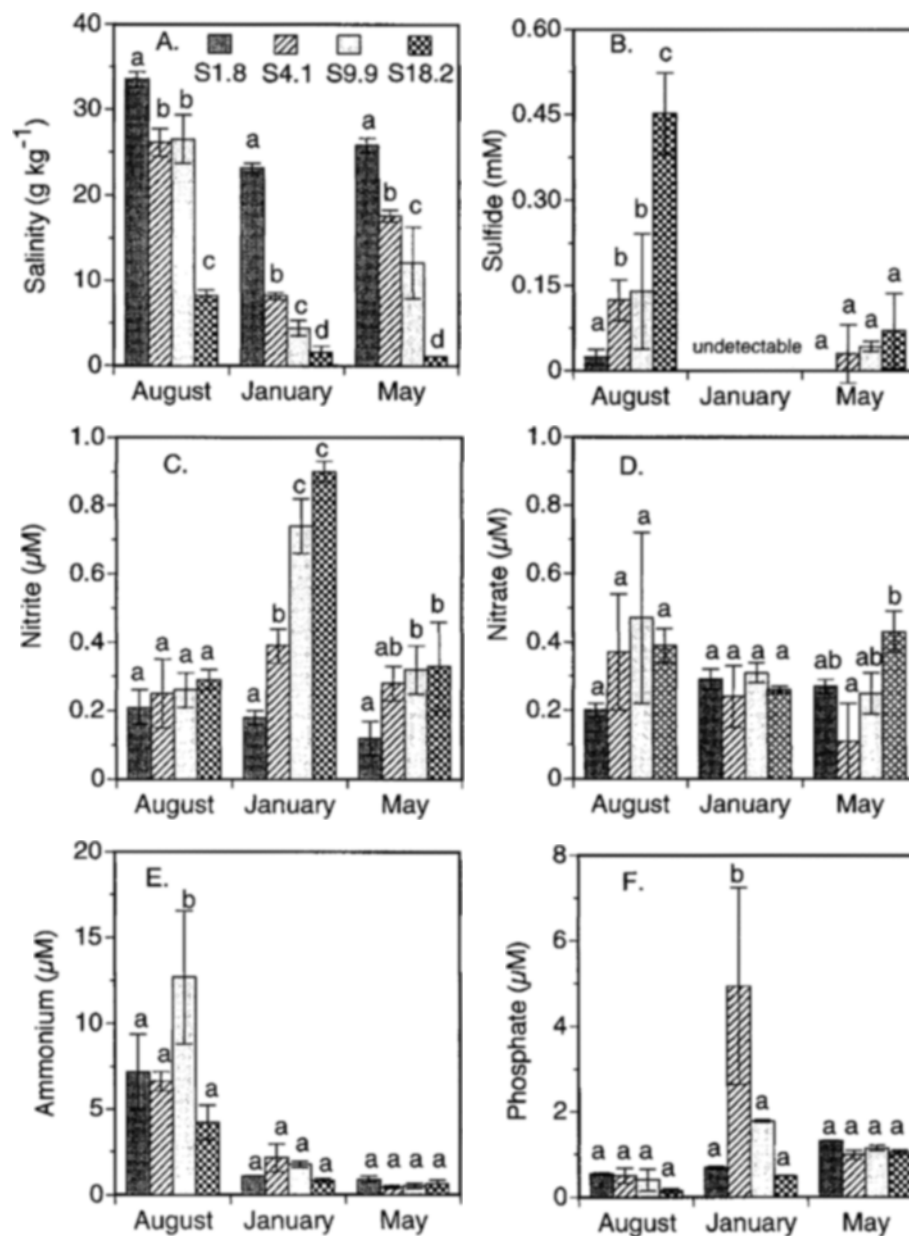


Fig. 4. Spatial and temporal variation in porewater stressors and nutrients including salinity (A), sulfide (B), nitrite (C), nitrate (D), ammonium (E), and phosphate (F) measured along the Shark River estuary during August 1994, January 1995, and May 1995. The values at each sampling date with the same letter are not significantly different among sites ($p > 0.05$). Values are mean ($n = 3$) \pm SE.

