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The dynamics of benthic nutrient pools and fluxes in tropical mangrove forests

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ABSTRACT

Variations in benthic nutrient pools and rates of dissolved nutrient exchange between the forest floor and tidal waters were examined over a 5-yr period in mixed *Rhizophora* forests lining Coral Creek on Hinchinbrook Island in Queensland, Australia. Seasonal and spatial changes in redox status, porewater and solid-phase nutrients, and in exchange rates were not consistent and did not correlate with temperature. Below-ground roots, on average, accounted for ~79%, 37% and 26% of bulk sediment TOC, total N and total P pools, respectively. Porewater nutrient concentrations were dominated by $Si(OH)_4^+$ and DON with consistently low levels of NO_2^- + NO_3^-. At most sampling periods, porewater NH_4^+ and PO_4^{3-} concentrations were higher in creek bank sediments than in mangrove sediments indicating uptake by trees. These sediments have low adsorption capacity (K = 0.17–0.47) for NH_4^+, but a moderate capacity (K = 0.8–4.8) for PO_4^{3-} adsorption. Most measured benthic fluxes of dissolved nitrogen and phosphorus showed uptake by sediments, prop roots and timber lying on the forest floor. Relative (per ha) estimates indicate that low-intertidal *Rhizophora* forests import ~2220 mmol N $ha^{-1}d^{-1}$ and ~496 mmol P $ha^{-1}d^{-1}$, with sediments accounting for nearly all uptake while Si is exported (~2475 mmol $ha^{-1}d^{-1}$. Mid-intertidal forests import ~1385, 93 and 4720 mmol $ha^{-1}d^{-1}$ of N, P and Si, respectively; sediments, prop roots and timber respectively account for 36%, 62% and 2% of the N import. Mid-intertidal sediments account for all net P uptake, but prop roots and sediments account for 60% and 40% of total Si uptake. On an absolute basis, low-intertidal forests (78 ha total area) in Coral Creek import ~881 kgN yr^{-1}, 436 kgP yr^{-1} and export 1963 kgSi yr^{-1}, and the mid-intertidal forests (338 ha total area) import ~2392 kgN yr^{-1}, 356 kgP yr^{-1} and 16300 kgSi yr^{-1}. The sum of these estimates equates to ~95% of the net annual import of total dissolved N and ~66% of the net annual import of total dissolved P into the Coral Creek tidal basin from adjacent coastal waters. By difference, ~14337 kgSi yr^{-1} is imported into the system. This indicates that mangrove forests are a very efficient sink of dissolved nitrogen, phosphorus and silicon in this tidally-driven coastal ecosystem. This import may be driven by the consistently high rates of microbial and plant growth and productivity within the forests.

1. Introduction

Mangrove forests and their associated waterways are a dominant intertidal ecosystem in the tropics. Most forests are very productive, and their associated food chains and nutrient cycles are often closely linked to those in adjacent coastal waters

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(Robertson and Alongi, 1992). The extent to which mangroves exchange dissolved and particulate nutrients with adjacent inshore waters depends upon several factors, including geomorphology, tidal regime, climate and groundwater inputs. Most forests appear to exchange substantial amounts of nutrients (e.g., northern Australia: Alongi *et al.,* 1992; Kenya: Hemminga *et al.,* 1994; Papua New Guinea: Robertson and Alongi, 1996; Mexico: Rivera-Monroy *et al.,* 1995), but some do not (e.g., southwest Florida: Twilley, 1985).

Physical characteristics are important, but it is less clear how rates, pathways and efficiency of organic matter decomposition and nutrient recycling within the forests affect the extent of nutrient exchange between mangroves and coastal waters. In a brief review, Wiebe (1989) suggested that mangroves are a sink for nutrients, particularly nitrogen, phosphorus and sulfur, but warned that such a generalization is tentative until early diagenesis and nutrient exchange processes are better understood. The comparatively few studies available indicate that mangrove sediments support an abundant microbial flora that is very active in mineralizing organic matter via several pathways (Stanley *et al.,* 1987; Alongi, 1988; Boto *et al.,* 1989; Kristensen *et al.,* 1991; Nedwell *et al.,* 1994).

Nevertheless, examination of specific decomposition pathways of organic matter (e.g., sulfate reduction, methanogenesis) and rates of nutrient turnover does not alone provide a clear understanding of the potential for nutrient exchange between mangroves and adjacent coastal waters. Mangroves are efficient at retaining and recycling nutrients via several mechanisms that reduce export, as suggested by Twilley *et al.* (1986) and Boto (1992). For instance, rapid uptake by the trees and adsorption to clays may exceed mineralization rates leading to retention, or even import, of some nutrients (Boto, 1992; Clough, 1992). This is plausible considering that most mangrove forests appear to be N- or P-limited, or both (Boto and Wellington, 1983). Similarly, the cell growth requirements of sedimentary microbes may balance with bacterial mineralization rates (Alongi, 1989). For example, in mangrove sediments on Hinchinbrook Island in northeastern Australia, Stanley *et al.* (1987) and Boto *et al.* (1989) found that, despite a sharp concentration gradient in DOC and DON concentrations between sediments and overlying tidal water, there was negligible flux across the sediment-water interface unless poisons were applied to the sediment surface, after which high rates of nutrient release were measured. This result was attributed to the very high rates of bacterial growth in surface sediments (Alongi, 1988) requiring nearly complete use of the available DOC and DON pool. Alongi (1989) argued that sedimentary bacteria act as a carbon sink in tropical mangrove forests. It is not known to what extent this nutritional demand is balanced with mineralization rates, particularly for other nutrient species. In addition, how are these processes balanced with tree requirements for nutrients? Boto and Wellington (1984) found that NH_4^+ pools can be depleted by tree uptake during

periods of rapid mangrove growth, but the relative amounts of free and adsorbed NH_4^+ and PO_4^{3-} in these sediments are not known.

A first-order nitrogen budget for the mangrove ecosystem on Hinchinbrook Island indicates that these forests import dissolved nitrogen and export particulate nitrogen mainly as leaves, twigs, bark and flowering parts, with the net exchange being a small import into the system (Alongi *et al.,* 1992). This budget was preliminary, so it is not known how temporal and spatial variations in particulate and dissolved sedimentary nutrient pools and sediment-water exchange rates contribute to nutrient exchange with coastal waters. It is also not clear if the considerably large standing mass of forest floor components such as fallen trunks and branches, and prop roots, play an important role in controlling nutrient exchange.

This paper describes a five-year study of variations with season and tidal elevation in concentrations of particulate and dissolved nutrients in mangrove sediments, and in nutrient exchange between the forest floor (sediments, fallen timber and prop roots) and overlying tidal waters, in the mangroves lining Coral Creek on Hinchinbrook Island. Relative (per ha) and absolute (the entire creek system) estimates of dissolved nutrient exchange were calculated in order to understand the contribution of mangrove forests to the overall nutrient budget of this tidally-driven coastal ecosystem.

2. Materials and methods

a. Study area. The study was conducted in forests lining Coral Creek at Missionary Bay (18° 13′ S, 146° 11′ E) on Hinchinbrook Island in Queensland, Australia (Fig. 1). This creek is one of eight large tidal waterways dissecting a large (50 km^2) mangrove ecosystem. Coral Creek is approximately 6 km long and 160 m in width at the mouth. Survey data (see summary in Boto and Bunt, 1981) and a hydrodynamic model (Wolanski *et al.,* 1980) indicate that approximately 457 ha of mixed *Rhizophora* forests line the creek and are almost completely inundated by semi-diurnal tides. The tidal range is ~2.7 m. There is minimal freshwater input except during periods of heavy monsoonal rains in summer. Creek water salinities rarely are lower than 33 even during monsoons (Wolanski and Gardiner, 1981).

A 360 m walkway traverses the forests near the creek mouth to facilitate access. Four sampling sites were located along the walkway (Fig. 1) on the basis of elevation above sea level. These stations were designated as the creek bank, low-, mid- and high-intertidal sites and were respectively located at elevations of ca. 0.0, 0.2, 0.9 and 1.2 m above Australian High Datum. These sites were sampled in October and December 1987, April and May 1988, April and June 1990, February and November 1991 and in September and December 1992.

The creek bank is ~3 m wide and drops off sharply at the tidal channel. It is vegetated by a sparse community of benthic diatoms, chlorophytes and phytoflagellates, and is inhabited mainly by *Uca* spp. In low- and mid-intertidal zones, three

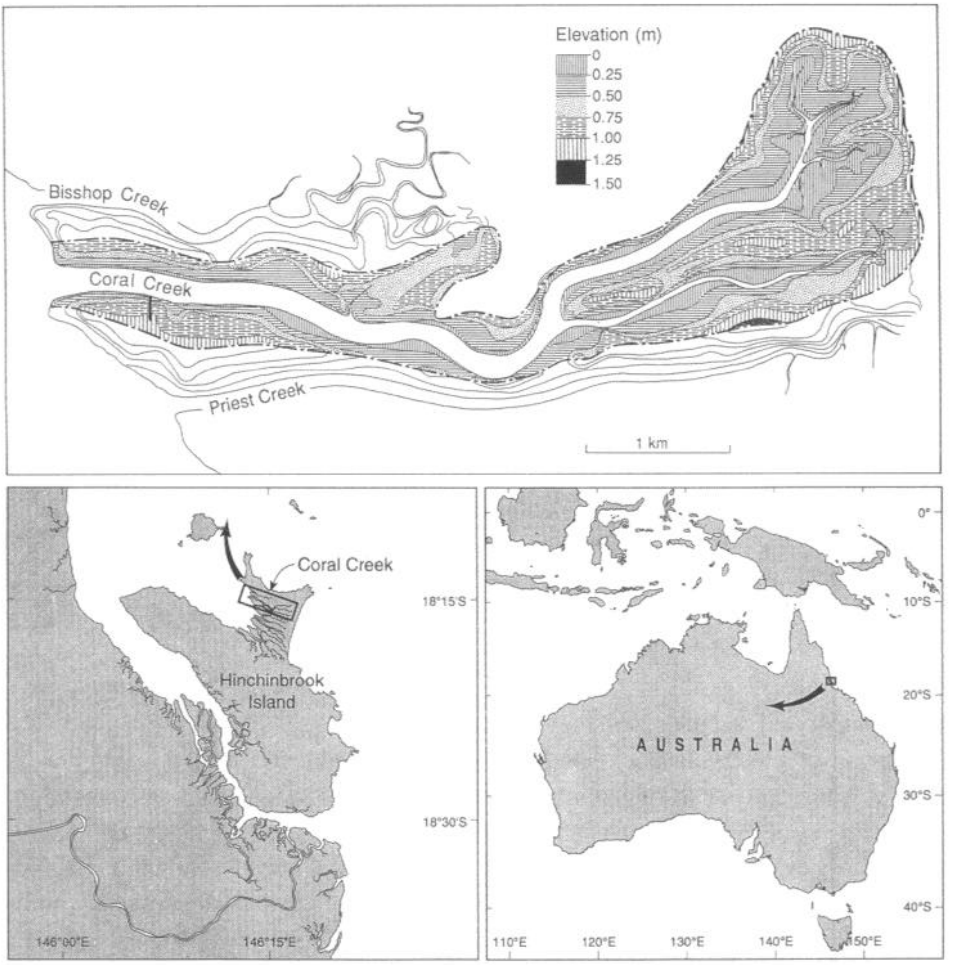

Figure 1. Map of Hinchinbrook Island and the Coral Creek system showing location of study sites near the creek mouth (vertical line) and tidal elevation in the adjacent mangrove forests.

