

## Seasonal variations in uptake and in situ regeneration of nitrogen in mangrove waters

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### Abstract

Seasonal changes of uptake of nitrogenous nutrients ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ , and urea) and regeneration ( $\text{NH}_4^+$  and  $\text{NO}_2^-$  production) in the plankton fraction of a mangrove ecosystem on the west coast of India were investigated. Nitrate was the major fraction of assimilable N (72%), followed by  $\text{NH}_4^+$  (16%),  $\text{NO}_2^-$  (6%), and urea (6%). Changes of nutrient concentrations followed clear seasonal cycles and were mainly regulated by in situ biological processes. The plankton took up  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in more or less equal proportions (39 and 44% respectively), followed by urea (11%) and  $\text{NO}_2^-$  (6%). Seasonal patterns of uptake were distinct, with a dominance of  $\text{NO}_3^-$  and  $\text{NO}_2^-$  uptake in the postmonsoon, followed by a dominance of  $\text{NH}_4^+$  and urea uptake in the premonsoon. The high and prolonged use of  $\text{NO}_3^-$  at the beginning of the productive season was due to a strong allochthonous supply of  $\text{NO}_3^-$ , dominance of microplankton, and low  $\text{NH}_4^+$  regeneration rates. Heterotrophs may take up all four nutrients and could account for half of the annual total N uptake. Ammonium and  $\text{NO}_2^-$  regeneration rates were among the highest known from nearshore waters and showed clear seasonal patterns. Production and use of  $\text{NH}_4^+$  were closely coupled. Nitrite production rates were related to  $\text{NH}_4^+$  production rates in a rectangular-hyperbolic fit. Nitrogen balance analyses showed that proximity to mangrove vegetation enhanced the flux rates, noninclusion of nitrification may lead to an overestimation of new production by 30%, and regeneration in the plankton fraction provided about 40% more N than was assimilated.

Since the demonstration that  $^{15}\text{N}$  is a sensitive tracer for measuring rates of nitrogen transformations in biological systems (Neess et al. 1962) and the postulation of the concepts of new and regenerated production (Dugdale and Goering 1967), there has been an increased interest in quantifying N fluxes in the marine environment. In the last three decades, the uptake of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ , representing the major fractions of new and regenerated N, has been investigated using  $^{15}\text{N}$  in a number of instances (*see* Dortch 1990). The ability to separate the new production fraction from the total production finds application in assessment of export of C and N to the deep sea (Eppley and Peterson 1979) and in models of biogeochemical cycles of N in the sea (Platt et al. 1991). The other component, regenerated production, is a useful indicator of ecological efficiency—under conditions of low new N fluxes, the ability of an ecosystem to sustain high levels of biological production depends entirely on the rates of internal recycling of N. This would be particularly true of tropical waters that, as a general rule, have low levels of ambient nitrogenous nutrients at any time of the year (Qasim and Wafar 1990).

A rough estimate from the data of Longhurst et al. (1995) shows that tropical waters account for between 20 and 40% of global marine primary production. Nevertheless, with a few exceptions, almost all studies on N uptake carried out so far are from high-latitude ecosystems (Wafar et al. 1995). The imbalance is still more marked with high-productivity

ecosystems such as coral reefs and mangroves. Both are structurally and functionally among the more complex coastal marine ecosystems (Qasim and Wafar 1990) and together account for more than 10% of global coastal primary production (Longhurst et al. 1995); yet studies on N cycles are few in coral reefs and nonexistent in mangroves.

In an earlier study on a mangrove ecosystem from the central west coast of India (Wafar et al. 1997), a model for prediction of litter fall was constructed and elemental flux, as C, N, and P, from mangrove vegetation to the aquatic food chain was quantified. Their study also showed that most of the terrestrial production ends up in mangrove waters. While this was important for sustaining the microbial food chain and nutrient regeneration in the water column, it was still inadequate for the N budget of the latter. The nitrogenous nutrition of the phytoplankton in mangrove waters, in order to agree with the high productivity generally ascribed to them, therefore, would have to depend on a strong supply of new N or rapid in situ N recycling. The present study was designed to examine this, by measuring over a seasonal cycle the uptake rates of the major assimilable N forms ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ , and urea) and in situ regeneration of  $\text{NH}_4^+$  and  $\text{NO}_2^-$ .

### Material and methods

The study site was an undisturbed mangrove forest of about 300 ha on the central west coast of India ( $16^\circ 12' - 16^\circ 14' \text{N}$ ;  $73^\circ 25' - 73^\circ 30' \text{E}$ ), fed by a small river and connected with the Arabian Sea by a single channel (Fig. 1). The study area experiences a monsoon climate; thus, the traditional seasonal breakup is into monsoon (June–September), postmonsoon (October–January), and premonsoon (February–May). Monsoon is characterized by heavy rainfall (2,500–3,000 mm), postmonsoon by dry and relatively cool climate and premonsoon by dry, hot, and humid conditions.

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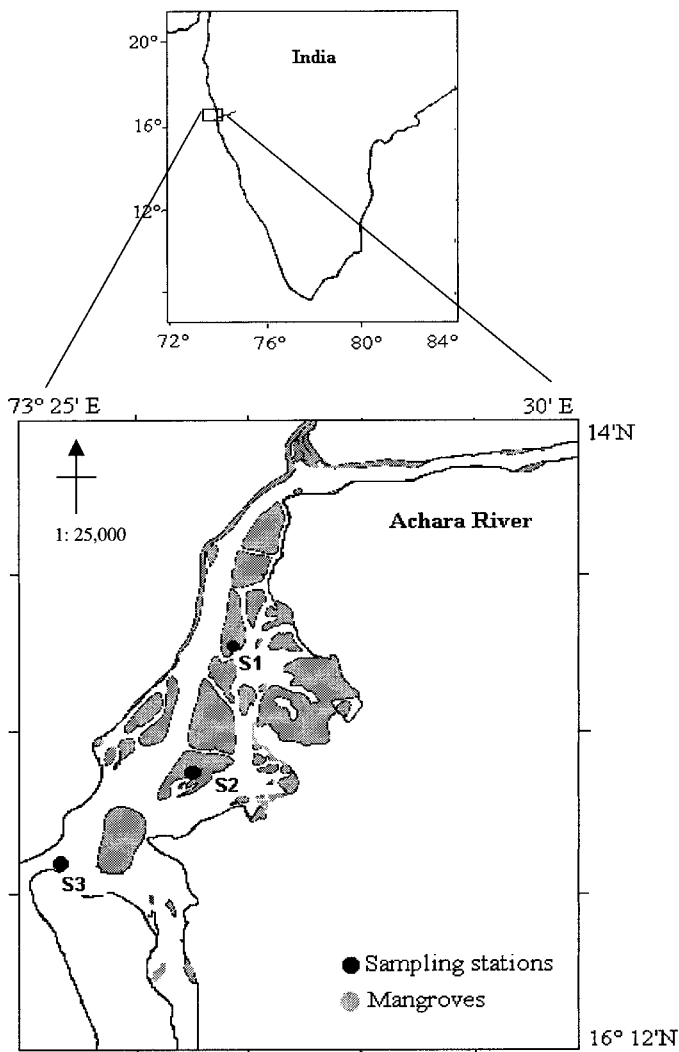


Fig. 1. Location of the Achara mangrove and the sampling stations.

The three sampling stations (Fig. 1) represent a gradient in mangrove vegetation, from dense (1) through moderate (2) to sparse (3). The mean depths of the water column at the three stations were 1.8, 2.1, and 2.7 m, respectively. Because of this shallowness and the tidal mixing, the water column at all stations remained vertically homogeneous throughout the year.

Water samples were collected from the surface and used for various analyses. Sampling at the three stations was done on three consecutive days during midtide. In each instance, collections began at between 0700 and 0800 h so that incubation for N uptake measurements could be started 2 h before local noon. The study period was from February 1997 to June 1998, with sampling at monthly intervals.

Temperature was measured with a laboratory thermometer (precision: 0.1°C). Salinity was calculated from the conductivity ratios measured in a Guildline Autosal model 8400A Salinometer. Concentrations of  $\text{NO}_3^-$  (Wood et al. 1967),  $\text{NO}_2^-$  (Bendschneider and Robinson 1952),  $\text{NH}_4^+$  (Koroleff 1970), and urea (Aminot and Kerouel 1982) were measured

in a Jasco ultraviolet/visible double beam spectrophotometer (2-nm band width), with analytical precisions respectively of  $\pm 0.1$ ,  $\pm 0.01$ ,  $\pm 0.05$ , and  $\pm 0.01 \mu\text{mol N L}^{-1}$ .

Particulate matter separated on preignited Whatman GF/F filter pads was used for determination of chlorophyll *a* (Chl *a*) by spectrophotometry (Strickland and Parsons 1972) and particulate organic nitrogen (PON) by the Kjeldahl method. In the latter case, titration of acid used to trap the steam-distilled  $\text{NH}_4^+$  with standard alkali was done with a micro-processor controlled Metrohm Dosimat-665 unit. Calibrations with standards gave an analytical precision of  $\pm 0.15 \mu\text{mol N}$ , comparable to that obtained with a CHN analyzer ( $\pm 0.1 \mu\text{mol N}$ ). Phytoplankton cells in acid-Lugol preserved samples were counted with an inverted microscope.

Samples for N uptake measurements were prefiltered through 200  $\mu\text{m}$  Nyltex net, transferred to 500-ml glass bottles, to which were added  $\text{Na}^{15}\text{NO}_3$ ,  $\text{Na}^{15}\text{NO}_2$ ,  $^{15}\text{NH}_4\text{Cl}$ , and  $\text{CO}$  ( $^{15}\text{NH}_3$ )<sub>2</sub> (97.4 atom percentage enrichment for  $\text{NO}_3^-$  and 95% for the other three—KOR isotopes, USA) at concentrations not more than 10% of the ambient. The bottles were placed in large troughs filled with seawater and incubated for 4 h under in situ conditions. The temperature was maintained at ambient by frequent change of seawater. Incident light on the incubation bottles was measured at hourly intervals during the incubation period using a LiCor photometer. At the end of the incubation, the particulate matter was recovered on preignited Whatman GF/F filter pads. All filtrations, including those for recovery of particulate matter for Chl *a* and PON measurements, were done under low vacuum.