low the critical value that influences mangrove complexity (Lugo et al. 1988). Our surveys of porewater sulfide and salinity measurements examined relatively dry (1994) and wet (1995) years in the Shark River watershed. Salinities in the upper region of the Shark River estuary near S18.2 reached 18 g kg^{-1} in June 1994, compared with salinities in this region $< 3 \text{ g kg}^{-1}$ through out 1995. The higher salinity and sulfide readings in August 1994 along the mangrove sites reflect this change in

freshwater input. Previous monthly surveys of the North River and Shark River estuaries also report salinities $< 30 \text{ g kg}^{-1}$ in mangrove regions (Heald 1969; Powell et al. 1989). Forest basal area was lowest in the oligohaline region and increased with higher salinity in the Shark River estuary, indicating that forest development was not limited by soil salinity.

In the absence of physiological stress by sulfide and salinity, soil nutrient availability is often impli-

TABLE 2. Summary of F statistics from repeated measures ANOVA of site and sampling date effects on porewater chemistry and nutrient availability. Statistical tests were conducted using univariate tests.

Sources	df	Salinity	Sulfide	NO ₂ ⁻	NO ₃ ⁻	NH ₄ ⁺	PO ₄ ³⁻
Site	3, 8	167.8***	31.62***	12.2**	1.3 ^{ns}	3.1 ^{ns}	2.7 ^{ns}
Date	2, 16	445.7***	50.82***	33.4***	0.9 ^{ns}	30.3***	5.17*
Site × Date	6, 16	28.9***	13.30***	7.3***	0.9 ^{ns}	2.1 ^{ns}	2.93*

Sources	df	Exchangeable NO ₂ ⁻ + NO ₃ ⁻	Exchangeable NH ₄ ⁺	Acid Fluoride PO ₄ ³⁻	Ammonification	P mineralization
Site	3, 8	8.15**	26.85***	108.5***	7.53*	4.10*
Date	2, 16	2.68*	17.28***	10.88***	75.70***	8.38**
Site × Date	6, 16	1.91*	3.84*	4.10*	7.88***	8.83***

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant.

cated as the principal factor determining variation in mangrove biomass and productivity. Most concentrations of porewater NH₄⁺ were < 10 μM in the study sites along the Shark River estuary and are lower than reported values for other mangrove soils, including Florida Bay (Rosenfeld 1979), Missionary Bay of Australia (Smith et al. 1991), Papua New Guinea (Alongi et al. 1993), and Belize (McKee 1995), which are all > 10 μM. Our values

were comparable to those reported in Indian River, Florida (< 25 μM, Carlson and Yarbrow 1988) and in dwarf mangroves of Belize (1.0 μM, Feller 1995). Inorganic PO₄³⁻ concentrations in porewaters in our study sites were < 2 μM, similar to mangrove soils in Australia (Smith et al. 1991) and Papua New Guinea (Alongi et al. 1993), and less than those observed in other forests in the Caribbean (Feller 1995; McKee 1995). The more productive