species of *Rhizophora* (*R. stylosa, R. apiculata* and *R. lamarckii*) occur as a mixed stand. *Ceriops tagal* co-dominates with *R. stylosa* and *R. lamarckii* in the high intertidal. The sediments at all three mangrove stations are well-sorted silts (15–20% clay by dry weight) containing large quantities of fine roots and are intensely bioturbated by sesarmid crabs to ~0.5 m depth (Boto and Wellington, 1984; Robertson, 1986; Smith *et al.,* 1991). Primary productivity, litterfall estimates, and other characteristics, such as basic sediment properties of these forests are described in Bunt and Williams (1980), Boto and Bunt (1981), Duke *et al.* (1981), Boto and Wellington (1983, 1984), Alongi (1988, 1994) and Clough and Scott (1989).

b. Sedimentological and root analyses. Samples were taken at low tide from each site using stainless steel cores which were inserted to a depth of 20 cm. Each core (7 cm i.d.) contained a recessed inner core tube made of PVC and subdivided into 2 cm rings. Replicate cores were taken close to trees (~10–50 cm) to ensure that below-ground root and rhizome biomass characteristic of the forest type were sampled. Porosity (ϕ = volume porewater/volume sediment) and mean dry sediment density (ρ_s = dry weight/dry volume) were measured by drying replicate 20 cc portions of sediment at 80°C to constant weight. Redox potential was measured at 2 cm intervals from duplicate cores (described above) modified with sampling ports on each 2 cm ring to allow insertion of a Model PRFO combination calomel reference-platinum electrode. The electrode was allowed to equilibrate for 10–15 min before readings were taken on a TPS LC80 mV-pH-temperature meter. Readings were taken at each site in winter (June 1990), summer (February 1991), late spring (November 1991) and early spring (September 1992).

Shallow below-ground root biomass was estimated in the three forest sites in September and December 1992 using the same cores as described above. Triplicate cores were taken to 20 cm depth and root and rhizome material at 2 cm intervals was gently washed on a 63 μm sieve. Material retained on the sieve was patted dry and weighted. Subsamples were dried, weighed and ground for elemental analyses. The mean ratio of wet weight to dry weight of roots was 5.54. The contribution of root-derived C, N and P to the bulk sediment nutrient pools was calculated by multiplying the elemental composition of the roots (see Results section *a*) by the dry weight of the roots per unit volume per depth interval (averaging all seasons) to obtain the total root C, N and P per unit volume (extrapolated to m^{-3}). The bulk sediment TOC, total N and total P concentrations (dry weight average of all seasons and the same depths) were multiplied by the sediment bulk density and porosity (see Table 3) to give the total nutrient pools extrapolated to m^{-3}. The percentage of C, N and P of the total sediment nutrient pool contributed by the roots was derived by dividing the total root nutrient pool by the total sediment nutrient pool.

c. Porewater and solid-phase nutrient analyses. Replicate (n = 2–3) cores were taken at each site for dissolved inorganic and organic nutrients and for solid-phase nutrients (total organic carbon, total nitrogen and total extractable phosphorus). Porewater samples were not taken at the creek bank in December 1987 and April 1988; at all sites, DON and DOP were measured only in April and June 1990, November 1991 and in September and December 1992.

Each core for interstitial water was sectioned at 2 cm intervals, placed immediately into acid-washed Petri dishes and the porewater extracted as soon as possible using a Teflon porewater extractor (Robbins and Gustinis, 1976) and subsequently processed as described in Alongi *et al.* (1993). In the first two seasons at all four sites, two additional cores were immediately placed into N_2-filled glove bags and sectioned. As

there were no significant ($P > 0.05$) differences in nutrient concentrations at all depths between cores cut under N_2 and those cut quickly in ambient air, on subsequent trips cores were cut under ambient conditions. Dissolved inorganic nutrients (NH_4^+, NO_2^- + NO_3^-, PO_4^{3-} and $Si(OH)_4^+$) were measured using standard automated techniques described by Ryle *et al.* (1981) and Ryle and Wellington (1982). DON and DOP concentrations were determined from a separate fraction of the same sample for inorganic nutrients following overnight digestion in a LaJolla UV photooxidation apparatus. Pre-digested N concentrations were subtracted from the post-digested NO_3^- levels to derive the DON concentrations. DOP concentrations were similarly determined by difference in P concentration before and after UV oxidation. Analytical precision was 1% for PO_4^{3-}, 1.5% for NO_2^- + NO_3^- and NH_4^+, and 3% for $Si(OH)_4^+$.

NH_4^+ adsorption in sediments at the four sites was estimated in February and November 1991 by KCl extraction using the procedure of Rosenfeld (1979). Briefly, ~100 g samples of sediment at each site (0–2 cm and 10–12 cm layers only) were squeezed as described above for free NH_4^+. Fifteen ml of 2 N KCl solution was added to each squeezed cake (triplicate samples), mixed and extracted for 1 h. The sediment was re-squeezed and the extracted solute analyzed for NH_4^+. The linear adsorption coefficient (K*) was calculated from the slope of the regression line of the plot of adsorbed (μmol g^{-1} dry wt sediment) vs. porewater (mM) NH_4^+. K, the *in situ* adsorption coefficient, was calculated using $K = (1 - \phi)/\phi$ (ρ_s K*) where ϕ = porosity and ρ_s = dry sediment density (Mackin and Aller, 1984).

PO_4^{3-} adsorption was measured at each site in September 1992 using the method of Krom and Berner (1980). Briefly, ~70 g samples of sediment kept in an N_2-filled glove bag were added to preweighed plastic containers containing an equal weight of filtered, deoxygenated creek water. Varying amounts of PO_4^{3-} from a 100 mM standard were added to each container, the containers sealed and shaken every few h until they were sampled at 24 h. Porewaters were isolated by centrifugation. K*, the linear adsorption coefficient, was estimated as the slope of the regression of ΔC (mass of adsorbed PO_4^{3-} added) vs. C (equilibrium concentration). K was calculated using the same equation as noted above for NH_4^+ adsorption.

Solid-phase nutrients were determined in December 1987 (forest sites only), May 1988 and in November 1991 from the same cores used for porewater squeezing. Subsamples were frozen and then dried at 80°C to constant weight and ground to a fine powder on an agate mill. Total organic carbon was determined on a Beckman TOC Analyser using the procedure of Sandstrom *et al.* (1986). Total nitrogen was measured on a Leco CHN Analyser, and total extractable phosphorus was determined on a Spectrametrics V plasma emission spectrometer following aqua regia and perchloric acid digestion. Analytical precision was 5% for total N and 3% for C and P.

d. Sediment-water exchange. Measurements of solute exchange were made at each site using a bell jar technique (Alongi *et al.,* 1993). Triplicate, clear (all dates) and darkened (April and June 1990, November 1991 and September 1992) glass bell jars (1 liter volume; 0.007 m^2 surface area) were placed into the sediment at low tide and allowed to fill naturally with the incoming tide. Preliminary experiments in August 1987 indicated that solute flux rates between sets of clear bell jars filled with filtered (0.45 μm) vs natural tidal water were not significantly ($P > 0.05$) different over a 3 h incubation period. Each bell jar had a propeller-driven, electric motor unit and sleeves for insertion of sampling tubes (see description in Boto *et al.,* 1989). Replicate 10 ml syringe samples were taken from a sampling port on each jar immediately following deployment and at 45 min intervals over a 3 h incubation period. The samples were filtered (0.45 μm cellulose acetate filters) and frozen immediately until analysis. Flux rates were calculated from the slope of the concentration-time plots using standard linear regression when the regression was significant at $P < 0.05$. Otherwise, net fluxes were recorded as nonsignificant.

e. Timber and prop root-tidal water exchange. In winter (June 1990) and summer (February 1991), the exchange rates of dissolved nutrients between fallen timber and prop roots with tidal water were estimated. In the timber experiments, three pieces (each ~1 kg wet weight) each of two 'ages' of *Rhizophora* spp. timber lying on the mid-intertidal forest floor were collected. These 'ages' were arbitrary, based on the degree of teredinid mollusc infestation: pieces with no bore holes ('young trunks') and pieces thoroughly (~80%) bored by molluscs ('mature trunks'). Each piece (total of 6) was gently washed with tidal water to remove surface mud, and placed into a plastic tray containing 10 l of coarse-filtered seawater, and covered with clear plastic to minimize evaporation. Three trays containing only filtered seawater served as controls. Every h for 6 h, replicate (20 ml) water samples were taken ~5 min after the water was gently stirred in each tray for determination of dissolved inorganic and organic nutrients. The wet and dry weight and area of each timber piece was determined at the end of each experiment. The mean ratio of wet weight to dry weight of timber was 1.54.