Regeneration of  $\text{NH}_4^+$  was measured by the isotope dilution technique (Glibert et al. 1982). Ammonium from the filtrate of the samples used for measurements of  $\text{NH}_4^+$  uptake was recovered by diffusion in basic pH (Kristiansen and Paasche 1989). Nitrification rates were measured by oxidation of  $^{15}\text{NH}_4^+$  in dark incubations. The  $\text{NO}_2^-$  for measurements of isotope ratios was extracted following the method described by Schell (1978).

$^{15}\text{N}:^{14}\text{N}$  isotope ratios of the particulate matter,  $\text{NH}_4^+$  extracted from the filtrate, and the  $\text{NO}_2^-$  extracted from the incubation medium were measured by emission spectrometry using a Jasco N-150 Nitrogen analyzer. As the PON was measured in a sample different from that incubated with  $^{15}\text{N}$ , the transport rate reported here is a product of specific uptake rate and initial PON concentration. Ammonium regeneration rates were calculated with either the equation of Laws (1984) or that of Glibert et al. (1982) depending on whether or not the  $\text{NH}_4^+$  concentrations in the medium changed measurably during the course of the incubation. Nitrification rates were calculated in the same way as for specific and absolute transport rates measured with  $^{15}\text{N}$  enriched nutrients (Lipschultz 1984).

All measurements were done in triplicate. As the standard deviations were less than 10% of the average at any time, only the latter are reported. The model II regression analysis was used throughout.

## Results

*Environmental parameters*—The monsoon-driven nature of the seasonality of environmental factors is reflected more

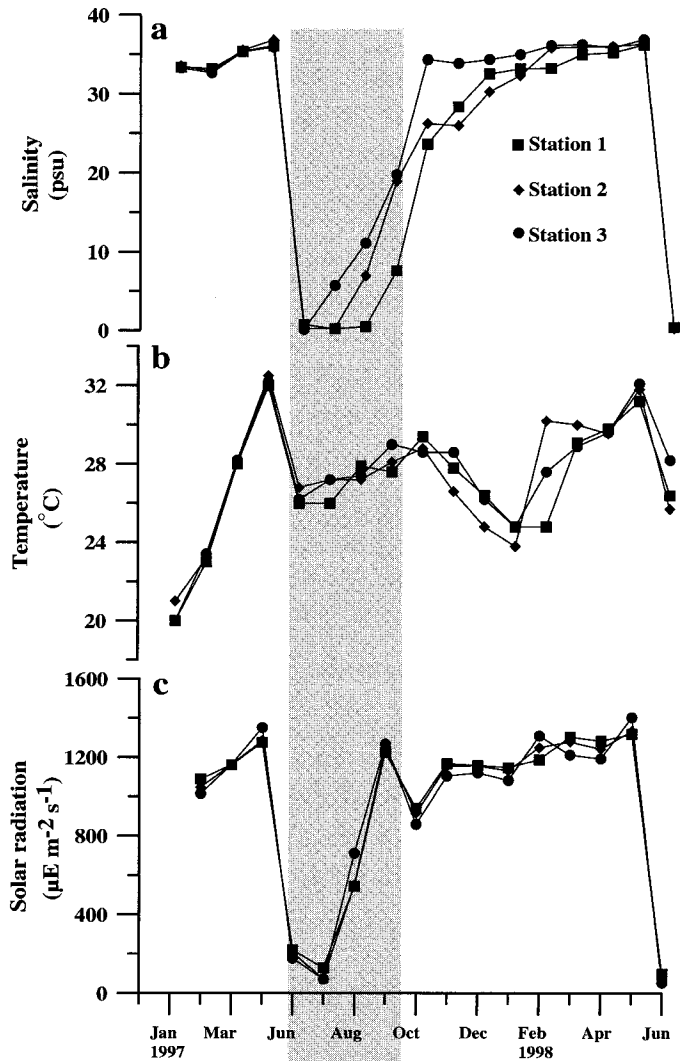


Fig. 2. Seasonal variations of (a) salinity, (b) temperature, and (c) incident solar radiation at stations 1, 2, and 3.

strongly in salinity (0–36) and incident light ( $<100\text{--}1,300 \mu\text{E m}^{-2} \text{s}^{-1}$ ) than in water temperature (20–32.5°C) (Fig. 2). The gradient in temperature between the stations was generally less than a degree or two, reflecting the diel variations. The salinity gradient ( $<1\text{--}10$ ) varied in a cyclic manner, with low gradients reflecting the dominance of seawater in summer and freshwater at the onset of the monsoon and the large ones, from the late monsoon through postmonsoon, an estuarine character.

**Nutrients**—Seasonal variations of  $\text{NO}_3^-$  concentrations (0.4–19.6  $\mu\text{mol N L}^{-1}$ ; average, 4.5  $\mu\text{mol N L}^{-1}$ ) at all stations were well defined (Fig. 3a), with a monsoon average (9.0  $\mu\text{mol N L}^{-1}$ ) four times higher than, and statistically different ( $F_{2,48} = 30.5$ ;  $p < 0.01$ ) from, that of the dry season ( $\sim 2 \mu\text{mol N L}^{-1}$ ). Spatial differences were, however, insignificant, with annual averages at the three stations lying between 4.1 and 4.7  $\mu\text{mol N L}^{-1}$ . Nitrite was present in measurable concentrations (0.03–0.8  $\mu\text{mol N L}^{-1}$ ; average, 0.2  $\mu\text{mol N L}^{-1}$ ) throughout the year and had a pattern of sea-

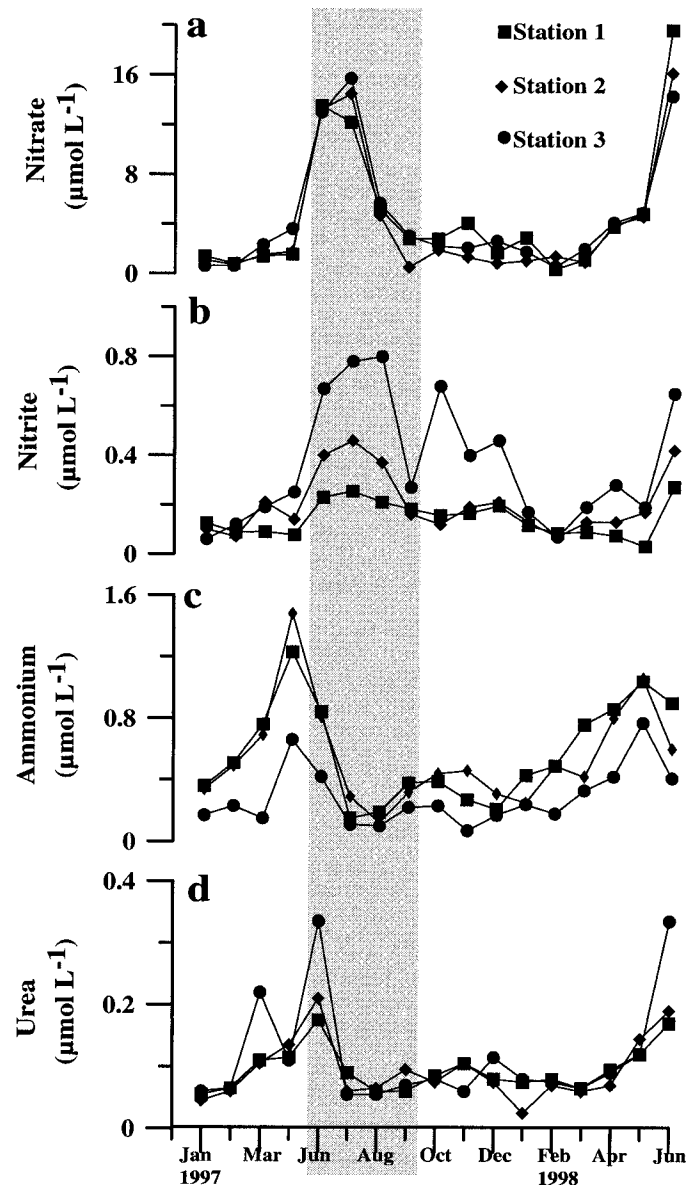


Fig. 3. Seasonal changes of concentrations of (a) nitrate, (b) nitrite, (c) ammonium, and (d) urea concentrations at stations 1, 2, and 3.

sonal change similar to that of  $\text{NO}_3^-$  (Fig. 3b), with a monsoon average of 0.4  $\mu\text{mol N L}^{-1}$  that was significantly higher than those of premonsoon and postmonsoon (0.1 and 0.2  $\mu\text{mol N L}^{-1}$ , respectively) seasons. Unlike the  $\text{NO}_3^-$ , however, spatial variations of  $\text{NO}_2^-$  were significant, with higher concentrations at the seaward station.

The pattern of seasonal changes of  $\text{NH}_4^+$  concentrations (0.1–1.5  $\mu\text{mol N L}^{-1}$ ; average, 0.5  $\mu\text{mol N L}^{-1}$ ) (Fig. 3c) was different from those of  $\text{NO}_3^-$  and  $\text{NO}_2^-$ , with a premonsoon high (average, 0.7  $\mu\text{mol N L}^{-1}$ ) decreasing through the monsoon (0.4  $\mu\text{mol N L}^{-1}$ ) and postmonsoon (0.3  $\mu\text{mol N L}^{-1}$ ) seasons. As expected with this nonconservative behavior, variations in  $\text{NH}_4^+$  concentrations between stations were significant ( $F_{2,48} = 5.1$ ;  $p < 0.05$ ). The pattern of changes of urea concentrations (0.05–0.35  $\mu\text{mol N L}^{-1}$ ) (Fig. 3d) was

Table 1. Average uptake rates ( $\text{nmol N L}^{-1} \text{ h}^{-1}$ ) of the four forms of nitrogen in the Achara mangrove (range in parentheses).