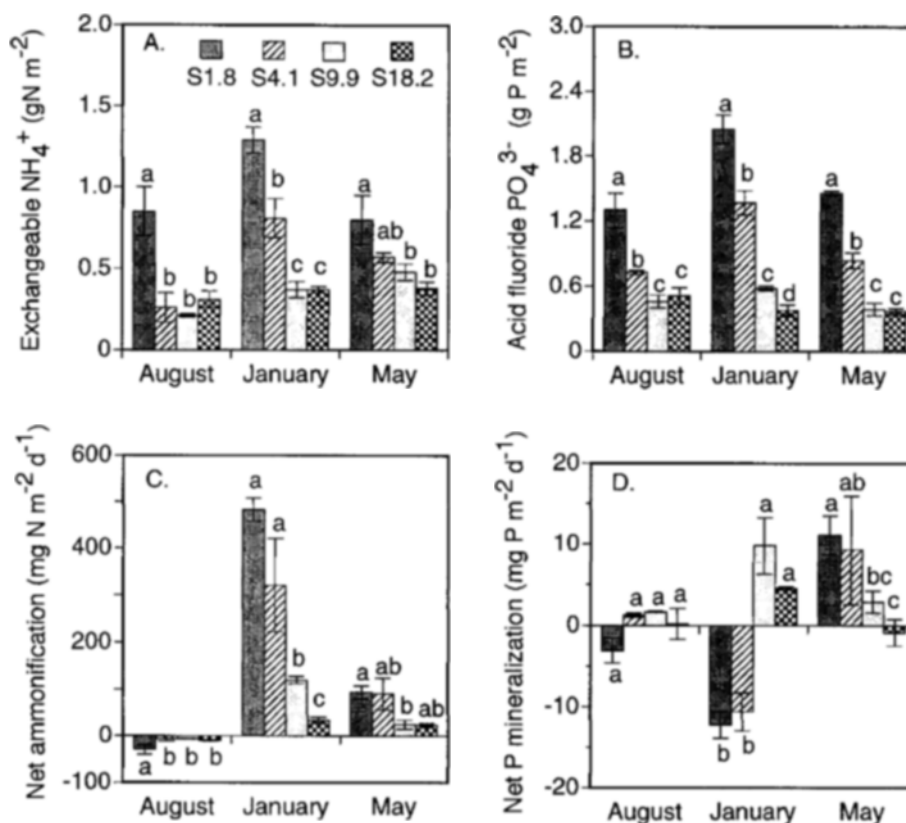


Fig. 5. Extractable ammonium (A), extractable phosphorus (B), net ammonification (C), and phosphorus mineralization (D) within the 0–20 cm soil at four mangrove sites along the Shark River estuary in August 1994, January 1995, and May 1995. Each value is the mean (\pm SE) of three stations. The values from different sites at each sampling date with the same letter are not significantly different among sites ($p > 0.05$).

TABLE 3. Soil carbon (C), nitrogen (N), and phosphorus (P) concentrations and bulk density along the Shark River estuary. Data are means of three sampling dates \pm SE. Correlation coefficients (r) are between respective soil variables for each site and distance from the mouth of the Shark River estuary.

Variables	S1.8	S4.1	S9.9	S18.2	r
Total C (%)	14.3 \pm 0.3	22.2 \pm 1.2	32.5 \pm 1.5	43.3 \pm 1.1	0.985*
Total N (%)	0.70 \pm 0.07	1.15 \pm 0.09	1.55 \pm 0.07	2.33 \pm 0.10	0.990**
Total P (%)	0.11 \pm < 0.01	0.12 \pm < 0.01	0.09 \pm < 0.01	0.06 \pm < 0.01	-0.960*
Bulk density (g cm ⁻³)	0.462	0.212	0.148	0.135	-0.751

* $p < 0.05$; ** $p < 0.01$.

mangrove sites at the mouth of Shark River estuary had similar porewater NH_4^+ and PO_4^{3-} concentrations as those forests in Belize with much less structure (Feller 1995). These comparisons of mangrove forest structure among sites along the Shark River estuary and with other mangrove locations indicate that porewater NH_4^+ and PO_4^{3-} concentrations, which are a minor fraction of the total N and P pools, are not a sensitive measure of soil fertility. Other forms of N and P, such as different pools of the exchangeable fractions, may be available for plant uptake and may contribute to soil fertility.

Nutrient turnover rates may be more important in determining nutrient limitation than simply concentration. Mangrove soils contain a high proportion of organic P, but most of this organic P tends to be recalcitrant (Alongi et al. 1992) or adsorbed and fixed by minerals as different chemical forms (Hesse 1962). Rapid immobilization of amended inorganic P in mangrove soils suggests that P adsorption by minerals can strongly immobilize inorganic PO_4^{3-} (Hesse 1962; Alongi et al. 1992). Our study showed that Ca-bound P was higher in the lower estuary than in the oligohaline zones along the Shark River estuary, indicating the significance of mineral processes at the mouth of the estuary. It has been demonstrated that carbonate can rapidly adsorb inorganic P released from mineralization of organic matter (DeKanel and Morse 1978; McGlathery et al. 1994). We observed little net P mineralization in mangrove sites along the Shark River estuary and low concentrations of inorganic PO_4^{3-} in soil porewaters. Both chemical fixation and microbial immobilization can contribute to the absence of inorganic PO_4^{3-} in mangrove soils along the Shark River estuary.