For the prop root experiments, prop roots of *Rhizophora* spp. were cut into three equal-length (~40 cm) pieces and classified as lower, middle and upper portions. The lower sections were heavily colonized by surface micro- and macroalgae, the middle sections were sporadically colonized, and the upper sections were usually free of colonizers. Each of three pieces from each of the three prop root sections (total of 9 pieces) were gently washed, the cut ends were sealed with wax, and placed into a plastic tray and treated as the wood pieces in the timber experiments. Similarly, three trays containing only filtered tidal water served as controls. Nutrient samples were taken using the same procedure as in the timber experiments over 6 h incubation

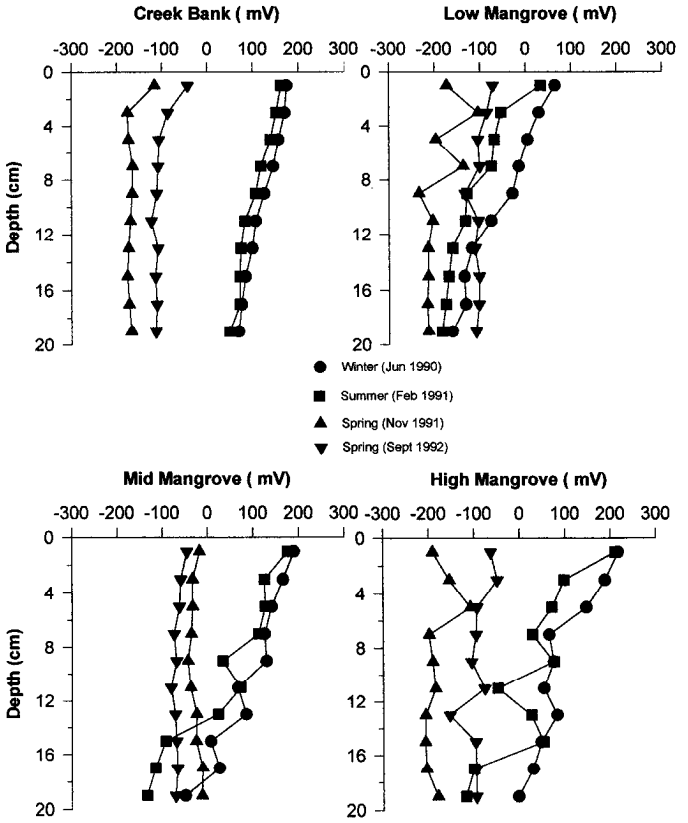

Figure 2. Mean vertical profiles of redox potential (mV) in creek bank and in low-, mid-, and high-intertidal mangrove sediments to a depth of 20 cm in winter (June 1990), summer (February 1991), late spring (November 1991) and early spring (September 1992).

periods. At the end of each experiment, fresh and dry weight and area of each piece was determined. The mean ratio of fresh weight to dry weight of prop roots was 2.37.

3. Results

a. Redox potential and roots. Redox potential (Fig. 2) varied significantly ($P < 0.05$) with season, sediment depth and intertidal position (3-way analysis of variance; Sokal and Rohlf, 1981). There were highly significant interactions (e.g., station × season × depth), obscuring clear differences among sites. Depending on season and depth, redox levels at these sites ranged widely from −240 to +210 mV. Redox values did not correlate with sediment temperature, as the most negative readings were measured in spring rather than summer (Fig. 2). Only half of the 16 profiles (all winter and summer) showed significant trends (runs test) of more negative readings with increasing sediment depth.

Shallow below-ground root and rhizome biomass ranged among forests as follows: in the low-intertidal, 530 (±80) kg wet weight m^{-3} sediment in September 1992 to 211 (±79) kg WW m^{-3} in December 1992; in the mid-intertidal, 755 (±100) kg WW m^{-3} sediment in September to 506 (±139) kg WW m^{-3} in December; and in the high-intertidal, 646 (±68) kg WW m^{-3} sediment in September to 435 (±109) kg WW m^{-3} in December. Root biomass at all sites was greater in spring than in summer, and increased with sediment depth only in the mid-intertidal forest, with similar amounts at all depths at other sites. Nutrient element composition of root and rhizome material was not significantly ($P > 0.05$) different between sites, and averaged 39.3% carbon, 0.58% nitrogen and 0.037% phosphorus by dry weight.

b. Solid-phase nutrients. Total organic carbon, total nitrogen and total phosphorus concentrations varied significantly ($P < 0.05$) among the four stations (Table 1). TOC concentrations were highest (and equivalent) in mid- and high-intertidal forests, averaging ~12.5% by sediment dry weight. In the low-intertidal forest and in the creek bank, TOC concentrations were lower, averaging 6.2% and 4.5% by sediment DW, respectively, but were not significantly ($P > 0.05$) different. The same pattern exists for total nitrogen, with a decline in concentration from the high-intertidal to the creek bank (Table 1). Both TOC and TN concentrations did not vary significantly ($P > 0.05$) with sediment depth or season at the four stations. In contrast, total phosphorus concentrations declined with increasing tidal elevation (Table 1) and decreased significantly ($P < 0.05$) at each station with increasing sediment depth (data not shown). Station differences for TP (all seasons) were: Creek bank = low > mid = high (SNK test; Sokal and Rohlf, 1981); seasonal differences were significant only in the mid-intertidal forest with highest concentrations in spring (Table 1). Stoichiometric ratios of sedimentary C:N:P increased from the creek bank to the high-intertidal forest (Table 1), averaging 262:9:1 in the creek bank, 392:13:1 in the low-intertidal forest, 1232:29:1 in the mid-intertidal forest and 1291:34:1 at the high-intertidal forest.

c. Porewater nutrients. Dissolved inorganic nutrient concentrations (Table 2; Figs. 3–5) varied significantly with season, station and sediment depth (3-way ANOVA's; $P < 0.05$). The highly significant interactions of depth by season by site precluded further analysis using SNK tests to test for station differences in grand means (Sokal and Rohlf, 1981). For instance, NH_4^+ concentrations in winter (June 1990) did not vary significantly with depth among forest sediments, but did increase significantly in the creek bank (Fig. 3, top left); in summer (December 1992) patterns were greatly different (Fig. 3, top right) among sites with sediment depth. Similar variations were exhibited by $NO_2^- + NO_3^-$ (Fig. 3, bottom), $Si(OH)_4^+$ (Fig. 4, bottom) and PO_4^{3-} (Fig. 5, top). There were no consistent seasonal patterns for porewater nutrients (Table 2).

Table 1. Mean (±1 SE) total organic carbon, total nitrogen and total extractable phosphorus concentrations (% sediment dry weight) and stoichiometric ratios (mole:mole) in low-, mid- and high-intertidal mangrove and creek bank sediments, averaged over 20 cm depth. Superscript numbers denote results of SNK tests; common numbers signify lack of significant ($P > 0.05$) differences between sites, and rank in concentration also corresponds to superscripted numbers with 1 being highest concentration.

		Location		
Season	Creek bank	Low	Mid	High
		TOC		
Summer (Dec 1987)	*	6.2 ± 2.5[2]	13.4 ± 1.4[1]	12.0 ± 2.5[1]
Autumn (May 1988)	4.2 ± 1.0[2]	5.8 ± 1.7[2]	13.1 ± 1.6[1]	13.4 ± 2.0[1]
Spring (Nov 1991)	4.8 ± 1.1[2]	6.7 ± 2.4[2]	11.1 ± 2.1[1]	12.5 ± 1.6[1]
Grand mean =	4.5[2]	6.2[2]	12.5[1]	12.5[1]
		TN		
Summer (Dec 1987)	*	0.24 ± 0.06[2]	0.36 ± 0.06[1]	0.39 ± 0.04[1]
Autumn (May 1988)	0.21 ± 0.03[2]	0.25 ± 0.03[2]	0.38 ± 0.05[1]	0.43 ± 0.07[1]
Spring (Nov 1991)	0.16 ± 0.03[2]	0.21 ± 0.04[2]	0.30 ± 0.03[1]	0.34 ± 0.04[1]
Grand mean =	0.19[2]	0.23[2]	0.35[1]	0.39[1]
		TP		
Summer (Dec 1987)	*	0.040 ± 0.013[1]	0.024 ± 0.004[2]	0.024 ± 0.003[2]
Autumn (May 1988)	0.046 ± 0.002[1]	0.041 ± 0.007[1]	0.024 ± 0.003[2]	0.025 ± 0.002[2]
Spring (Nov 1991)	0.043 ± 0.003[1]	0.042 ± 0.002[1]	0.034 ± 0.005[2]	0.027 ± 0.002[3]
Grand mean =	0.045[1]	0.041[1]	0.027[2]	0.025[2]
		C:N:P		
Summer (Dec 1987)	*	400:13:1	1442:33:1	1292:36:1
Autumn (May 1988)	236:10:1	365:14:1	1410:35:1	1385:38:1
Spring (Nov 1991)	288:8:1	412:11:1	843:20:1	1196:28:1
Grand mean =	262:9:1	392:13:1	1232:29:1	1291:34:1

*not sampled.

Although not statistically significant, there were some general trends among stations. First, inorganic nutrient concentrations at all four sites were dominated by $Si(OH)_4^+$, followed in decreasing order of abundance by NH_4^+, PO_4^{3-} and NO_2^- + NO_3^- (Table 2). Second, low but consistent, levels of NO_2^- + NO_3^- were always detected and were equivalent among the four sites (Fig. 3, bottom). Third, NH_4^+ concentrations were higher in the creek bank sediments than in the forest sediments (Table 2). Fourth, on most sampling intervals, PO_4^{3-} and $Si(OH)_4^+$ concentrations were highest in creek bank and high-intertidal sediments compared to low- and mid-intertidal forest sediments (Table 2).

DON (Fig. 4, top) and DOP (Fig. 5, bottom) concentrations exhibited equally wide variations (3-way ANOVA's) among stations and seasons with sediment depth

(Table 2). The lack of a consistent seasonal pattern among sites is similar to the lack of a pattern for inorganic species, but general patterns do emerge. On average, DON concentrations increased with increasing tidal elevation (Table 2) from a grand mean of ~60 μM in creek bank sediments to a grand mean of ~128 μM in high-intertidal sediments. The pattern for DOP was similar, but the grand mean concentrations in the mid- and high-intertidal sediments were not different (Table 2).

The adsorption experiments (Table 3) showed that K for NH_4^+ ranged from 0.17 for creek bank sediments to a high of 0.47 for mid-intertidal sediments. That is, of the NH_4^+ produced by detrital decomposition, 17–47% more is associated with the sediment than is dissolved in the porewater. The adsorption coefficients (K) measured for PO_4^{3-} were considerably greater (Table 4), ranging from a low of 0.8 for creek bank sediments to a high of 4.8 for the low-intertidal sediments. This indicates that nearly 1 to 5 times more PO_4^{3-} is associated with the sediment than is dissolved in the interstitial water.

d. Rates of nutrient regeneration. Rates of sediment-water exchange (Table 5) on the creek bank were usually dominated by $Si(OH)_4^+$, DON and NH_4^+ release. Rates of release for PO_4^{3-} and DOP were slower, and $NO_2^- + NO_3^-$ fluxes were into the sediment. At the low- and mid-intertidal *Rhizophora* sites, nearly all measured fluxes of nitrogen and phosphorus showed uptake; $Si(OH)_4^+$ was usually released from the low-intertidal, but, on average, taken up by mid-intertidal sediments (Table 5). At the high-intertidal station, most trials showed no flux of NH_4^+, but significant and consistent uptake of $NO_2^- + NO_3^-$ and release of DON; the measurable flux rates of $Si(OH)_4^+$, PO_4^{3-} and DOP were fast compared to the other sites. There were no significant ($P > 0.05$) differences in flux rates between sets of clear and darkened bell jars used at all four stations in April and June 1990, November 1991 and September 1992 (data not shown). Across all sites and trials, rates of nutrient flux neither correlated ($P > 0.05$) with temperature (r range of -0.12 to $+0.19$) nor with oxygen uptake (August, October and December 1987, April and May 1988, and September 1992; oxygen data from Alongi, 1994). The only significant correlation was between PO_4^{3-} and $Si(OH)_4^+$ flux ($r = +0.69$; $P < 0.01$).