Station	$\text{NO}_3^-$	$\text{NH}_4^+$	$\text{NO}_2^-$	Urea
1	144 (13–386)	368 (8–1,194)	21 (5–94)	14.5 (0–31.5)
2	100 (10–274)	235 (4–822)	19 (4–44)	13 (0.1–31.5)
3	58 (1.8–125)	29 (5–80)	6 (1–13)	9 (0–42.5)

similar to that of  $\text{NH}_4^+$  except that the peak was in June instead of May. The seasonal as well as spatial variations, however, were not statistically significant.

Nitrate was the major fraction ( $71 \pm 18\%$ ) of assimilable N at any time of the year, followed by  $\text{NH}_4^+$  ( $16 \pm 13\%$ ), urea ( $6 \pm 4\%$ ), and  $\text{NO}_2^-$  ( $6 \pm 4\%$ ).

**PON, Chl *a* and cell counts**—PON concentrations were substantially higher in the monsoon (average,  $121.9 \mu\text{mol N L}^{-1}$ ) than in the dry season (averages of  $48.9$  and  $44.2 \mu\text{mol N L}^{-1}$ , respectively, in premonsoon and postmonsoon months) (Fig. 4a). The spatial gradient also was significant: PON concentrations were highest ( $85.8 \pm 43.6 \mu\text{mol N L}^{-1}$ ) at Sta. 1 and decreased seaward ( $72.5 \pm 36.7$  and  $48.6 \pm 51.6 \mu\text{mol N L}^{-1}$  at the next two stations).

Unlike the PON, Chl *a* concentrations ( $0.1$ – $21.6 \mu\text{g L}^{-1}$ ) were higher in the dry months ( $9.8$  and  $10 \mu\text{g L}^{-1}$ , respectively, in premonsoon and postmonsoon seasons) than in the wet season ( $4.2 \mu\text{g L}^{-1}$ ) (Fig. 4b). Variations in Chl *a* concentrations between the stations were also less marked. Nanoplankton ( $20$ – $1 \mu\text{m}$ ) were the major contributors to Chl *a* in premonsoon and monsoon months ( $66$  and  $76\%$  respectively), whereas microplankton ( $200$ – $20 \mu\text{m}$ ) accounted for  $81\%$  of the Chl *a* in the postmonsoon.

Consistent with the changes of Chl *a*, the phytoplankton cell counts were higher in the dry months (averages of  $559 \times 10^3$  and  $626 \times 10^3 \text{ cells L}^{-1}$ , respectively, in premonsoon and postmonsoon months) than during the monsoon (average of  $232 \times 10^3 \text{ cells L}^{-1}$ ). In general, diatoms were the major group of phytoplankton ( $58.8\%$ ), followed by dinoflagellates ( $21.1\%$ ), blue-green algae ( $19.6\%$ ), and coccolithophores ( $0.5\%$ ). Among the species that were present in significant numbers, the nitrogen-fixing *Trichodesmium erythraeum* is of particular interest: it occurred in bloom proportions ( $7$ – $10 \times 10^5 \text{ cells L}^{-1}$ ) in May and was responsible for the premonsoon peak.

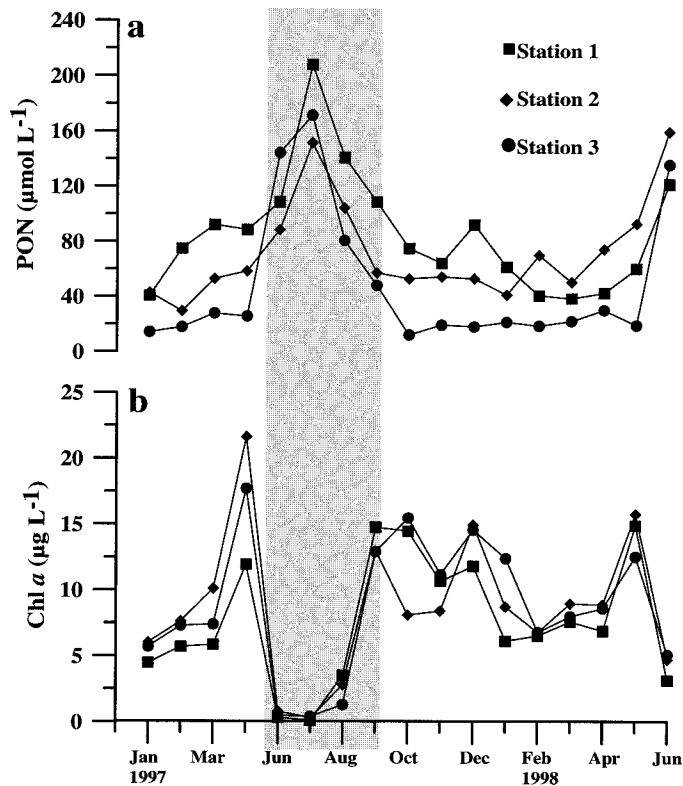


Fig. 4. Seasonal changes of concentrations of (a) particulate organic nitrogen and (b) Chl *a* at stations 1, 2, and 3.

**N uptake rates**—Annual averages (Table 1) show that  $\text{NH}_4^+$  was the major form of N taken up within the mangrove zone (stations 1 and 2) followed by  $\text{NO}_3^-$ , urea, and  $\text{NO}_2^-$ . At these two stations, uptake of regenerated N accounted for more than two-thirds of the total N uptake. At the seaward station, however, uptake of  $\text{NO}_3^-$  exceeded that of  $\text{NH}_4^+$  by almost a factor of two. Variations in rates of uptake of  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , and  $\text{NO}_2^-$  between the three stations were statistically significant ( $F_{2,45}$  for  $\rho\text{NO}_3^-$  3.53,  $p < 0.05$ ;  $F_{2,45}$  for  $\rho\text{NH}_4^+$  6.93,  $p < 0.01$ ;  $F_{2,45}$  for  $\rho\text{NO}_2^-$  4.93,  $p < 0.01$ ).

Within the annual cycle, uptake rates of all four nutrients varied through an order of magnitude or more (Table 1), entraining substantial seasonality. They were lowest in the case of all four nutrients during the monsoon, but the patterns of subsequent changes were not similar (Fig. 5). Im-

Table 2. Summary of regression analyses of uptake rates versus Chl *a*.

N nutrient	Intercept	Slope (95% CI)	Average uptake ( $\text{nmol N L}^{-1} \text{ h}^{-1}$ )	Heterotrophic uptake as % of average uptake
$\text{NO}_3^-$ (low uptake)	23.0	2.9 (1.2, 4.5)	44	52
$\text{NO}_3^-$ (high uptake)	49.0	18.4 (6.3, 30.3)	223	22
$\text{NH}_4^+$ (low uptake)	21.3	4.8 (0.5, 9.4)	59	36
$\text{NH}_4^+$ (high uptake)	44.4	31.6 (16, 88)	356	12
$\text{NO}_2^-$ (at Sta. 1)	4.6	1.6 (0.2, 3.2)	16	29
Urea (at Sta. 1)	4.6	1.3 (0.15, 2.45)	26	35
Urea (at Sta. 2)	3.3	1.3 (0.5, 1.85)	30	22
All nutrients (pooled data)	179.0	18.7 (0.6, 36.5)	339	53

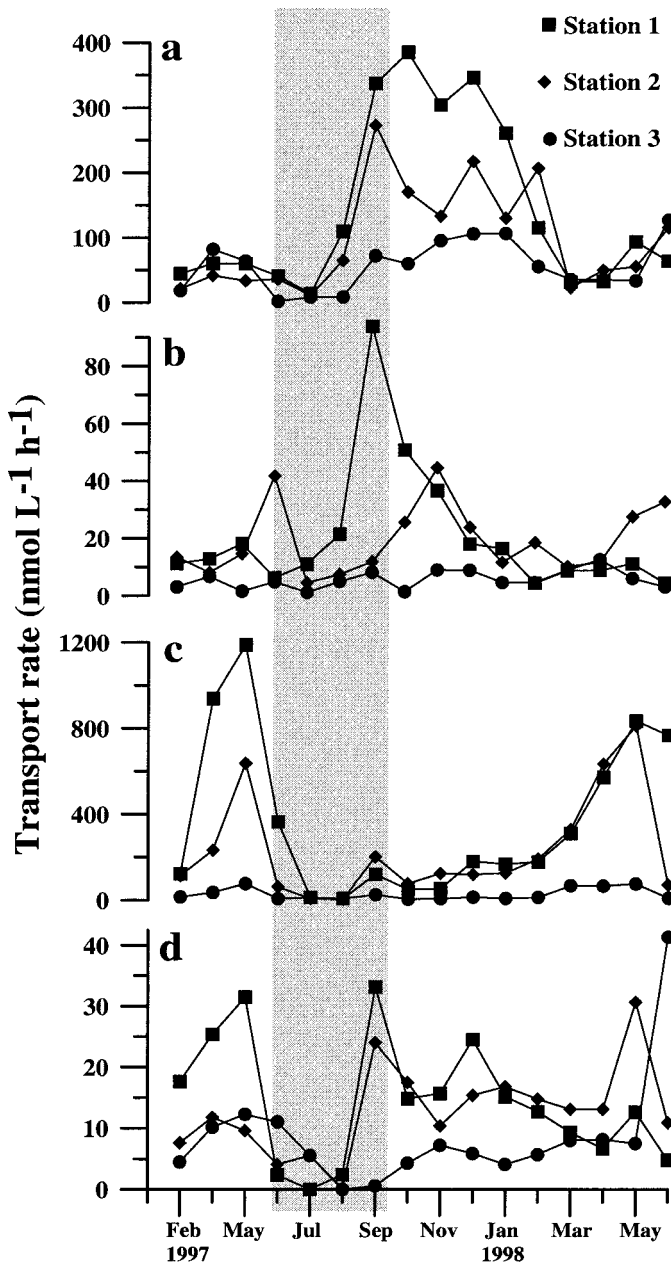


Fig. 5. Seasonal variations in the transport rates of (a) nitrate, (b) nitrite, (c) ammonium, and (d) urea at stations 1, 2, and 3.