Net NH_4^+ production also declined with P concentrations along the estuarine gradient of Shark River estuary. Net ammonification rates in mangrove soils along the estuary in January (35–239 mg N m⁻² d⁻¹) and May (18–70 mg N m⁻² d⁻¹) are comparable to other macrophyte systems, such as subtropical seagrasses (28–294 mg N m⁻² d⁻¹, Boon et al. 1986) and freshwater marsh (44 mg N m⁻² d⁻¹, Bowden 1984). However, net ammonifi-

cation was negligible at all mangrove sites in August, with evidence of N immobilization; in January, when the water level was lowest, ammonification rates were highest. Litter fall of all three mangrove species peaks from June to August in southwest Florida, and most of this litter is deficient in N as indicated by C:N generally > 50 (Heald 1969; Twilley et al. 1986; Lawton-Thomas 1997). Nitrogen isotope studies of both $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ have demonstrated the strong potential for N immobilization in mangrove sediments with similar N concentrations and C:N as those of the sites in our study (Rivera-Monroy et al. 1995; Rivera-Monroy and Twilley 1996). There are indications from our study that patterns of N immobilization may be seasonal in response to changes in hydroperiod, as well as the quantity and quality of leaf litter.

Relative N mineralization (N mineralization per unit of total N) is a useful index to compare overall soil quality as a factor determining N mineralization rates (Pastor et al. 1987). Relative N mineralization decreased exponentially with distance from the mouth of the estuary (Fig. 8A). This indicates that the proportion of recalcitrant organic N in mangrove soils increases rapidly with distance from the Gulf of Mexico toward the upstream mangrove-marsh ecotone. Nitrogen mineralization was not correlated with either total C, total N, or C:N. This suggests that ammonification rates in this mangrove region are independent of total N concentration. Mean rates of net ammonification were significantly correlated with acid-fluoride extractable P concentrations ($r^2 = 0.94$, $p < 0.05$), suggesting that N mineralization was associated with P availability (Fig. 8B). Highly significant correlations of microbial activity with P components indicate that microbial activity is probably P-limited in mangrove soils in New Guinea, which then may limit N mineralization (Alongi et al. 1993). These indicators suggest a very complex interaction between substrate quality along with N and P mineralization rates that control the availability of these two nutrients for mangrove productivity.

The landward decline of mangrove basal area and biomass was associated with a decrease in sev-