The rates of dissolved nutrient exchange between young and mature *Rhizophora* trunks and tidal water (Table 6) showed some uptake of inorganic N and net release of $Si(OH)_4^+$, with little or no flux of PO_4^{3-}, DON and DOP. There were no clear differences between young and mature trunks (Table 6).

The rates of nutrient exchange between tidal water and *Rhizophora* prop roots (Table 7) indicated uptake of N (including DON) and $Si(OH)_4^+$ mainly in summer. There was little or no flux of P; winter-summer differences were inconsistent. On average, there was greater uptake of NH_4^+ by lower prop root sections, but no clear differences among the three sections for the other nutrients (Table 7).

Table 2. Mean (±1 SE) porewater nutrient concentrations (μM) in creek bank and in low-, mid- and high-intertidal mangrove sediments, averaged over 20 cm depth, with season. Superscript numbers denote results of SNK tests; common numbers signify lack of significant differences ($P > 0.05$) between sites, and rank in concentration also corresponds to superscripted numbers with 1 being highest concentration. Highly significant interactions precluded SNK tests of site differences for grand means of all nutrient species (see Results section *c*).

	Location			
Season	Creek bank	Low	Mid	High
		PO_4^{3-}		
Spring (Oct 1987)	10.4 ± 6.6^{1,2}	3.0 ± 1.8^{3}	7.4 ± 6.5^{2}	15.3 ± 17.9^{1}
Summer (Dec 1987)	*	2.3 ± 1.3^{1,2}	3.1 ± 1.3^{1}	1.8 ± 0.8^{2}
Autumn (Apr 1988)	*	3.5 ± 4.2^{1}	3.5 ± 1.9^{1}	2.0 ± 0.6^{2}
Autumn (May 1988)	1.7 ± 0.7^{3}	1.2 ± 0.7^{3}	4.9 ± 4.1^{1}	2.0 ± 1.1^{2}
Autumn (Apr 1990)	3.2 ± 5.0^{1}	0.6 ± 0.4^{3}	0.3 ± 0.3^{3}	1.7 ± 1.9^{2}
Winter (Jun 1990)	1.6 ± 0.4^{1}	0.9 ± 1.0^{2}	0.8 ± 0.8^{2}	1.5 ± 1.4^{1,2}
Summer (Feb 1991)	5.9 ± 3.3^{1}	0.8 ± 0.3^{2}	0.8 ± 0.3^{2}	3.1 ± 2.6^{1}
Spring (Nov 1991)	2.5 ± 3.8^{1}	0.8 ± 0.3^{2}	3.6 ± 3.7^{1}	2.8 ± 1.7^{1}
Spring (Sept 1992)	2.9 ± 3.4^{1}	0.3 ± 0.3^{2}	0.3 ± 0.4^{2}	2.0 ± 1.7^{1}
Summer (Dec 1992)	2.4 ± 1.0^{2}	0.9 ± 1.1^{3}	3.8 ± 3.1^{1}	1.4 ± 1.4^{3}
Grand mean =	3.8	1.4	2.9	3.4
		NH_4^+		
Spring (Oct 1987)	154.2 ± 29.8^{1}	8.6 ± 3.4^{3}	8.9 ± 3.6^{3}	23.0 ± 26.6^{2}
Summer (Dec 1987)	*	15.4 ± 8.5^{2}	57.6 ± 25.6^{1}	13.0 ± 7.5^{2}
Autumn (Apr 1988)	*	22.8 ± 13.0^{1}	15.1 ± 10.2^{1,2}	7.9 ± 5.9^{2}
Autumn (May 1988)	69.5 ± 35.6^{1}	35.2 ± 17.2^{2}	37.5 ± 11.3^{2}	18.1 ± 4.0^{3}
Autumn (Apr 1990)	207.1 ± 192.9^{1}	31.7 ± 1.9^{2}	24.4 ± 9.4^{3}	16.2 ± 6.5^{4}
Winter (Jun 1990)	86.2 ± 28.9^{1}	27.7 ± 11.1^{2}	20.8 ± 11.4^{2,3}	18.9 ± 8.3^{3}
Summer (Feb 1991)	234.7 ± 54.6^{1}	20.8 ± 5.8^{3}	17.7 ± 12.0^{3}	34.5 ± 29.0^{2}
Spring (Nov 1991)	146.2 ± 4.5^{1}	58.4 ± 41.1^{2}	46.0 ± 31.5^{2,3}	30.5 ± 15.9^{3}
Spring (Sept 1992)	76.1 ± 42.2^{1}	21.8 ± 22.4^{2}	16.6 ± 16.7^{2}	17.7 ± 17.9^{2}
Summer (Dec 1992)	83.1 ± 55.8^{1}	10.0 ± 10.2^{3}	46.2 ± 48.2^{2}	85.2 ± 90.4^{1}
Grand mean =	131.9	25.2	29.1	26.5
		$NO_2^- + NO_3^-$		
Spring (Oct 1987)	0.5 ± 0.3^{3}	1.4 ± 1.8^{2}	0.5 ± 0.2^{3}	2.6 ± 3.2^{1}
Summer (Dec 1987)	*	1.2 ± 1.0^{2}	1.0 ± 0.2^{2}	3.6 ± 2.1^{1}
Autumn (Apr 1988)	*	1.5 ± 1.5^{1}	0.6 ± 0.3^{2}	0.8 ± 0.7^{2}
Autumn (May 1988)	0.5 ± 0.4^{1}	0.6 ± 0.2^{1}	0.7 ± 0.4^{1}	0.8 ± 0.8^{1}
Autumn (Apr 1990)	1.6 ± 0.7^{2}	1.4 ± 0.2^{2}	4.2 ± 5.6^{1}	3.5 ± 0.8^{1}
Winter (Jun 1990)	2.0 ± 1.1^{1}	1.7 ± 0.9^{1}	1.6 ± 1.3^{1,2}	1.2 ± 0.3^{2}
Summer (Feb 1991)	0.2 ± 0.0^{1}	0.2 ± 0.0^{1}	0.2 ± 0.0^{1}	0.2 ± 0.0^{1}
Spring (Nov 1991)	1.7 ± 1.8^{1}	0.6 ± 0.3^{2}	0.5 ± 0.0^{3}	0.9 ± 0.4^{2}
Spring (Sept 1992)	3.2 ± 3.5^{1}	4.9 ± 1.3^{1}	1.0 ± 0.6^{2}	1.0 ± 0.5^{2}
Summer (Dec 1992)	1.1 ± 0.5^{3}	2.8 ± 2.1^{2}	2.6 ± 2.3^{2}	4.0 ± 6.3^{1}
Grand mean =	1.4	1.6	1.3	1.9

Table 2. (Continued)

Season	Location			
	Creek bank	Low	Mid	High
		$Si(OH)_4^+$		
Spring (Oct 1987)	236.4 ± 31.7[1]	230.5 ± 23.1[1]	88.3 ± 63.5[2]	220.9 ± 43.1[1]
Summer (Dec 1987)	*	147.3 ± 15.4[2]	128.3 ± 40.7[2]	253.0 ± 73.9[1]
Autumn (Apr 1988)	*	126.4 ± 61.5[2]	102.6 ± 43.8[2]	139.6 ± 44.7[1]
Autumn (May 1988)	159.1 ± 48.6[1]	107.4 ± 22.1[2]	105.1 ± 23.3[2]	176.2 ± 73.1[1]
Autumn (Apr 1990)	188.8 ± 47.4[2]	92.6 ± 75.7[3]	39.3 ± 20.2[4]	262.3 ± 73.8[1]
Winter (Jun 1990)	177.5 ± 49.1[2]	164.3 ± 95.7[2]	103.8 ± 42.9[3]	320.5 ± 126.6[1]
Summer (Feb 1991)	125.2 ± 25.4[2]	67.4 ± 29.6[3]	80.8 ± 32.3[2,3]	191.8 ± 98.9[1]
Spring (Nov 1991)	691.6 ± 140.0[1]	442.0 ± 200.9[2]	578.5 ± 187.0[1,2]	739.6 ± 212.3[1]
Spring (Sept 1992)	208.8 ± 70.6[1]	82.3 ± 40.4[2]	136.9 ± 147.3[2]	218.4 ± 59.9[1]
Summer (Dec 1992)	226.1 ± 60.3[1,2]	194.1 ± 53.3[2,3]	144.5 ± 115.5[3]	263.3 ± 152.4[1]
Grand mean =	251.7	165.4	150.8	278.6
		DON		
Autumn (Apr 1990)	38.1 ± 42.3[2]	105.6 ± 96.4[1]	40.4 ± 37.1[2]	143.2 ± 87.7[1]
Winter (Jun 1990)	77.1 ± 57.8[2]	85.8 ± 56.0[2]	102.2 ± 70.7[1]	172.3 ± 109.8[1]
Spring (Nov 1991)	156.4 ± 102.2[1,2]	102.6 ± 49.2[2]	206.1 ± 122.7[1]	183.2 ± 37.2[1]
Spring (Sept 1992)	22.8 ± 16.1[2]	63.1 ± 60.2[1]	68.1 ± 34.9[1]	61.1 ± 32.1[1]
Summer (Dec 1992)	5.3 ± 5.8[3]	72.1 ± 16.0[2]	118.4 ± 123.9[1]	78.3 ± 69.3[1,2]
Grand mean =	59.9	85.8	107.0	127.6
		DOP		
Autumn (Apr 1990)	4.6 ± 2.5[1,2]	4.7 ± 3.9[1,2]	2.5 ± 2.0[2]	6.2 ± 4.2[1]
Winter (Jun 1990)	2.9 ± 1.7[2]	3.9 ± 3.9[2]	7.0 ± 5.7[1]	7.9 ± 6.3[1]
Spring (Nov 1991)	1.4 ± 3.4[3]	2.2 ± 2.7[2,3]	3.7 ± 1.9[2]	6.1 ± 2.6[1]
Spring (Sept 1992)	1.1 ± 1.0[2]	1.5 ± 1.6[1]	2.1 ± 1.4[1]	1.4 ± 1.4[1,2]
Summer (Dec 1992)	0.1 ± 0.0[3]	1.3 ± 1.0[2]	7.7 ± 9.4[1]	1.6 ± 3.0[2]
Grand mean =	2.0	2.7	4.6	4.6

*Not sampled.