mediately after the monsoon,  $\text{NO}_3^-$  was the major N source (average 65%: range 56–82%) for uptake. This high importance persisted through early premonsoon months to the seasonal minimum in March–April. Ammonium, on the other hand, was relatively little used (average 21%: range 7–26%) during postmonsoon months but became a major N nutrient in premonsoon (average 67%: range 30–87%). Seasonal changes of uptake rates of  $\text{NO}_2^-$  and urea were relatively less marked. In the case of  $\text{NO}_2^-$ , changes at stations 1 and 2 (excluding the single high value in June 1997) showed postmonsoon peaks, but not at Sta. 3, where there was no clear pattern. On an average,  $\text{NO}_2^-$  uptake rates in the postmonsoon were twice as high as in the premonsoon. In the case

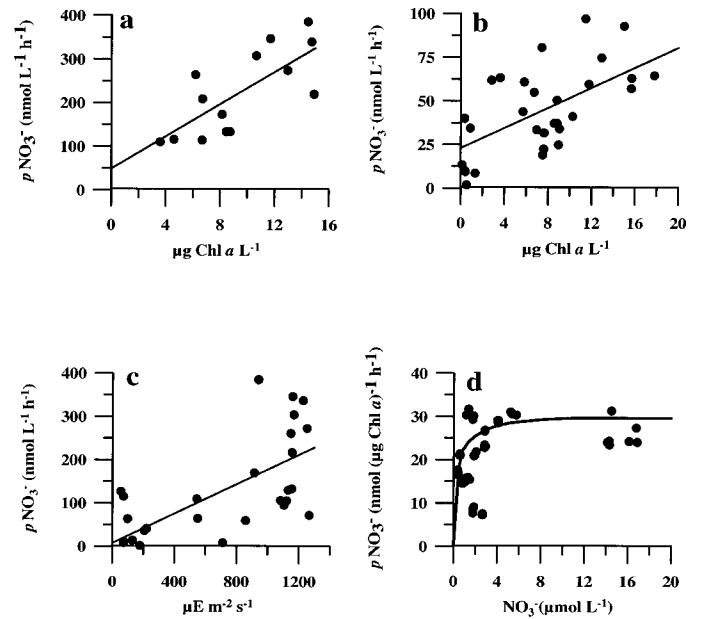


Fig. 6. Relationship between (a) Chl *a* and high nitrate uptake rates, (b) Chl *a* and low nitrate uptake rates, (c) incident light and nitrate uptake rates, and (d) ambient nitrate and chlorophyll-specific nitrate uptake rates.

of urea, a premonsoon peak, as was the case with  $\text{NH}_4^+$ , was seen at all stations. Nevertheless, uptake rates in the postmonsoon season were often relatively high. Notwithstanding the minor variations in the uptake rates of the four nutrients between some months, the pattern of new N-based uptake in the postmonsoon giving way progressively to regenerated N-based uptake in the premonsoon was distinct.

Nitrate uptake rates were independent of concentrations but related to Chl *a* concentrations, with statistically different slopes (Table 2) between uptake rates higher than  $100 \text{ nmol L}^{-1} \text{ h}^{-1}$  when  $\text{NO}_3^-$  was the major N source (Fig. 6a), and those lower (Fig. 6b). Phytoplankton-mediated uptake rates were about six times higher during the postmonsoon and early premonsoon than the rest of the year. Heterotrophic uptake (the intercept), on the other hand, varied only by a factor of two. When the premonsoon values were excluded,  $\text{NO}_3^-$  uptake rates were also related linearly with light (Fig. 6c). When normalized to Chl *a*, they were related with the nitrate concentrations in a rectangular-hyperbolic fit (Fig. 6d). A  $V/S$  versus  $S$  plot ( $r = 0.92$ ) gave a maximum  $\text{NO}_3^-$  uptake of  $25 \text{ nmol N } (\mu\text{g Chl } a)^{-1} \text{ h}^{-1}$  and a half saturation constant of  $0.8 \mu\text{mol N L}^{-1}$ .

Ammonium uptake rates were concentration dependent (Fig. 7a). As was the case with  $\text{NO}_3^-$ , they were also related to Chl *a* concentrations with different slopes and intercepts (Table 2) between periods when uptake rates were higher (February–May) and the rest of the year (Fig. 7b,c). As with  $\text{NO}_3^-$ , phytoplankton-mediated  $\text{NH}_4^+$  uptake rates varied by a factor of six between these two periods. Heterotrophic uptake (the intercept), on the other hand, varied by a factor of two. Neither absolute nor Chl-normalized uptake rates correlated with light. However, Chl-normalized  $\text{NH}_4^+$  uptake was linearly related to  $\text{NH}_4^+$  concentrations (Fig. 7d).

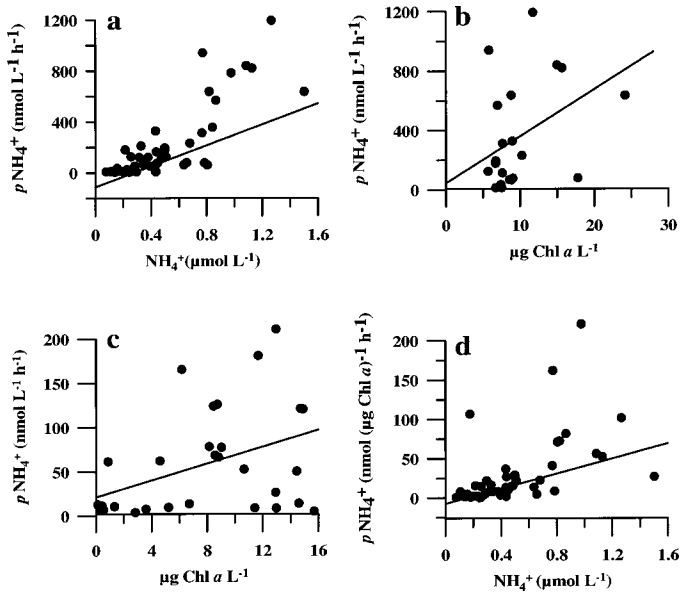


Fig. 7. Relationship between (a) ambient ammonium and ammonium uptake rates, (b) Chl *a* and high ammonium uptake rates, (c) Chl *a* and low ammonium uptake rates, and (d) ambient ammonium and chlorophyll-specific ammonium uptake rates.

Nitrite and urea uptake rates, both as absolute and Chl-normalized, were concentration and light independent. Nitrite uptake rates at Sta. 1 were related linearly with Chl *a* ( $r = 0.55$ ,  $p < 0.01$ ) (Fig. 8a), giving an intercept of 4.6  $\text{nmol N L}^{-1} \text{h}^{-1}$ . In the case of urea, relationships of uptake rates with Chl *a* were good at stations 1 ( $r = 0.61$ ;  $p < 0.01$ ) and 2 ( $r = 0.81$ ;  $p < 0.01$ ) (Fig. 8b,c) giving intercepts of 4.4 and 2.2  $\text{nmol N L}^{-1} \text{h}^{-1}$ . Since the slopes (1.3 and 1.25  $\text{nmol N } (\mu\text{g Chl } a)^{-1} \text{h}^{-1}$ ) were similar, this suggests that the heterotrophic uptake of urea was about one and a half times higher at Sta. 1 than at Sta. 2.

**Ammonium regeneration**—The pattern of changes of  $\text{NH}_4^+$  regeneration rates ( $10\text{--}1,500 \text{ nmol N L}^{-1} \text{h}^{-1}$ ) was notable for the seasonality (Fig. 9a): lowest rates in the monsoon, slightly higher but almost constant rates in postmonsoon, and a rapid increase in premonsoon to a peak in May. These are remarkably similar to the changes of  $\text{NH}_4^+$  uptake rates (Figs. 9a and 5c) indicating a close coupling between these two processes. Regression analysis of pooled data of  $\text{NH}_4^+$  uptake and regeneration rates gave a  $U/R$  ratio of 0.63 (95% confidence interval [CI] = 0.48, 0.77,  $r = 0.86$ ,  $p < 0.001$ ). Between the three stations, however, the  $U/R$  ratios varied with a statistical significance and decreased from Sta. 1 (0.85, 95% CI = 0.6, 1.21,  $r = 0.89$ ,  $p < 0.001$ ), through Sta. 2 (0.53, 95% CI = 0.44, 0.60,  $r = 0.96$ ,  $p < 0.001$ ), to Sta. 3 (0.13, 95% CI = 0.08, 0.17,  $r = 0.9$ ,  $p < 0.001$ ) indicating the increasing importance of regeneration over uptake toward the interior, riverine end. The pattern of changes of ambient  $\text{NH}_4^+$  concentrations was also similar to that of  $\text{NH}_4^+$  regeneration at the three stations (Figs. 3c and 9a), with statistically significant correlations ( $r = 0.81, 0.77$ , and  $0.75$  respectively,  $p < 0.001$ ).