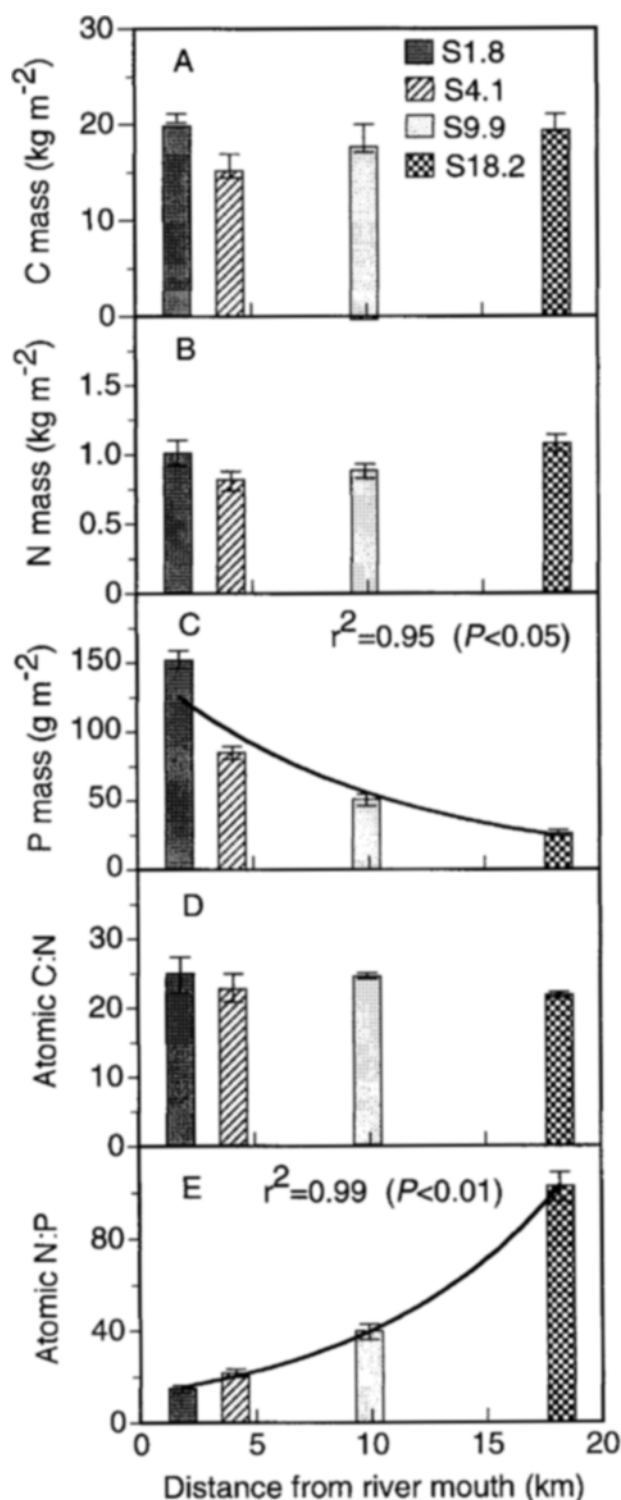


Fig. 6. Changes of soil carbon (C), nitrogen (N), and phosphorus (P) within 0–40 cm soil in mangrove forests from the marine site (S1.8) to the oligohaline site (S18.2) along the Shark River estuary of the Everglades National Park. Data are mean of three sampling dates \pm SE.

eral indices of soil fertility along the axis of the Shark River estuary. The greater decrease in TP in mangrove soils compared with more constant total N concentrations from the lower to the upper estuary results in N:P < 20 in the lower estuary, 40 in the intermediate zone, and > 80 in the upper estuary. The lower relative availability of P per unit of N indicates P was a limiting nutrient to mangroves in the oligohaline zone of this estuary. The higher concentrations of TP at the mouth of the Shark River estuary, along with lack of stress from salinity and sulfide, result in optimum conditions for mangrove growth in this region. Fertilization studies in other mangrove forests (Boto et al. 1984; Boto and Wellington 1984; Feller 1995; Twilley 1995), including the marl soils of the southeastern Everglades (Koch and Snedaker 1997), have revealed that P availability can be a major factor limiting annual growth of mangrove forests in soils having low salinity or sulfide concentrations. Changes in species composition and basal area along this soil fertility gradient in Shark River estuary indicates that *L. racemosa* is more dominant in the higher nutrient sites of the lower estuary, whereas *R. mangle* dominates in the upper estuary at the lower nutrient site. Simulations of forest development using the relationship of species-specific response to soil fertility indicate that most, but not all, of the shift in community composition and basal area along the estuarine gradient can be explained with relative soil TP concentrations (Chen and Twilley 1998).