4. Discussion

a. Contribution of mangrove forests to nutrient exchange with coastal waters. The composition and behavior of the benthic nutrient pools and fluxes support the notion that nutrient cycling processes in the forests drive the import of dissolved N, P and Si into this tidally-dominated ecosystem. Estimates on a per hectare basis for the low- and mid-intertidal forests clarify the contribution the various forest floor components make to nutrient exchange. The calculations (see assumptions and empirical values used in Table 8) show that the low-intertidal forests import ~2220 mmol N $ha^{-1}d^{-1}$ and ~496 mmol P $ha^{-1}d^{-1}$, with sediments accounting for 84% and 100% of the N and P uptake, respectively. Fallen timber and prop roots account for little of the net exchange. In contrast, Si is exported from the low-intertidal forest

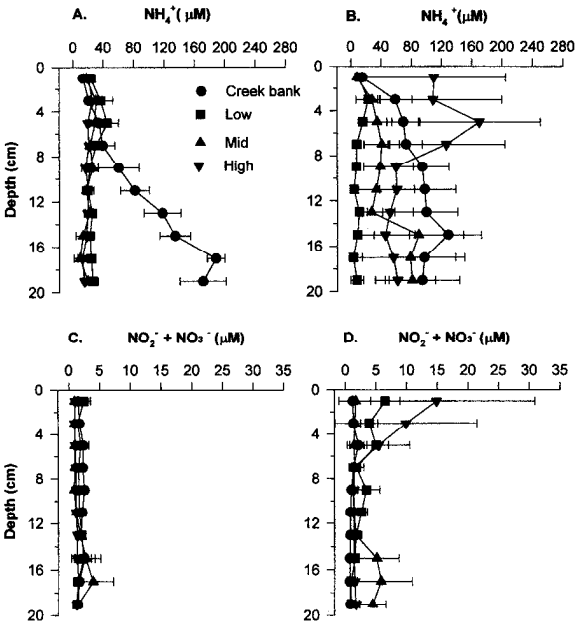

Figure 3. Mean (±1 SE) vertical depth profiles of porewater NH_4^+ in (A) winter (June 1990), (B) summer (December 1992) and of porewater NO_2^- + NO_3^- in (C) winter (June 1990) and (D) summer (December 1992) at the four stations.

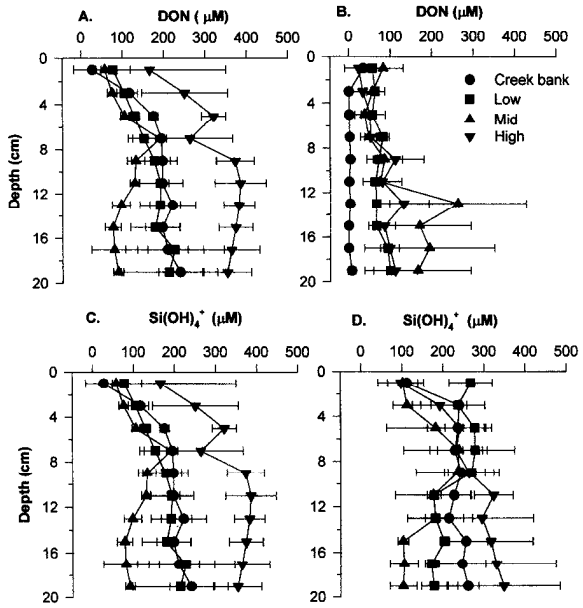

Figure 4. Mean (±1 SE) vertical depth profiles of porewater DON in (A) winter (June 1990) and (B) summer (December 1992) and of porewater $Si(OH)_4^+$ in (C) winter (June 1990) and (D) summer (December 1992) at the four stations.

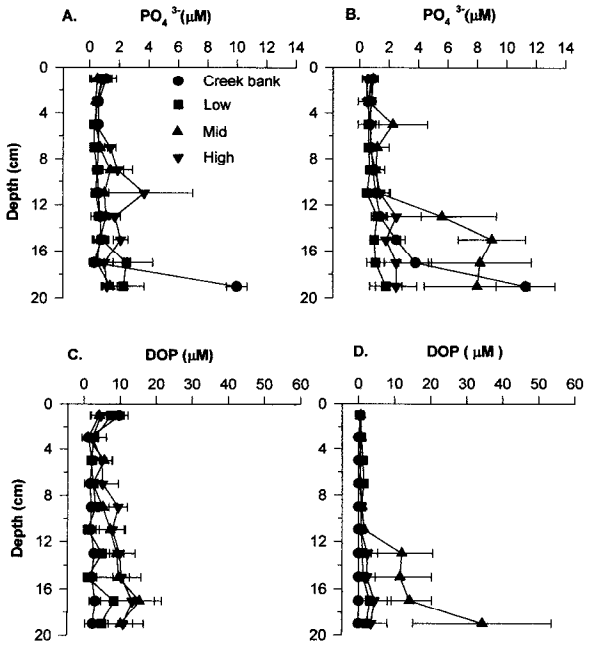

Figure 5. Mean (±1 SE) vertical depth profiles of porewater PO_4^{3-} in (A) winter (June 1990) and (B) summer (December 1992) and of porewater DOP in (C) winter (June 1990) and (D) summer (December 1992) at the four stations.

(~2475 mmol Si $ha^{-1}d^{-1}$), mainly by sediments and by some release from trunks, but prop roots take up nearly 28% of the total release by sediment and fallen timber. Sediment uptake accounts for ~6% and ~28% of the N and P required for net forest primary production requirements.

For the mid-intertidal forests, calculations indicate that these forests import ~1385 mmol N $ha^{-1}d^{-1}$ and ~93 mmol P $ha^{-1}d^{-1}$, with sediments, prop roots and timber respectively accounting for 36%, 62% and 2% of the N import, and sediments accounting for all of the net P uptake. As in the low-intertidal forests, timber and prop roots account for little of the P exchange. In contrast to the low-intertidal forests, Si is imported into the mid-intertidal forests, at an estimated rate of

Table 3. Measured values of linear adsorption coefficient for NH_4^+ (K*, ml g^{-1}), the *in situ* adsorption coefficient (K), mean porosity (σ = volume water/volume sediment), and mean dry sediment density (ρ_s = dry weight/dry volume, g ml^{-1}), values from both trials combined. All regressions were significant ($P < 0.001$).

Location	K*	σ	ρ_s	K
Creek bank	0.72	0.74	0.68	0.17
Low-intertidal	1.18	0.73	0.61	0.26
Mid-intertidal	2.26	0.73	0.56	0.47
High-intertidal	1.41	0.72	0.60	0.32

Table 4. Measured values of linear adsorption coefficient (K*, ml g^{-1}) for PO_4^{3-}, the dimensionless *in situ* adsorption coefficient (K), and the exchangeable PO_4^{3-} initially on sediment (C_i, μmol g^{-1}), September 1992.

Location	K*	K	C_i
Creek bank	3.45	0.8	0.0244
Low-intertidal	21.3	4.8	0.0043
Mid-intertidal	21.4	4.4	0.0044
High-intertidal	13.4	3.1	0.0531

4720 mmol Si $ha^{-1}d^{-1}$, with prop roots and sediments accounting for ~60% and 40% of Si uptake. As in the low-intertidal forests, fallen timber releases some (~175 mmol $ha^{-1}d^{-1}$) dissolved Si. Sediment uptake accounts for ~2%, 5% and 100% of the N, P and Si required for net forest primary production requirements in the mid-intertidal forests. Estimates cannot be made for the high-intertidal forests as some data such as timber lying on the forest floor are unavailable. The contribution of the creek banks to nutrient exchange also was not estimated because an accurate assessment of bank area cannot be made as many banks are unstable and vary in width over time.

Absolute estimates of the total amount of dissolved N, P and Si imported by nearly all of the mangrove forests lining Coral Creek can be made by multiplying the relative estimates (Table 8) by the total area of the low- and mid-intertidal forests. In Coral Creek, the total area of mangrove forests is 457 ha, of which the low- and mid-intertidal forests inhabit 78 and 338 ha, respectively, with the remaining area colonized by high-intertidal forests and some salt pan (Boto and Bunt, 1981; Alongi *et al.,* 1992). Extrapolating to the entire creek, the calculations indicate that for total dissolved nitrogen the low-intertidal forests import 880.5 kg N yr^{-1} and that the mid-intertidal forests import 2391.6 kg N yr^{-1} for a total estimated import of 3274.6 kg N yr^{-1} into the Coral Creek mangroves. The calculations for total dissolved P show that the low-intertidal forests import 435.6 kg P yr^{-1} with the mid-intertidal forests importing 355.6 kg P yr^{-1} for a total import of 791.2 kg P yr^{-1} into the creek. For total dissolved Si, the low-intertidal forests export 1963.4 kg Si yr^{-1} and the mid-intertidal forests import 16300.7 kg Si yr^{-1}, for a net import of 14337.3 kg Si yr^{-1} into Coral Creek.

How do these absolute estimates compare with the net annual rates of dissolved nutrient exchange between Coral Creek and adjacent coastal waters? Calculating net annual exchange by fitting tidal cycle changes in nutrient concentrations in Coral Creek to a hydrodynamic model (Wolanski *et al.,* 1980) and to water volume exchange (2.1×10^6 m^3) over an average tidal run, Boto and Wellington (1988) and Alongi *et al.* (1992) estimated a net annual import into Coral Creek of total dissolved N of 3463.2 kg N yr^{-1} and a net annual import of total dissolved P of 1194.8 kg P yr^{-1}. Comparing these estimates to those for the mangroves indicates that the import of total dissolved nitrogen by the forests equates to ~95% (3274.6/3463.2) of the net annual import of total dissolved N into Coral Creek from adjacent coastal waters.

Table 5. Rates of dissolved nutrient flux (μmol m^{-2} h^{-1}) in clear bell jars sampled over a 3 h period in mangroves and on the creek bank. Values depict mean ± 95% C.I. Negative values indicate net flux into the sediment. Temperatures are mean sediment temperatures over each sampling period. *not measured.