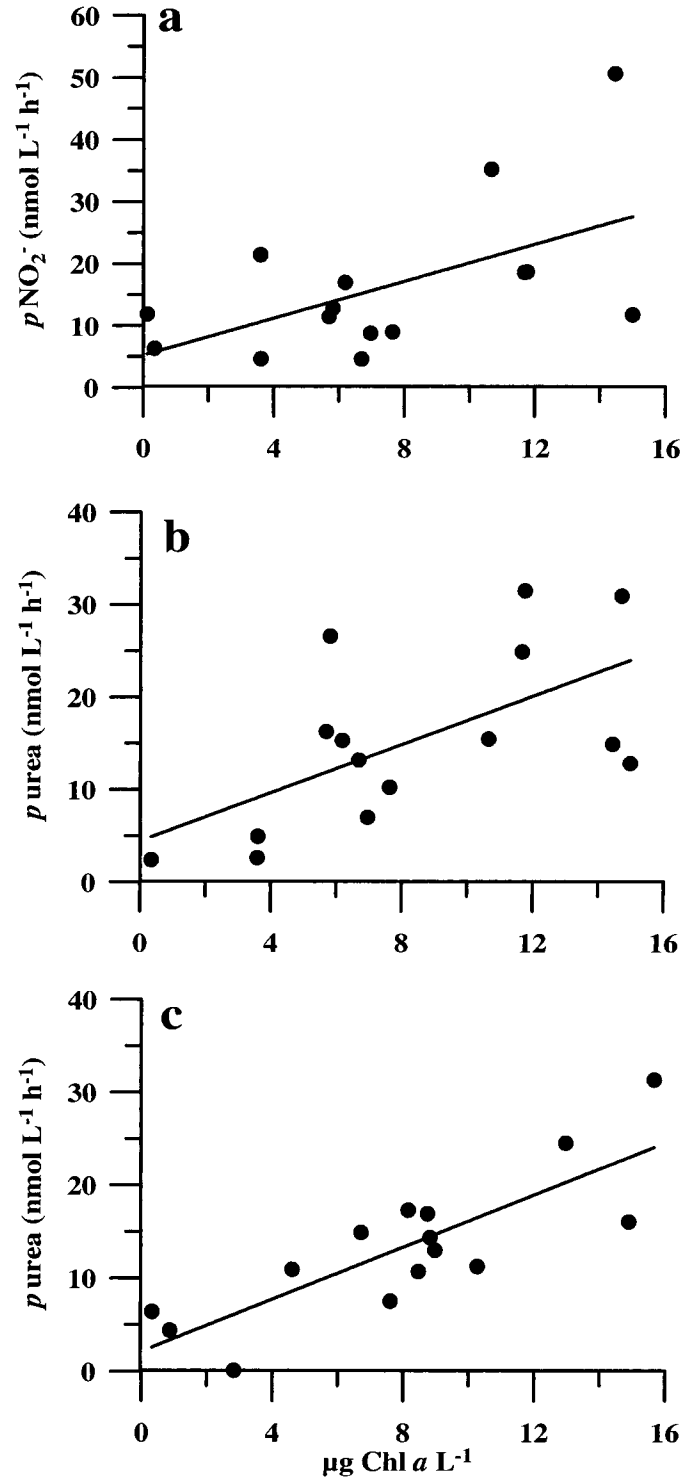


Fig. 8. Relationship between (a) Chl *a* and nitrite uptake rates, (b) Chl *a* and urea uptake rates at Sta. 1, and (c) Chl *a* and urea uptake rates at Sta. 2.

**Nitrification**—Seasonal changes of nitrification rates ( $0.1\text{--}96.7 \text{ nmol N L}^{-1} \text{h}^{-1}$ ) were remarkable for the steady increase from near-trace values in June to a peak in May (Fig. 9b). The nitrification rates were strongly  $\text{NH}_4^+$  concentration dependent ( $r = 0.88$ ,  $p < 0.001$ , Fig. 10) and, to some

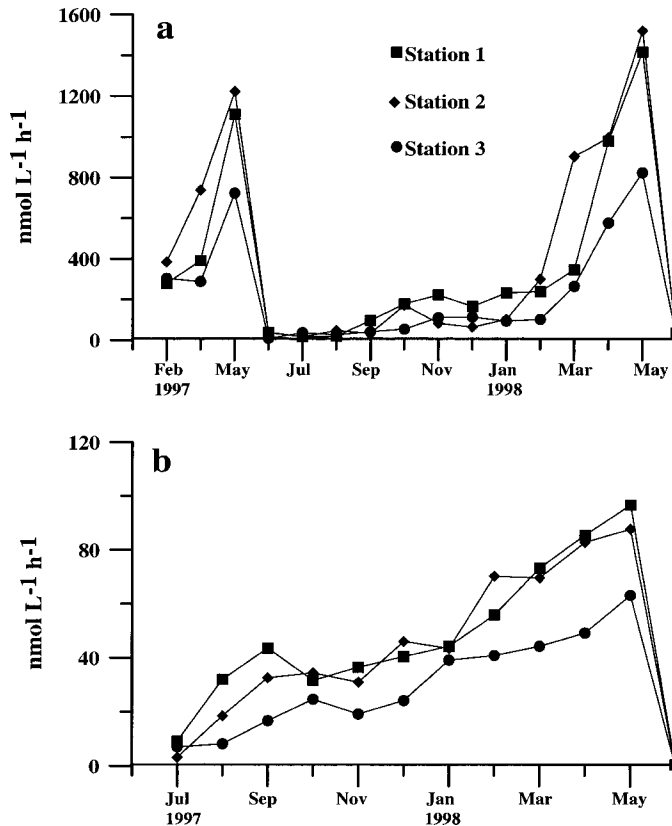


Fig. 9. Seasonal changes of (a) ammonification and (b) nitrification rates at stations 1, 2, and 3.

extent, temperature dependent ( $r = 0.48$ ,  $p < 0.01$ ). Variations in nitrification rates between the stations were not significant.

## Discussion

**Nitrogenous nutrients—concentrations and sources—** Though mangroves are generally regarded as productive coastal marine ecosystems in the tropics (Qasim and Wafar 1990), measurements of concentrations of nutrients, especially of N, that sustain this production have been few and far between. Several cover only part of the annual cycle, and only a few, such as those in the mangroves of Australia (Boto and Wellington 1988; Trott and Alongi 1999), Pakistan (Harrison et al. 1997), Mexico (Rivera-Monroy et al. 1995), and India (Krishnamurthy et al. 1975), present seasonal cycles. None of these studies included all assimilable forms of N.

The clear seasonality in the changes of nutrient concentrations in our study is different from the uniform concentrations observed during the dry season in the Australian mangroves (Trott and Alongi 1999) or the lack of a pattern in Pakistan mangroves (Harrison et al. 1997). What we consider of interest in the seasonal changes of N nutrients in this mangrove is the extent to which in situ processes control ambient concentrations. Freshwater advection was the major source of  $\text{NO}_3^-$  only in the monsoon and early postmonsoon months (Figs. 2 and 3). The rapid increase in salinity and

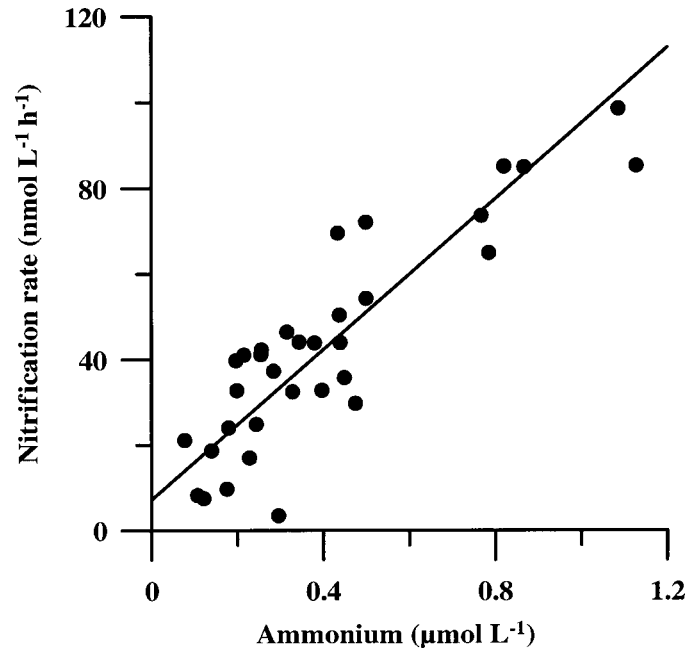


Fig. 10. Variations of nitrification rates as a function of substrate concentrations.

the steady increase in nitrification rates from September onward demonstrate that in situ  $\text{NO}_3^-$  production then becomes progressively important as a source, so much so that changes in  $\text{NO}_3^-$  concentrations in premonsoon months (February–May) could be explained by changes in nitrification rates (Fig. 11). With an average nitrification rate of  $68.6 \text{ nmol N L}^{-1} \text{ h}^{-1}$  at this time, production of  $\text{NO}_3^-$  to a level equivalent to the average ambient concentration ( $3.1 \text{ } \mu\text{mol N L}^{-1}$ ) would require hardly a few days. We have not measured  $\text{NO}_3^-$  production rates directly, but since  $\text{NO}_2^-$  accumulation was not evident, presumably oxidation of  $\text{NO}_2^-$  is as rapid as its formation.

The importance of in situ production is even more striking

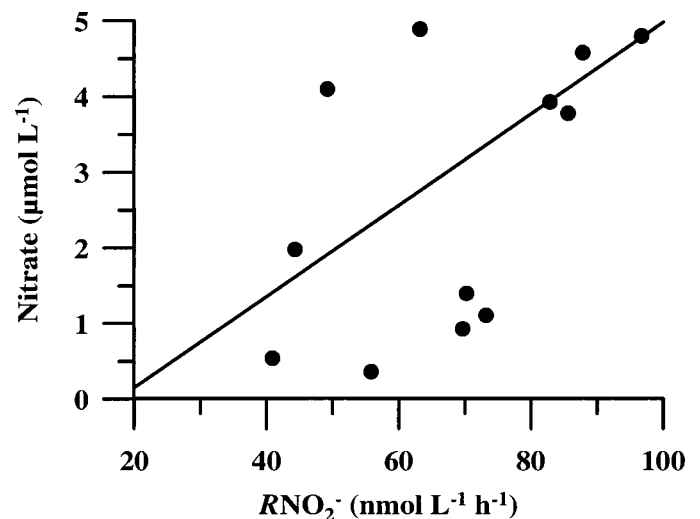


Fig. 11. Relationship between nitrification rates and nitrate concentrations.

in the case of  $\text{NH}_4^+$ . This is borne out by the incidence of seasonal minimum concentrations of  $\text{NH}_4^+$  during peak monsoon (July–August) months (Fig. 2) and the close similarity in the pattern of changes of ambient  $\text{NH}_4^+$  concentrations and  $\text{NH}_4^+$  regeneration rates at all three stations (Figs. 3c and 9a). The only exception was in June when fresh rains could have scoured the sediments and caused the release of  $\text{NH}_4^+$ . The average  $\text{NH}_4^+$  regeneration rates for monsoon, postmonsoon, and premonsoon were 30, 130, and 660  $\text{nmol N L}^{-1} \text{h}^{-1}$ , respectively. With these rates the turnover time of  $\text{NH}_4^+$  at average ambient levels (0.4, 0.3, and 0.7  $\mu\text{mol N L}^{-1}$ ) would be less than 2 h in dry months and not higher than 14 h in the wet season. These time scales (for  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) are less than the flushing time for west coast estuaries in non-monsoon months (Qasim and Wafar 1990). Biological, rather than physical, processes are therefore important in regulating the nutrient levels in this mangrove. There is no reason to doubt that  $\text{NH}_4^+$  and  $\text{NO}_2^-$  (and  $\text{NO}_3^-$ ) production rates in other mangroves could be less than what we have measured, and in that event biological control of nutrient concentrations could be a common feature to all mangroves.