The relative bulk concentrations of P and their chemical fractions in mangrove soils contribute to our understanding of P dynamics along the Shark River estuary. There are two major sources of nutrients to this estuary: discharge from Shark River Slough and sediment resuspension from the near-shore boundary along the southwest coast of Florida. In our study, sequential extractions of P indicated a significant decrease in Ca-bound P and increase in residual P from the lower to the upper estuary. Significantly higher Ca-bound P as a percentage of TP near the mouth of Shark River estuary suggests that the greater bulk density concentration of P at the marine sites may be related to sediment deposited from the Gulf of Mexico. Shallow mangrove soils in the marsh-mangrove ecotone of the upper estuary receive little mineral sediment and have a greater proportion of organic P. Increased soil concentrations of both total and Ca-bound P with salinity, along with higher soil bulk density, were used as boundary conditions in simulations of soil processes at three sites along the Shark River estuary (Chen and Twilley 1999). These simulations, using Pb-210 estimates of sedimentation at S4.1, demonstrated that the Gulf of

TABLE 4. Phosphorus (P) fractionation at 0–20 cm depth in soils from mangrove forests along the Shark River estuary. Data are means \pm SE ($n = 3$). Changes in superscript letters with the mean P concentration for each fraction indicate significant differences among sites (Tukey's $p < 0.05$).

Site	Soil P Components (g P m ⁻²)				
	Labile P	Fe/Al-bound P	Hydrolyzable organic P	Ca-bound P	Residual P
S1.8	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
S4.1	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
S9.9	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
S18.2	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
p =	0.003	< 0.001	< 0.001	< 0.001	0.013

Mexico was a major source of P for mangroves in the lower estuary. Surveys of water quality parameters in the Whitewater and Florida Bay regions found distinct inner and outer mangrove zones of similar influence (Boyer et al. 1997). Inner mangrove zones had lower TP concentrations and higher TN:TP (TN is total N) than outer zones, matching the spatial characteristics of the mangrove soils in the mangrove zones of our study. These water quality surveys, along with indicators of higher concentrations of P availability in the northwest region of Florida Bay (Fourqurean et al. 1992), suggest P is transported in dissolved and suspended forms to this region from the coastal boundary current that passes by the mouth of the Shark River estuary. Phosphorus transported along the southwest coast of Florida appears to regulate mangrove forest development and productivity at the lower regions of the Shark River estuary.

Accelerated nutrient loadings, especially P, from different anthropogenic sources in the watersheds

of south Florida can change the vegetation characteristics of oligotrophic regions of the Everglades (Davis 1994). Soil P from areas near the Everglades Agriculture Area (EAA) range from 0.12% to 0.16% (Craft and Richardson 1993a; DeBusk et al. 1994) and decrease to 0.05% to 0.07% in regions south along the Shark River Slough (Davis 1991; Koch and Reddy 1992; Craft and Richardson 1993a,b; Reddy et al. 1993; DeBusk et al. 1994). In our study, TP concentrations in the upper estuary site (0.06%) are similar to those concentrations in lower regions of Shark River Slough. However, P concentrations near the mouth of Shark River estuary (0.12%) are similar to the upper limits of total soil P in the marshes adjacent to eutrophic soils of EAA. Based on bulk density values, P content per unit volume of soil at the mouth of Shark River estuary (0.21 mg cm⁻³ and 0.38 mg cm⁻³ in S4.1 and S1.8, respectively) are even higher than those in the enriched area in Water Conservation Area 2A which is part of the Everglades, where P content ranges from 0.12 mg cm⁻³ to 0.2 mg cm⁻³ (Koch and Reddy 1992; Reddy et al. 1993; Craft and Richardson 1993a). These gradients in TP represent a gradual shift from more mineral soil at the coastal margin to organic soil at the headwater regions of Shark River Slough. The enrichment of soils with TP results in sensitive changes to wetland vegetation, demonstrating the potential effects of natural (e.g., sea-level rise and storm frequency) and anthropogenic (e.g., fertilization and freshwater diversion) forcing on landscape vegetation dynamics in this coastal ecotone. We hypothesize that upstream marshes in Shark River Slough effectively reduce surface water P concentrations. This leads to relatively low P inputs and contributes to the limited mangrove structure in the oligohaline zone (along with possible effects of hydroporoid). Marine inputs of P are a significant contribution to the optimum conditions described by Davis (1940) for mangrove forest development along the southwestern Everglades. These patterns in vegetation dynamics and soil properties in the coastal zone suggest that the entire Everglades