Season	°C	NH_4^+	$NO_2^- + NO_3^-$	DON	PO_4^{3-}	DOP	$Si(OH)_4^+$
			Creek bank				
Spring (10/87)	27	0	−2 ± 1	*	0	*	−90 ± 15
Autumn (5/88)	25	0	−3 ± 1	*	−2 ± 1	*	90 ± 20
Autumn (4/90)	24	270 ± 15	−2 ± 1	85 ± 30	4 ± 1	4 ± 1	315 ± 20
Winter (6/90)	20	130 ± 60	0	150 ± 75	9 ± 1	3 ± 1	330 ± 20
Summer (2/91)	28	65 ± 10	−3 ± 1	30 ± 4	0	2 ± 1	475 ± 30
Spring (11/91)	23	0	−5 ± 2	260 ± 60	0	0	0
Spring (9/92)	27	50 ± 10	−3 ± 1	50 ± 10	0	0	0
Grand mean =		74	−3	115	2	2	160
			Low-Intertidal				
Winter (8/87)	18	0	0	*	−3 ± 1	*	0
Spring (10/87)	27	−2 ± 1	−2 ± 1	*	−3 ± 1	*	−30 ± 10
Summer (12/87)	29	0	−2 ± 1	*	0	*	140 ± 30
Autumn (4/88)	25	0	0	*	0	*	0
Autumn (5/88)	24	−3 ± 1	−3 ± 1	*	0	*	0
Autumn (4/90)	24	−15 ± 7	1 ± 1	−60 ± 25	−1 ± 1	−1 ± 1	130 ± 40
Winter (6/90)	20	−15 ± 7	−1 ± 1	0	−1 ± 1	0	0
Summer (2/91)	27	17 ± 5	0	−30 ± 3	2 ± 1	0	160 ± 70
Spring (11/91)	25	0	−3 ± 2	0	0	−25 ± 10	0
Spring (9/92)	25	−22 ± 5	−4 ± 1	0	−1 ± 1	−2 ± 1	0
Grand mean =		−4	−1	−18	−1	−6	40
			Mid-Intertidal				
Winter (8/87)	20	0	0	*	0	*	0
Spring (10/87)	26	0	0	*	−1 ± 1	*	0
Summer (12/87)	29	0	−3 ± 1	*	−2 ± 1	*	−320 ± 50
Autumn (4/88)	26	0	−2 ± 1	*	0	*	−40 ± 15
Autumn (5/88)	24	0	−3 ± 1	*	−2 ± 1	*	30 ± 10
Autumn (4/90)	23	−5 ± 3	−5 ± 1	−1 ± 1	−1 ± 1	−1 ± 1	0
Winter (6/90)	20	0	−1 ± 1	0	−1 ± 1	0	−60 ± 10
Summer (2/91)	27	−30 ± 15	−5 ± 1	−2 ± 1	0	−2 ± 1	90 ± 30
Spring (11/91)	24	0	−4 ± 1	0	0	0	0
Spring (9/92)	25	−15 ± 4	−3 ± 1	0	−2 ± 1	0	0
Grand mean =		−5	−3	−1	−1	−1	−30
			High-Intertidal				
Winter (8/87)	22	0	0	*	0	*	0
Spring (10/87)	28	5 ± 1	−5 ± 1	*	0	*	0
Summer (12/87)	30	0	0	*	0	*	0
Autumn (4/88)	27	0	−2 ± 1	*	−1 ± 1	*	0
Autumn (5/88)	23	0	−5 ± 1	*	5 ± 1	*	250 ± 50
Autumn (4/90)	22	30 ± 8	−2 ± 1	0	15 ± 2	10 ± 2	590 ± 25
Winter (6/90)	20	0	−1 ± 1	0	4 ± 1	0	560 ± 70
Summer (2/91)	29	0	−2 ± 1	30 ± 5	15 ± 2	0	360 ± 60
Spring (11/91)	24	0	−3 ± 9	0	0	−30 ± 8	290 ± 65
Spring (9/92)	28	0	−3 ± 1	40 ± 20	−1 ± 1	0	0
Grand mean =		4	−2	14	4	−4	205

Table 6. Rates of dissolved nutrient flux (μmol kg^{-1} WW log d^{-1}) from young and mature dead trunks on the floor of the *Rhizophora* forests (low- and mid-intertidal). Values are mean ± 95% C.I. and were extrapolated to a daily basis assuming average tidal inundation* of 8 and 6 h in the low- and mid-intertidal forests over a calendar year. Negative values denote uptake by trunks.

Age	Season	NH_4^+	$NO_2^- + NO_3^-$	DON	PO_4^{3-}	DOP	$Si(OH)_4^+$
Young	Winter (6/90)	0	−1 ± 1	0	2 ± 1	0	0
	Summer (2/91)	−6 ± 1	−2 ± 1	0	−1 ± 1	0	30 ± 10
Mature	Winter (6/90)	0	−1 ± 1	0	0	0	0
	Summer (2/91)	−7 ± 1	−2 ± 1	0	0	0	60 ± 25

*See first footnote, Table 8.

The uptake of total dissolved phosphorus by the mangrove forests equates to ~66% (791.2/1194.8) of the net annual import of total dissolved P into the creek. These high proportions suggest that the mangrove forests inhabiting Coral Creek effectively take up nearly all of the total dissolved nitrogen, and nearly two-thirds of the total dissolved phosphorus, imported on a net annual basis into the system from the adjacent nearshore waters. Water-column concentrations and net tidal exchange of dissolved Si were not measured, but the total import figure for the low- and mid-intertidal forests similarly suggests net import of Si into Coral Creek driven largely by mangrove uptake. These estimates indicate that the mangrove ecosystem of Coral Creek acts as an efficient sink for dissolved nutrients. There is considerable uncertainty in these estimates considering that (1) the contribution of creek banks and high-intertidal forests were not included, (2) mean values were used and extrapolated from small-scale measurements to a large area and (3) the propagation of error from multiplying several estimates may be large. The impact of the high-intertidal forests may be minimal considering that they constitute only 9% of

Table 7. Rates of dissolved nutrient flux (μmol kg^{-1} fresh weight prop root d^{-1}) from the lower, middle and upper portions of prop roots of *Rhizophora* spp. from the low- and mid-intertidal. Values are mean ± 95% C.I. and were calculated to a daily basis assuming average tidal inundation* of 8 and 6 h in the low- and mid-intertidal forests over a calendar year. Negative values denote uptake by prop roots.

Root section	Season	NH_4^+	$NO_2^- + NO_3^-$	DON	PO_4^{3-}	DOP	$Si(OH)_4^+$
Lower	Winter (6/90)	−13 ± 5	0	0	0	0	11 ± 5
	Summer (2/91)	−8 ± 4	−2 ± 1	−16 ± 3	−1 ± 1	0	−140 ± 50
Middle	Winter (6/90)	0	0	0	1 ± 1	1 ± 1	0
	Summer (2/91)	−1 ± 2	−6 ± 1	−11 ± 4	0	0	−80 ± 15
Upper	Winter (6/90)	0	0	−15 ± 7	0	0	0
	Summer (2/91)	0	−1 ± 1	0	−1 ± 1	0	−30 ± 10

*See first footnote, Table 8.

Table 8. Areal (per ha) estimates of nutrient exchange of total dissolved N, P and Si from low- and mid-intertidal *Rhizophora* forests with Coral Creek water, averaged over seasons, from mean flux rates for sediments (Table 5), trunks (Table 6) and prop roots (Table 7). Values are mmol ha^{-1} d^{-1}, assuming average daily tidal inundation* of 8 and 6 h for the low- and mid-intertidal forests, respectively. Estimates of standing wet weight of trunks** were obtained by multiplying the dry weight trunk data of Robertson and Daniel (1989) by the wet to dry weight conversion factor for trunks (see Methods section *e*). Estimates of fresh weight of prop roots*** were calculated by fitting the tree density data of Robertson and Daniel (1989) and Robertson (unpubl. data) to the allometric equations for *Rhizophora* prop roots in Clough and Scott (1989) and multiplying by the fresh to dry weight conversion factor for prop roots (see Methods section *e*). These data are available only for the low- and mid-intertidal forests. Values in parentheses indicate percentage contribution to net forest primary production calculated by dividing the nutrient exchange data by the total net forest primary production estimates for these forests in Bunt *et al.* (1979) and Clough *et al.* (1995). Si contribution was estimated by multiplying biomass by the Si content for *Rhizophora* spp. in Spain and Holt (1980). Negative values indicate import from tidal water.

Element	Component	Low-intertidal forest	Mid-intertidal forest
Nitrogen	Trunks	−45	−30
	Prop roots	−305	−860
	Sediments	−1870 (6%)	−495 (2%)
	Total	**−2220**	**−1385**
Phosphorus	Trunks	4	3
	Prop roots	0	0
	Sediments	−500 (28%)	−90 (5%)
	Total	**−496**	**−93**
Silicon	Trunks	250	175
	Prop roots	−975	−2745
	Sediments	3200	−1800 (100%)
	Total	**2475**	**−4720**

*Average daily tidal inundation was calculated from the tidal and survey data obtained from the National Tidal Facility, Flinders University and from the Australian Survey Office (Federal Government Department of Administrative Services), respectively.

**Values are 11,193 kg wet weight of wood ha^{-1} in the low-intertidal forest and 10,640 kg WW of wood ha^{-1} in the mid-intertidal forest. These values were multiplied by the average flux rates of trunks (Table 6) to derive the nutrient exchange rates for fallen timber on a per ha basis.

***Values are 24,556 kg fresh weight of prop roots ha^{-1} in the low-intertidal forest and 92,293 kg fresh wt of prop roots ha^{-1} in the mid-intertidal forest. These values were multiplied by the average flux rates of the summed portions of prop roots (Table 7) to derive the nutrient exchange rates for prop roots on a per ha basis.

total forest area compared with 17% and 74% of total forest area within the mid- and low-intertidal zones, respectively (Alongi *et al.,* 1992). Further, nutrient release from the creek bank sediments (Table 5) may offset the rates of nutrient uptake by the high-intertidal sediments.