**Nitrogen uptake**—Nitrate and  $\text{NH}_4^+$  were the major nutrients used by phytoplankton, more or less in equal proportions ( $38.7 \pm 26.0\%$  and  $44.3 \pm 29.5\%$ , respectively, of total N uptake). Uptake of urea ranked third ( $11.0 \pm 11.3\%$ ), followed by that of  $\text{NO}_2^-$  ( $6.0 \pm 5.3\%$ ). This situation is different from most other coastal waters where uptake of  $\text{NH}_4^+$  has often been shown to exceed substantially that of  $\text{NO}_3^-$  (Dortch 1990). Besides, the seasonal patterns were distinctly different, with a dominance of  $\text{NO}_3^-$  (and, along with  $\text{NO}_2^-$ , new N in the classical sense) uptake in postmonsoon followed by a dominance of  $\text{NH}_4^+$  (and, along with urea, regenerated N) uptake in the premonsoon.

The high and prolonged use of  $\text{NO}_3^-$  at the beginning of the productive season could have been due to several facts. The first is the high ambient  $\text{NO}_3^-$  concentrations, compared with  $\text{NH}_4^+$ . Under these conditions,  $\text{NO}_3^-$  is taken up more (Wafar et al. 1983; Carpenter and Dunham 1985; Pennock 1987) or at least as much as  $\text{NH}_4^+$  (L'Helguen et al. 1996). The adequate  $\text{NO}_3^-$  supply during the postmonsoon can be seen by the following comparison. Use of a conservative mixing line ( $\text{NO}_3^- = 10.38 - 0.23 \text{ salinity}$ ,  $r = -0.80$ ,  $p < 0.01$ ) showed that the average reduction in  $\text{NO}_3^-$  input through diminished freshwater flow at monthly intervals between September and January was 0.3–2.9  $\mu\text{mol N L}^{-1}$ . The measured nitrification rates, raised with a photoperiod of 12 h, for the same time intervals gave inputs of an order of magnitude higher (10–15  $\mu\text{mol N L}^{-1}$ ), compensating adequately for the reduction in allochthonous supply of  $\text{NO}_3^-$ . The second is the dominance of microplankton. Large-sized cells have a distinct preference for  $\text{NO}_3^-$  over  $\text{NH}_4^+$  (Malone 1980; Kokkinakis and Wheeler 1987); our data agree with this. Microplankton constituted 80% of phytoplankton biomass and subsisted almost exclusively on nitrate (98% of nitrate taken up by unfractionated plankton) (Heredia 2000). The third is the low  $\text{NH}_4^+$  concentrations at this time (Fig. 3c) and hence possibly a lack of inhibition of  $\text{NO}_3^-$  uptake.

The decrease in  $\text{NO}_3^-$  uptake rates from January was, however, quite rapid. As the light regime was still favorable and

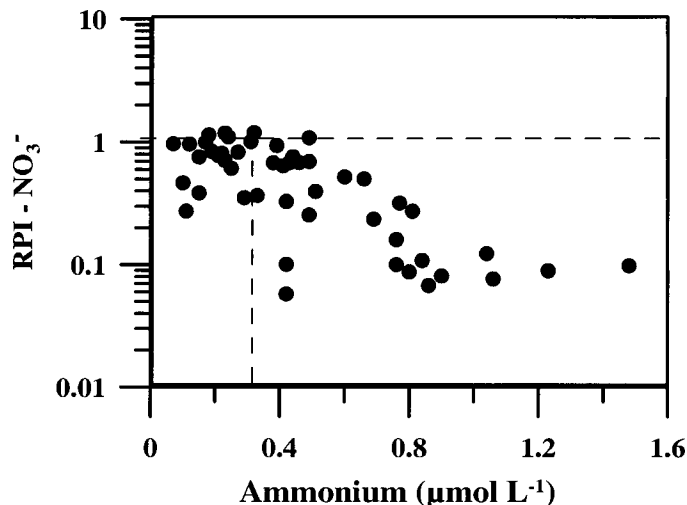


Fig. 12. Ambient ammonium concentrations and relative preference indices for nitrate.

the increasing nitrification rates would have supplied more  $\text{NO}_3^-$  than during the postmonsoon, this could only be due to an inhibition of  $\text{NO}_3^-$  uptake by increasing  $\text{NH}_4^+$  concentrations (Fig. 3c). The relative preference indices (McCarthy et al. 1977) for  $\text{NO}_3^-$ , though not without bias in interpretation (Stolte and Riegman 1996), were nearer to 1 only at  $\text{NH}_4^+$  concentrations  $< 0.3 \mu\text{mol N L}^{-1}$  and began to decrease appreciably at higher concentrations (Fig. 12). Sufficiently high  $\text{NH}_4^+$  concentrations can bring about a sustained reduction of  $\text{NO}_3^-$  uptake (Paasche and Kristiansen 1982; Dortch 1990; L'Helguen et al. 1996). The threshold concentrations at which this occurs range from 0.1  $\mu\text{mol N L}^{-1}$  in oligotrophic waters to 2  $\mu\text{mol N L}^{-1}$  in polluted estuaries. In our study this was about 0.3  $\mu\text{mol N L}^{-1}$ . Ammonium concentrations in the premonsoon were  $> 0.3 \mu\text{mol N L}^{-1}$  at all stations, and this, coupled with the intense regeneration, could have induced the shift to an enhanced use of  $\text{NH}_4^+$  in this season.

The pattern of high and prolonged  $\text{NO}_3^-$  use preceding high  $\text{NH}_4^+$  uptake is unknown from any other estuarine ecosystem. Relating concentration changes of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  with Chl *a* in permanently well-mixed temperate coastal waters, Wafar et al. (1983) suggested that the spring N source for phytoplankton was  $\text{NO}_3^-$ , and only when this has been reduced to low levels does  $\text{NH}_4^+$  assume an importance. High  $\text{NO}_3^-$  uptake rates measured in deep well-mixed waters with  $^{15}\text{N}$  (L'Helguen et al. 1996) in spring conformed with this, but, interestingly, in shallow sectors  $\text{NH}_4^+$  uptake became important early in spring itself (Maguer et al. 1996), in a pattern that was reminiscent of waters that become seasonally stratified. Obviously, a strong supply of  $\text{NO}_3^-$  at the beginning of the productive season coupled with a physical mixing that allows phytoplankton continued access to  $\text{NO}_3^-$  would then lead to a prolonged use of  $\text{NO}_3^-$ . These conditions are met with in the mangrove waters in the form of seasonal advection of  $\text{NO}_3^-$  with freshwaters and tidal mixing, augmented with high in situ nitrification.

The large seasonal variations in the uptake of individual N compounds even out when their sums are considered. For

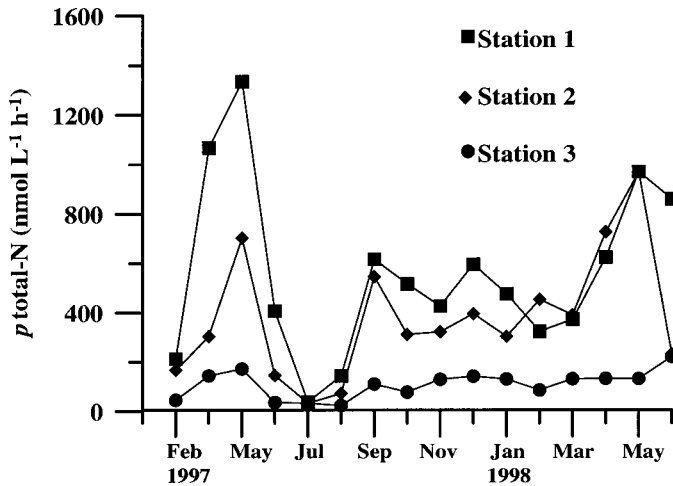


Fig. 13. Seasonal changes of total N uptake rates at stations 1, 2, and 3.

part of the year (September to March/April), the total N uptake varied within narrow ranges at all three stations. It then increased to peak values in May and declined subsequently to low values in June–July (Fig. 13). These changes bear a good resemblance and a reasonably good correlation ( $r = 0.33$ ;  $p < 0.05$ ) to those of incident light (Fig. 2c) but not to the sums of all four nutrients. This pattern is a marked exception to the generally held belief that in nearshore tropical ecosystems, it is the nutrient supply rather than light that regulates planktonic productivity (Qasim and Wafar 1990). The lack of nutrient control was due to exceptionally high in situ N regeneration rates (*see below*) more than to allochthonous supply, to the extent that even at their lowest, the total assimilable N concentrations were still not less than  $1 \mu\text{mol N L}^{-1}$ .