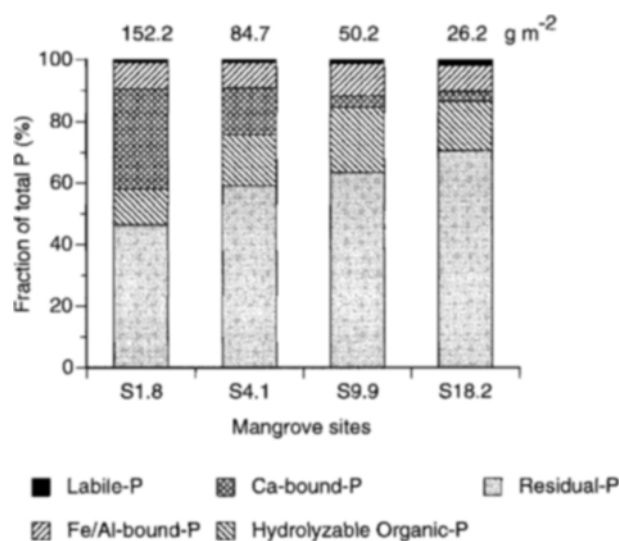


Fig. 7. Changes in phosphorus (P) fractionations as a percent of total P within the 0–20 cm soil at four mangrove sites along the Shark River estuary. The concentration of total P at each site is given above the respective bar.

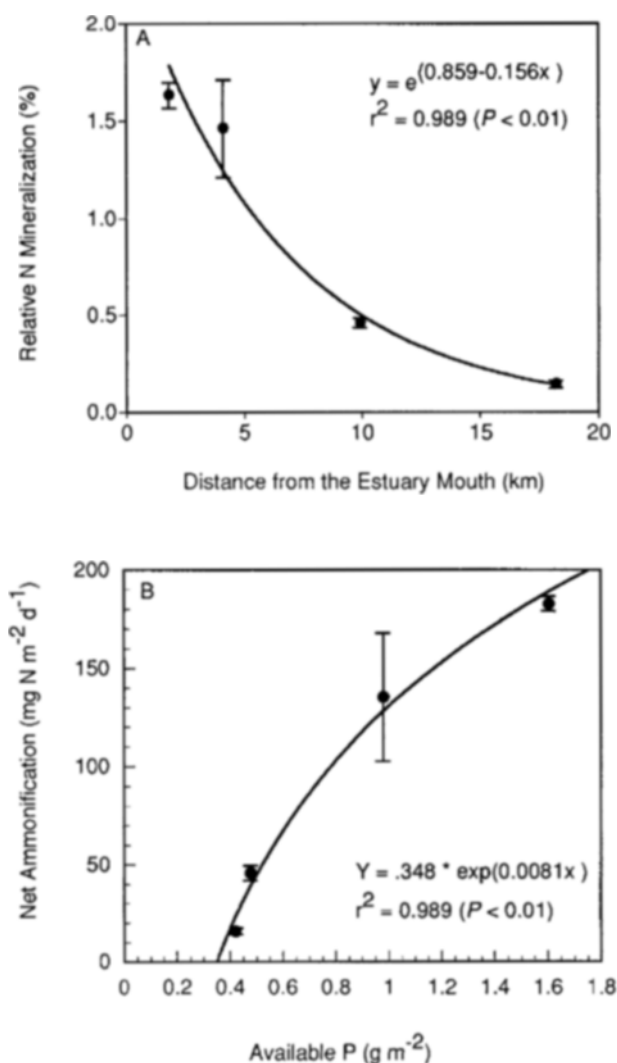


Fig. 8. A) The relative ammonification rate of mangrove soils in relation to location of sites along the Shark River estuary. Relative ammonification is calculated as the net total amount of ammonium mineralized (0–20 cm) during three periods of 15-d incubation as a percentage of mean total N present initially. B) Net ammonification rate in relation to the amount of available phosphorus in soil to depth of 20 cm. Values are mean ($n = 3$ stations) \pm SE.

landscape from freshwater uplands to the coastal margin are sensitive to the management of water quality and quantity, particularly those practices that influence the distribution of P.

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