It is likely that net exchange processes in other mangrove systems would be different considering the lack of groundwater input and freshwater runoff into Coral Creek. In Terminos Lagoon, Mexico, Rivera-Monroy *et al.* (1995) found that a fringe mangrove forest acts as a sink of NH_4^+ and $NO_2^- + NO_3^-$ and as a source of particulate N and DON with rainfall and river discharge controlling the magnitude and direction of N flux. The net annual fluxes of inorganic nitrogen from the Mexican fringe forest were higher than those measured for Coral Creek, particularly during the rainy season, but DON fluxes were less and in a different direction. In Brazil, Ovalle *et al.* (1990) found that nutrient exchange was balanced between mangroves and coastal waters, but Wattayakorn *et al.* (1990) estimated low rates of TN and inorganic nitrogen export from the Klong Ngao mangroves in Thailand. Thong *et al.* (1993) indicated that mangrove sediments are a major source of dissolved nitrogen in Malaysian mangroves dominated by a large tidal range. However, the data are insufficient to estimate the contribution of nutrient exchange processes within mangroves to the overall nutrient budgets of these coastal systems as calculated for Coral Creek.

b. Factors controlling benthic nutrient pools and fluxes. The lack of seasonality in the benthic nutrient pools and fluxes is not surprising, considering that earlier studies found no seasonality in creek water salinity and nutrient concentrations (Boto and Wellington, 1988), and in crab (Robertson, 1986; Smith *et al.,* 1991) and benthic microbial activity (Iizumi, 1986; Alongi, 1988; Boto and Robertson, 1990) in these forests. Lack of seasonality can be attributed to a small seasonal range in temperature (Table 5). These forests do show some seasonality in rates of litterfall (Duke *et al.,* 1981), but rates of net forest primary production and photosynthesis are fairly constant during the course of the year, being more responsive (and variable) to diel changes in solar insolation and to day-to-day climate variations, such as atmospheric pressure and cloud cover, than to seasonal cues (Clough, 1992).

There was a high degree of spatial heterogeneity in the porewater pools, both with depth into the sediment and with tidal elevation to the extent that it was not possible to statistically distinguish site differences. These variations were undoubtedly due to many factors, but there are two dominant features—crabs and below-ground roots—that must account for most of the among- and within-site variation. It is plausible to suggest that these two features are the major factors regulating redox status and early diagenetic pathways that are, in turn, ultimately regulated by rates of organic matter supply (i.e., litterfall).

Recent studies (Robertson, 1986; Smith *et al.,* 1991) show that sesarmid crabs in these forests are voracious consumers of leaf litter, to the extent that leaf litter export is reduced by 30% when consumption by crabs is taken into account (Robertson, 1986). The high density of crab burrows is conspicuous in these forests. It is likely that intense bioturbation increases the microtopography of the forest floor, altering

sediment granulometry and nutrient concentrations. In a series of experiments, Smith *et al.* (1991) tested the hypothesis that reduction of the crab fauna would lead to an increase in sediment sulfide concentrations, alter nutrient levels, and decrease forest growth and productivity. They found elevated concentrations of porewater sulfides and NH_4^+ in crab removal plots compared with controls. No differences were found for porewater PO_4^{3-} and $NO_2^- + NO_3^-$, but forest growth was less in the removal plots. Moreover, trees in the removal plots had significantly less reproductive output than trees in control plots. Smith *et al.* (1991) hypothesized that the burrowing activities of grapsid crabs stimulates sediment turnover, affecting some nutrients and thus creating a sediment milieu suitable for the growth and production of *Rhizophora.*

The presence of below-ground roots may also regulate sediment redox and nutrient pools. Several studies have found that redox status and sulfide concentrations are frequently correlated with the presence of mangrove roots and rhizomes (Carlson *et al.,* 1983; Andersen and Kristensen, 1988; McKee *et al.,* 1988; Kristensen *et al.,* 1991). Several workers (Boto and Wellington, 1984; Alongi, 1988; Kristensen *et al.,* 1991) have found that most mangrove sediments are anoxic, but rarely sulfidic. Such appears to be the case in the Hinchinbrook Island sediments where redox varies greatly among replicate cores with sediment depth and season at each site. Differences between the creek bank and mangrove sediments were not significantly different in most seasons (Fig. 2), despite the fact that mangroves translocate oxygen to their roots. Few redox readings were more negative than −150 mV and many were positive, despite the fact that these sediments are silt-dominated and carbon-rich. Free sulfide concentrations in these sediments are extremely patchy, ranging from 35–130 μM with a mean of ~50 μM (Smith *et al.,* 1991). These values are at the low end of the range compared with salt marsh and other organic-rich sediments (Bradley and Morris, 1990; Howarth, 1993). Kristensen *et al.* (1991) ascribed the anoxic, but non-sulfidic, state of mangrove sediments in Thailand to crab bioturbation and the translocation of dissolved organic matter and gases via the roots. Similar to this study, they found a high degree of variation between replicate cores which they attributed to the patchiness of crab burrows and below-ground root biomass.

Redox state as affected by below-ground roots and crab bioturbation may in turn affect adsorption capacity of porewater constituents (Boto, 1992). The adsorption experiments described here indicate that NH_4^+ adsorption was low compared with other marine sediments (Rosenfeld, 1979; Mackin and Aller, 1984), but that PO_4^{3-} adsorption was a significant retention factor limiting P availability. The adsorption coefficient (K) for NH_4^+ ranged from a low of 0.17 on the creek bank to a maximum of 0.47 in the mid-intertidal sediments. In other marine sediments, K typically ranges from 1.0–1.7 (Mackin and Aller, 1984). The low adsorption capacity of NH_4^+ in mangrove sediments may be attributed to low sediment porosity, density, and cation exchange capacity (Boto, 1992), and to low adsorption capacity of roots and rhizomes

(Clough *et al.,* 1983). In comparison, PO_4^{3-} adsorption was high, with K ranging from a low of 0.8 in the creek bank to significantly higher values (3–5) in the mangrove sediments. Krom and Berner (1980) indicated that in anoxic sediments, K for PO_4^{3-} is ~1–2, much lower than in post-oxic and oxic sediments because iron oxides (important in PO_4^{3-} adsorption in oxic sediments) are converted to iron sulfides in anoxic deposits.

Below-ground roots (at least to 63 μm in size and to a depth of 20 cm) account for most of the total organic carbon and a significant fraction of the total particulate nitrogen and phosphorus pools in these sediments. Estimates were made of the percentage of bulk sediment C, N and P accounted for by below-ground biomass (see Methods section *b*). In the low-intertidal forest, root and rhizomes account for 66–100% of bulk sediment TOC, 24–40% of total N, and 9–15% of total P. In the mid-intertidal, below-ground biomass accounts for 89–93% of TOC, 48–49% of total N and 39–40% of total P. Root biomass accounts for 59–65% of bulk sediment TOC, 29–31% of total N and 27–28% of total P in the high-intertidal forest. Averaging sites, mean percentages were 78.5% of sediment TOC, 36.9% of total N and 26.1% of total P. These pools vary little over time or with sediment depth implying little change in below-ground biomass. Seasonal change in root biomass is minimal and more likely to vary spatially as a function of tree density than over time in these forests (Robertson, pers. comm.).

The significant contribution of roots to the bulk sediment nutrient pools may explain the highly skewed C:N:P ratios of from 392:13:1 in the low-intertidal to 1291:34:1 at the high-intertidal site. C:N:P stoichiometry in sediments is rarely in agreement with the theoretical Redfield ratio of 106:16:1, but these ratios are greatly different compared to other marine sediments (Tyson, 1994). The contribution of roots is evident considering that the C:N:P ratio of roots is 2744:35:1, and that the mean ratio in creek bank sediments is less than in mangrove sediments. In these forests, Boto and Wellington (1984) found that organic matter constitutes ~30% of the dry weight of the sediment over the top 40 cm, and that 80% of root biomass is contained in the top m, with significant quantities of roots to a depth of 2 m. The high proportion of root and woody material also explains the low porosity and dry sediment densities (Table 3) of these sediments. Low density and porosity values have been measured in other organic-rich, mangrove sediments (Kristensen *et al.,* 1991).

Differences in the size of the porewater pools are also dependent on tree growth and on rates of microbial activity, representing a balance between mineralization and assimilation (Boto *et al.,* 1985; Alongi *et al.,* 1993; Nedwell *et al.,* 1994). The smaller size of the NH_4^+ pool in the mangrove sediments compared with in the creek bank can be attributed to uptake by mangroves (Boto *et al.,* 1985; Clough, 1992). Microbially-mediated processes such as nitrification, nitrogen fixation, denitrification, and ammonification result in the production or loss of porewater solutes and gases, but these processes have rarely been measured in mangrove sediments

(Wiebe, 1989; Nedwell *et al.,* 1994). A model of nitrogen cycling within the Hinchinbrook sediments (Alongi *et al.,* 1992) indicates that ammonification and production of DON are major N processes compared with denitrification. The cycling of P and Si is unknown in these sediments, but the consistent uptake of PO_4^{3-}, the rapid rates of Si flux, and the per ha estimates of PO_4^{3-} and $Si(OH)_4^+$ exchange, suggest similarly rapid P and Si cycling.

The consistent uptake of nitrite and nitrate across the sediment-water interface, and by prop roots and fallen timber, represent either the first stages of denitrification ($NO_3^- \rightarrow N_2O$ and N_2), nitrate respiration ($NO_3^- \rightarrow NH_4^+$), uptake by autotrophs (sediment microalgae, algae on prop roots and timber) or immobilization in detritus (Rice and Hanson, 1984). There is little or no microalgae on the surface of these muds and no net primary production (Alongi, 1994). Several other studies have similarly observed uptake of nitrate from the overlying water to the sediments, but in all cases, the uptake was ascribed to assimilation by microalgae (Alongi *et al.,* 1993; Morell and Corredor, 1993). Fluxes of DON and DOP were also frequently into the sediment, but possible reasons are problematic given that these pools consist of unknown and complex mixtures of organic compounds (Stanley *et al.,* 1987). The uptake of DIN by the prop roots and timber agrees well with the nitrogen fixation study of Boto and Robertson (1990) suggesting that algae and other flora colonizing the surfaces of prop roots and timber are actively growing and assimilating nutrients from the tidal water.

In conclusion, it is apparent that while a large proportion of the solid-phase nutrients are tied up in below-ground biomass, the dissolved nutrient pools and flux rates are closely linked to plant assimilation mechanisms and to mineralization processes by microbes. These nutrient cycling processes are highly dynamic and rapid, leading to net import of dissolved N, P and Si to the extent that mangrove forests are a finely balanced and highly efficient sink for dissolved nutrients in this tropical coastal ecosystem.

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REFERENCES

Alongi, D. M. 1988. Bacterial productivity and microbial biomass in tropical mangrove sediments. Microb. Ecol., *15,* 59–79.