**Carbon productivity**—Conversion of total N uptake rates with a C:N ratio of 6.25 (by atoms) gave the following carbon productivity equivalents:  $42 \pm 25 \mu\text{g C L}^{-1} \text{h}^{-1}$  (range:  $3\text{--}100 \mu\text{g C L}^{-1} \text{h}^{-1}$ ) for Sta. 1,  $28 \pm 18 \mu\text{g C L}^{-1} \text{h}^{-1}$  (range:  $3\text{--}55 \mu\text{g C L}^{-1} \text{h}^{-1}$ ) for Sta. 2, and  $8 \pm 4 \mu\text{g C L}^{-1} \text{h}^{-1}$  (range:  $2\text{--}16 \mu\text{g C L}^{-1} \text{h}^{-1}$ ) for Sta. 3. The values for Sta. 1, where mangrove plants were abundant, were of the same order as measured in some other west coast mangrove waters by  $^{14}\text{C}$  assimilation (e.g., Pant et al. 1980) and elsewhere (e.g., Teixeira et al. 1969) by oxygen balance. The large differences between stations 1 and 3 clearly show that association with mangrove vegetation enhances plankton productivity.

**Heterotrophic uptake**—The high PON content and its lack of relationship with Chl *a* suggest a high detritus content in POM and, by inference, a greater role for heterotrophic activity in N assimilation. A substantial amount of N assimilation in marine microbial populations is associated with nonphotosynthetic organisms (Eppley et al. 1977; Laws et al. 1985). They have primarily a preference for  $\text{NH}_4^+$  (Wheeler and Kirchman 1986) but can also take up other forms of N, especially  $\text{NO}_3^-$  (Kirchman et al. 1994), with rates ranging

from less than one-third of  $\text{NH}_4^+$  uptake (Kirchman et al. 1994) to an equivalent extent (Kirchman and Wheeler 1998).

Heterotrophic uptake of N has been evaluated in various ways: as equivalent to N uptake by the picoplankton ( $<1 \mu\text{m}$ ) fraction (e.g., Probyn and Painting 1985); by using metabolic inhibitors on the  $<1 \mu\text{m}$  fraction (Wheeler and Kirchman 1986); by correcting the uptake rates measured in the  $<1 \mu\text{m}$  fraction with a ratio of uptake to Chl *a* in the unfractionated sample (Kirchman et al. 1994), a ratio of bacterial to picophytoplankton production in the  $<1\text{-}\mu\text{m}$  fraction (Kirchman and Wheeler 1998), or rates of  $^{14}\text{CO}_2$  incorporation into protein (Hoch and Kirchman 1995); and by a comparison of the pattern of changes in N uptake rates and Chl *a* in the picoplankton fraction (Le Corre et al. 1996). Since the picoplankton was not separated in the present study due to difficulties in filtration and recovery of sufficient PON for emission spectrometry and since particles (and bound bacteria) are likely to be spread over a large size range, we evaluated the share of heterotrophs by a regression analysis of N uptake with Chl *a*.

Situations where linear fits between N uptake and Chl *a* had a  $p < 0.05$  or lower (Table 2) showed that all the four compounds were taken up by heterotrophs to varying extents, ranging from a low of  $3\text{--}4.5 \text{ nmol N L}^{-1} \text{h}^{-1}$  with urea and  $\text{NO}_2^-$  to  $44 \text{ nmol N L}^{-1} \text{h}^{-1}$  with  $\text{NH}_4^+$  when its uptake was high. In most instances, however, the intercepts were not statistically different from zero, but when the sum of all four nutrients was considered (Table 2) there was a distinct improvement in the correlation ( $p < 0.01$ ) and the statistical significance of the intercept ( $179 \pm 95 \text{ nmol N L}^{-1} \text{h}^{-1}$ ). The regression intercept approach may not be the right way of estimating heterotrophy if the distributions of chlorophyll and heterotrophs covary in space and time, which is probably the case here. However, as the intercept derived thus is a minimum estimate and the estimated heterotrophic uptake is statistically valid, some reliance on the importance of heterotrophs, if not on the actual value itself, can still be had.

Heterotrophic uptake could be an important component ( $\sim 50\%$ ) of planktonic N uptake in mangrove waters (Table 2). Proportions of the order of  $20\text{--}30\%$  (Glibert 1982; Kirchman and Wheeler 1998) or even more (Fuhrman et al. 1988) of bacterial  $\text{NH}_4^+$  uptake in total  $\text{NH}_4^+$  uptake are not uncommon ( $\text{NH}_4^+$  is the only form considered in most studies). Our results, however, differ in the sense that this happens in a high nutrient ecosystem where bacterial N uptake can be expected not to exceed  $10\%$  of total N uptake (Glibert 1982; Hoch and Kirchman 1995). A stationwise plot (Fig. 14) of estimated heterotrophic uptake of N (using the uptake/Chl *a* ratio of 19 from the regression) along with total N uptake clearly shows a sharp gradient in the former between stations and a dominance in the monsoon. These reflect the spatial and seasonal differences in the abundance of PON (Fig. 4a) and suggest that the quantity of PON is a prime factor for a high proportion of heterotrophic N uptake. The quality of the PON substrate could be even more important: decomposition experiments with mangrove litter (Wafar et al. 1997) showed that efflux of elements from the particulate to the dissolved pool was rapid in the first two weeks. The nature of this DOM is unknown at present, but, as hypothesized by Hoch and Kirchman (1995), this could be one of the factors

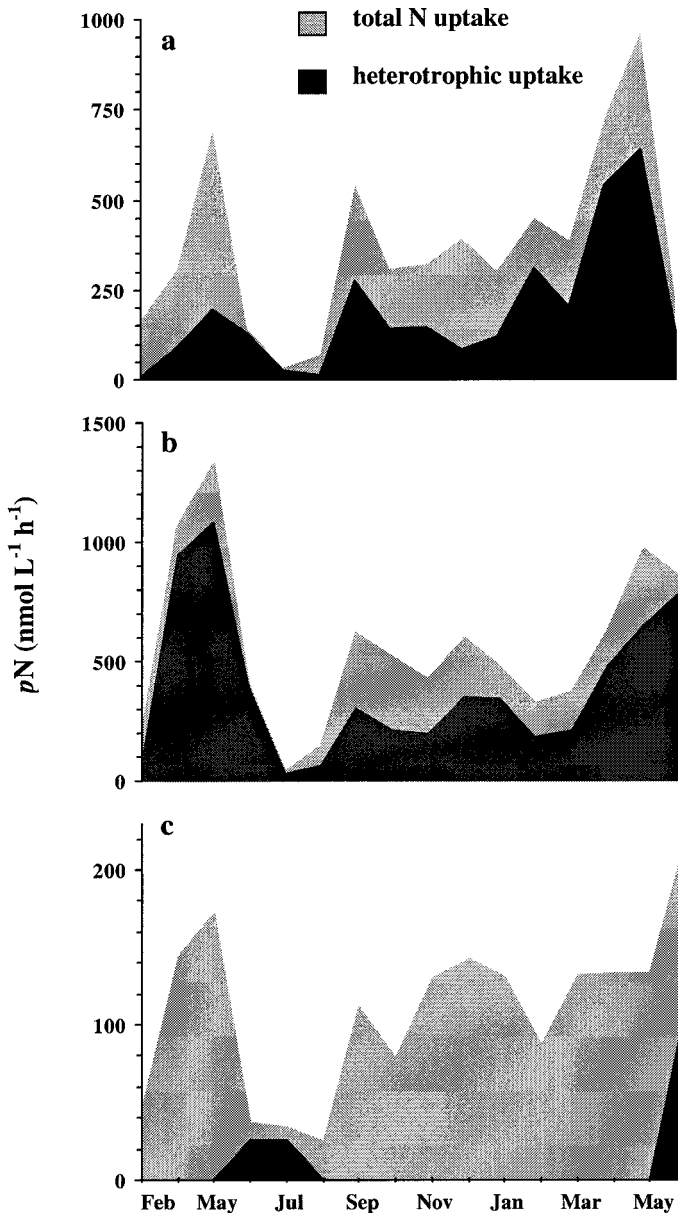


Fig. 14. Seasonal changes of total N uptake and heterotrophic uptake rates at stations (a) 1, (b) 2, and (c) 3.

that determine the high heterotrophic uptake rates in mangrove waters.

**N regeneration**—Ammonium regeneration rates measured are among the highest reported so far for nearshore waters (Glibert 1982; Lipschultz et al. 1986; Bode and Dortch 1996) and are probably characteristic of high detritus ecosystems. Grazers (ciliates and flagellates) and DON mineralizers are the major producers of  $\text{NH}_4^+$  in the  $<200\text{-}\mu\text{m}$  fraction (Paasche and Kristiansen 1982; Probyn 1987; Le Corre et al. 1996). The relative importance of these groups is unassessable with the present data, but the high PON content and the  $>50\%$  efflux of elements from the litter within 2 weeks of the onset of decomposition (Wafar et al. 1997) suggest that mineralization of DON could have been an im-

portant source of  $\text{NH}_4^+$ . Among the environmental parameters, temperature, as expected from the pattern of seasonal changes (Figs. 2b and 9a), had an influence ( $r = 0.65$ ,  $p < 0.01$ ) on  $\text{NH}_4^+$  production.

Uptake and regeneration of  $\text{NH}_4^+$  in short-term experiments are closely coupled, but their rates are not always in balance. The  $U/R$  ratio may exceed one (e.g., Harrison et al. 1983), be less than that (e.g., Hanson and Robertson 1988), or vary as a function of season, depth, and plankton size fraction (Le Corre et al. 1996).

Ammonium production almost always exceeded its uptake; the daytime production was in excess of assimilatory N requirements ( $U/R$  ratio of 0.63). The good relationship of nitrification rates with  $\text{NH}_4^+$  concentrations (Fig. 10) (and  $\text{NH}_4^+$  production rates—see below) suggests that a part of  $\text{NH}_4^+$  production also fluxes to the nitrification pathway. The ammonium uptake to  $\text{NH}_4^+$  regeneration ratio for the period when  $\text{NO}_2^-$  regeneration was also measured (July 1997–June 1998) was 0.41. This increased to 0.48 when the latter was included with  $\text{NH}_4^+$  uptake, still leaving excess  $\text{NH}_4^+$  production. Nevertheless, the ambient  $\text{NH}_4^+$  concentrations were low and the  $\text{NH}_4^+$  uptake by plankton was concentration dependant. This suggests that other autotrophs (benthic algae and the mangrove vegetation) would constitute potential sinks for  $\text{NH}_4^+$  mineralized in the water column.