—— 1989. The fate of bacterial biomass and production in marine benthic food chains, *in* Recent Advances in Microbial Ecology, T. Hattori, Y. Ishida, Y. Maruyama, R. Y. Morita and A. Achida, eds., Japan Sci. Soc. Press, Toyko, 35–359.

—— 1994. Zonation and seasonality of benthic primary production and community respiration in tropical mangrove forests. Oecologia, *98,* 320–327.

Alongi, D. M., K. G. Boto and A. I. Robertson. 1992. Nitrogen and phosphorus cycles, *in* Tropical Mangrove Ecosystems, A. I. Robertson and D. M. Alongi, eds., Am. Geophys. Union, Washington D.C., 251–292.

Alongi, D. M., P. Christoffersen and F. Tirendi. 1993. The influence of forest type on microbial-nutrient relationships in tropical mangrove sediments. J. Exp. Mar. Biol. Ecol., *171,* 201–223.

Andersen, F. O. and E. Kristensen. 1988. Oxygen microgradients in the rhizosphere of the mangrove *Avicennia marina.* Mar. Ecol. Prog. Ser., *44,* 201–204.

Boto, K. G. 1992. Nutrients and mangroves, *in* Pollution in Tropical Aquatic Systems, D. W. Connell and D. W. Hawker, eds., CRC Press, Boca Raton, 129–145.

Boto, K. G., D. M. Alongi and A. J. L. Nott. 1989. Dissolved organic carbon-bacteria interactions at sediment-water interface in a tropical mangrove system. Mar. Ecol. Prog. Ser., *51,* 243–251.

Boto, K. G. and J. S. Bunt. 1981. Tidal export of particulate organic matter from a northern Australian mangrove system. Estuar. Coast. Shelf Sci., *13,* 247–255.

Boto, K. G. and A. I. Robertson. 1990. The relationship between nitrogen fixation and tidal exports of nitrogen in a tropical mangrove system. Estuar. Coast. Shelf Sci., *31,* 531–540.

Boto, K. G., P. Saffigna and B. F. Clough. 1985. Role of nitrate in the nitrogen nutrition of the mangrove *Avicennia marina.* Mar. Ecol. Prog. Ser., *21,* 259–265.

Boto, K. G. and J. T. Wellington. 1983. Phosphorus and nitrogen nutritional status of a northern Australian mangrove forest. Mar. Ecol. Prog. Ser., *11,* 63–69.

—— 1984. Soil characteristics and nutrient status in northern Australian mangrove forests. Estuaries, *7,* 61–69.

—— 1988. Seasonal variations in concentrations and fluxes of dissolved organic and inorganic material in a tropical, tidally-dominated, mangrove waterway. Mar. Ecol. Prog. Ser., *50,* 151–160.

Bradley, P. M. and J. T. Morris. 1990. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora.* Ecology, *71,* 282–287.

Bunt, J. S., K. G. Boto and G. Boto. 1979. A survey method for estimating potential levels of mangrove forest primary production. Mar. Biol., *52,* 123–128.

Bunt, J. S. and W. T. Williams. 1980. Studies in the analysis of data from Australian tidal forests ('mangroves'). I. Vegetational sequences and their graphical representation. Aust. J. Ecol., *5,* 385–390.

Carlson, P. R., L. A. Yarbro, C. F. Zimmermann and J. R. Montgomery. 1983. Porewater chemistry of an overwash mangrove island. Florida Sci., *46,* 239–249.

Clough, B. F. 1992. Primary productivity and growth of mangrove forests, *in* Tropical Mangrove Ecosystems, A. I. Robertson and D. M. Alongi, eds., Am. Geophys. Union, Washington, D.C., 225–249.

Clough, B. F., K. G. Boto and P. M. Attiwill. 1983. Mangrove and sewage: a re-evaluation, *in* Biology and Ecology of Mangroves, Tasks for Vegetation Science 8, H. J. Teas. ed., Dr. W. Junk, The Hague, 151–161.

Clough, B. F., J. E. Ong and G. W. Gong. 1995. Estimating leaf area index and photosynthetic production in mangrove forest canopies. Oecologia (submitted).

Clough, B. F. and K. Scott. 1989. Allometric relationships for estimating above-ground biomass in six mangrove species. Forest Ecol. Man., *27,* 117–127.

Duke, N. C., J. S. Bunt and W. T. Williams. 1981. Mangrove litterfall in northeastern Australia. I. Annual totals by component species. Aust. J. Bot., *29,* 547–553.

Hemminga, M. A., F. J. Slim, J. Kazunga, G. M. Ganssen, J. Nieuwenhuize and N. M. Kruyt. 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). Mar. Ecol. Prog. Ser., *106,* 291–301.

Howarth, R. W. 1993. Microbial processes in salt-marsh sediments, *in* Aquatic Microbiology, T. E. Ford, ed., Blackwell Scientific Publications, Boston, 239–259.

Iizumi, H. 1986. Soil nutrient dynamics, *in* Workshop on Mangrove Ecosystem Dynamics, S. Cragg and N. Polunin, eds., UNDP/UNESCO Regional Project RAS/79/002, New Delhi, 171–180.

Kristensen, E., M. Holmer and N. Bussarawit. 1991. Benthic metabolism and sulfate reduction in a south-east Asian mangrove swamp. Mar. Ecol. Prog. Ser., *73,* 93–103.

Krom, M. D. and R. A. Berner. 1980. Adsorption of phosphate in anoxic marine sediments. Limnol. Oceanogr., *25,* 797–806.

Mackin, J. E. and R. C. Aller. 1984. Ammonium adsorption in marine sediments. Limnol. Oceanogr., *29,* 250–257.

McKee, K. L., I. A. Mendelssohn and M. W. Hester. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans.* Am. J. Bot., *75,* 1352–1359.

Morell, J. M. and J. E. Corredor. 1993. Sediment nitrogen trapping in a mangrove lagoon. Estuar. Coast. Shelf Sci., *37,* 203–212.

Nedwell, D. B., T. H. Blackburn and W. J. Wiebe. 1994. Dynamic nature of the turnover of organic carbon, nitrogen and sulphur in the sediments of a Jamaican mangrove forest. Mar. Ecol. Prog. Ser., *110,* 223–231.

Ovalle, A. R. C., C. E. Rezende, L. D. Lacerda and A. A. R. Silva. 1990. Factors affecting the hydrochemistry of a mangrove tidal creek, Sepetiba Bay, Brazil. Estuar. Coast. Shelf Sci., *31,* 639–650.

Rice, D. L. and R. B. Hanson. 1984. A kinetic model for detritus nitrogen: role of the associated bacteria in nitrogen accumulation. Bull. Mar. Sci., *35,* 326–340.

Rivera-Monroy, V. H., J. D. Day, R. R. Twilley, F. Vera-Herrera and C. Coronado-Molina. 1995. Flux of nitrogen and sediment in a fringe mangrove forest in Terminos Lagoon, Mexico. Estuar. Coast. Shelf Sci., *40,* 139–160.

Robbins, J. A. and J. Gustinis. 1976. A squeezer for efficient extraction of pore water from small volumes of anoxic sediment. Limnol. Oceanogr., *21,* 905–909.

Robertson, A. I. 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. J. Exp. Mar. Biol. Ecol., *102,* 237–248.

Robertson, A. I. and D. M. Alongi. (eds.) 1992. Tropical Mangrove Ecosystems. Am. Geophys. Union, Washington, D.C., 329 pp.

—— 1996. The role of riverine mangrove forests in carbon flux to the tropical ocean: a preliminary mass balance for the Fly Delta. Geo-Mar. Lett., (in press).

Robertson, A. I. and P. A. Daniel. 1989. Decomposition and the annual flux of detritus from fallen timber in tropical mangrove forests. Limnol. Oceanogr., *34,* 640–646.

Rosenfeld, J. K. 1979. Ammonium adsorption in nearshore anoxic sediments. Limnol. Oceanogr., *24,* 356–364.

Ryle, V. D., H. R. Mueller and P. Gentien. 1981. Automated analysis of nutrients in tropical seawater. Aust. Inst. Mar. Sci. Oceanogr. Ser., OS-81-4, 24 pp.

Ryle, V. D. and J. T. Wellington. 1982. Reduction column for automated determination of nitrates. Analytical Lab Note No. 19, Aust. Inst. Mar. Sci., Townsville, 3 pp.

Sandstrom, M. W., F. Tirendi and A. Nott. 1986. Direct determination of organic carbon in modern reef sediments and calcareous organisms after dissolution of carbonate. Mar. Geol., *70,* 321–329.

Smith III, T. J., K. G. Boto, S. D. Frusher and R. L. Giddins. 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. Estuar. Coast. Shelf Sci., *33,* 419–432.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, 859 pp.

Spain, A. V. and J. A. Holt. 1980. The elemental status of the foliage and branchwood of seven mangrove species from northern Queensland. Division of Soils Divisional Report No. 49, CSIRO, Australia, 8 pp.

Stanley, S. O., K. G. Boto, D. M. Alongi and F. T. Gillan. 1987. Composition and bacterial utilization of free amino acids in tropical mangrove sediments. Mar. Chem., *22,* 13–30.

Thong, K. L., A. Sasekumar and N. Marshall. 1993. Nitrogen concentrations in a mangrove creek with a large tidal range. Hydrobiol., *254,* 125–132.

Twilley, R. R. 1985. The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. Estuar. Coast. Shelf Sci., *20,* 543–557.

Twilley, R. R., A. E. Lugo and C. Patterson-Zucca. 1986. Litter production and turnover in basin mangrove forests in southwest Florida. Ecology, *67,* 670–683.

Tyson, R. V. 1994. Sedimentary Organic Matter. Chapman and Hall, London, 544 pp.

Wattayakorn, G., E. Wolanski and B. Kjerfve. 1990. Mixing, trapping and outwelling in the Klong Ngao mangrove swamp, Thailand. Estuar. Coast. Shelf Sci., *31,* 667–688.

Wiebe, W. J. 1989. Phosphorus, sulfur, and nitrogen cycles in mangrove forests, *in* Recent Advances in Microbial Ecology, T. Hattori, Y. Ishida, Y. Maruyama, R. Y. Morita, and A. Uchida, eds., Japan Sci. Soc. Press, Tokyo, 312–317.

Wolanski, E. and R. Gardiner. 1981. Flushing of salt from mangrove swamps. Aust. J. Mar. Freshwat. Res., *32,* 681–683.

Wolanski, E., M. Jones and J. S. Bunt. 1980. Hydrodynamics of a tidal creek-mangrove swamp system. Aust. J. Mar. Freshwat. Res., *31,* 431–450.

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