**Nitrification**—Though subject to inhibition by light, nitrifying bacteria are known to be still active within the euphotic zone, especially near its base or at the primary  $\text{NO}_2^-$  maximum (Ward 1986), and to mineralize  $\text{NH}_4^+$  to an extent that even exceeds the rates of  $\text{NO}_3^-$  assimilation in the open ocean (Dore and Karl 1996) and neritic waters (Gentilhomme and Raimbault 1995). Water column nitrification rates in the marine environment are highly variable, but most productive estuarine and coastal areas have higher rates than oceanic waters (Kaplan 1983). Typical rates in the primary  $\text{NO}_2^-$  maximum in oceanic waters range between 20 (Olson 1981; Ward et al. 1984) and 40  $\text{nmol N L}^{-1} \text{d}^{-1}$  (Dore and Karl 1996). In neritic waters, they are an order of magnitude higher, up to 20  $\text{nmol N L}^{-1} \text{h}^{-1}$  (Gentilhomme and Raimbault 1995). In unpolluted estuaries, they could be still one more order of magnitude higher, up to 1,200  $\text{nmol N L}^{-1} \text{d}^{-1}$  (compilation in Berounsky and Nixon 1993).

The average nitrification rate of 40  $\text{nmol N L}^{-1} \text{h}^{-1}$ , equivalent to a daily rate of close to 1,000  $\text{nmol N L}^{-1}$ , and the range ( $24\text{--}2,000 \text{ nmol N L}^{-1} \text{d}^{-1}$ ) measured in this study are among the highest values reported (Berounsky and Nixon 1993). What is remarkable is that, unlike in other eutrophic environments, these high nitrification rates appear to be supported by low  $\text{NH}_4^+$  concentrations (Fig. 10). Though the latter did relate linearly with nitrification rates, the low ambient concentrations and the high planktonic uptake rates suggest that it would be the rate of  $\text{NH}_4^+$  production rather than its in situ concentrations that regulates nitrification. The relation between nitrification rates and  $\text{NH}_4^+$  regeneration rates did indeed obey Michaelis-Menton kinetics (Fig. 15) and the  $V/S$  versus  $S$  plot was an extremely good fit ( $r = 0.95$ ,  $p < 0.001$ ). The predicted maximum nitrification rate was 100  $\text{nmol N L}^{-1} \text{h}^{-1}$ , which was attained in the month of May (97  $\text{nmol N L}^{-1} \text{h}^{-1}$ ). The  $\text{NH}_4^+$  regeneration rate

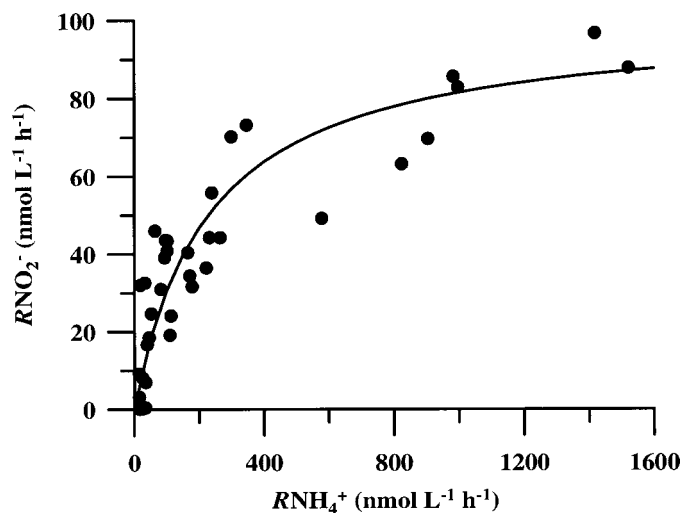


Fig. 15. Relationship between nitrification rates and ammonium regeneration rates.

required to sustain half the maximum nitrification rate was about  $225 \text{ nmol N L}^{-1} \text{ h}^{-1}$ . This way of relating rate of product formation with rate of substrate formation rather than its concentration might appear unusual, but in our opinion this is a more realistic way of evaluating the coupling between the two processes, especially when the substrate is partitioned with yet another process.

Other environmental variables that regulate nitrification are oxygen concentrations, temperature, and suspended load. The percent saturation of dissolved oxygen at all stations was rarely below 100, and hence could not have influenced nitrification rates. Besides, marine nitrifiers can grow and oxidize their substrate at very low oxygen tensions (Kaplan 1983). Temperature, on the other hand, could have had an influence ( $r = 0.51$ ), but it could be fortuitous since the patterns of changes of temperature,  $\text{NH}_4^+$  concentrations, and  $\text{NH}_4^+$  regeneration rates were more or less similar. Turbidity can also enhance nitrification rates (Helder and DeVries 1983; Owens 1986). This could have been an important factor regulating nitrification in the present study: though the analysis of variance did not show significant differences between nitrification rates among the three stations, there was still a gradient in the averages between the first two and the third (50, 47, and  $31 \text{ nmol N L}^{-1} \text{ h}^{-1}$ ). This was proportional to the gradient in average PON concentrations (86, 73, and  $49 \text{ nmol N L}^{-1}$ ).

While the coupling between  $\text{NH}_4^+$  production and its use in the planktonic food chain was quite close, this was not true with nitrification rates and uptake rates of  $\text{NO}_3^-$  and  $\text{NO}_2^-$ . The pattern of changes in these (Figs. 5a,b and 9b) showed that these rates were in balance only during February–May. As these were the months when the freshwater flow was virtually nonexistent, uptake rates in excess of nitrification rates during the rest of the year could only have been supported by  $\text{NO}_3^-$  and  $\text{NO}_2^-$  input through freshwater advection. Integration of  $\text{NO}_3^-$  and  $\text{NO}_2^-$  uptake and  $\text{NO}_2^-$  production from July to January gave rates of 0.42 and  $0.07 \text{ mmol N L}^{-1}$ , respectively, indicating that about 80% of

Table 3. N uptake and regeneration rates ( $\text{mmol L}^{-1} \text{ yr}^{-1}$ ) in the Achara mangrove.

Station	$\rho\text{NO}_2^-$	$\rho\text{NO}_3^-$	$\rho\text{NH}_4^+$	$\rho\text{Urea}$	$\text{RNH}_4^+$	$\text{RNO}_2^-$
1	0.10	0.76	1.77	0.055	2.41	0.2
2	0.08	0.53	1.47	0.065	2.41	0.19
3	0.02	0.27	0.17	0.035	1.31	0.12
Average	0.07	0.52	1.14	0.05	2.04	0.17

$\text{NO}_3^-$  and  $\text{NO}_2^-$  taken up during the monsoon and postmonsoon was sustained by allochthonous inputs.

*Nitrogen balance*—Uptake and regeneration rates integrated for an annual cycle are given in Table 3. Figure 16 shows the seasonwise breakup of the integrated rates for the three stations. The assumptions made in these calculations are: uptake of  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ , and urea occur over a 12 h photoperiod; nighttime assimilation of  $\text{NH}_4^+$  is half of the daytime rate (Le Corre et al. 1996);  $\text{NH}_4^+$  regeneration rates do not differ between day and night (Glibert 1982; Selmer 1988); and nitrification occurs only in the night (12 h per day). Uptake rates of  $\text{NO}_3^-$  and  $\text{NO}_2^-$  are strongly light dependant (MacIsaac and Dugdale 1972), whereas those of urea and  $\text{NH}_4^+$  are not (L'Helguen 1991), with only a 20–25% reduction at night compared with day. Annual uptake of  $\text{NH}_4^+$  and urea are, therefore, conservative estimates.

Three interesting features become evident. The first is the remarkably higher flux rates at stations 1 and 2 than at Sta. 3. As these were in close proximity to the mangrove vegetation, this is suggestive of an influence of terrestrial productivity on planktonic N fluxes. However, this was not as substantial as expected. Wafar et al. (1997) calculated that the average flux of PON and DON from mangrove litter fall into a  $1 \text{ m}^2$  water area beneath was  $27.1 \text{ mg N d}^{-1}$ , equivalent (with an average depth of 1 m) to about  $0.7 \text{ mmol N L}^{-1} \text{ yr}^{-1}$ . This was about 26–33% of the N taken up by plankton at these two stations ( $2.69$  and  $2.15 \text{ mmol N L}^{-1} \text{ yr}^{-1}$ ). This range is similar to that calculated by Wafar et al. (1997) using historic data on  $^{14}\text{C}$  assimilation, DOC excretion by phytoplankton, and Redfield ratios. Even when the N supply through advection ( $0.42 \text{ mmol N L}^{-1}$ ) is added, this falls short by more than 50% of the N required for sustaining the planktonic productivity, suggesting that rapid in situ recycling is far more important as a N source than external inputs.

The second concerns the overestimation of new production by nonconsideration of in situ nitrification. The concepts of new production (Dugdale and Goering 1967) and  $f$ -ratio (Eppley and Peterson 1979) necessitate a flux of  $\text{NO}_3^-$  from external sources. Nitrification, however, could be an important internal source of  $\text{NO}_3^-$  (Olson 1981; Ward et al. 1982) and may support between 47 and 142% of the measured  $\text{NO}_3^-$  assimilation, as was shown from ALOHA time-series data in the North Pacific (Dore and Karl 1996), or between 20 and 115%, as was shown in coastal waters (Prisco and Downes 1985) or the totality, as was shown for the Algerian current (Gentilhomme and Raimbault 1995). In our study, the fraction of  $\text{NO}_3^-$  uptake that could have been supported by nitrification varied from <1% in monsoon months to

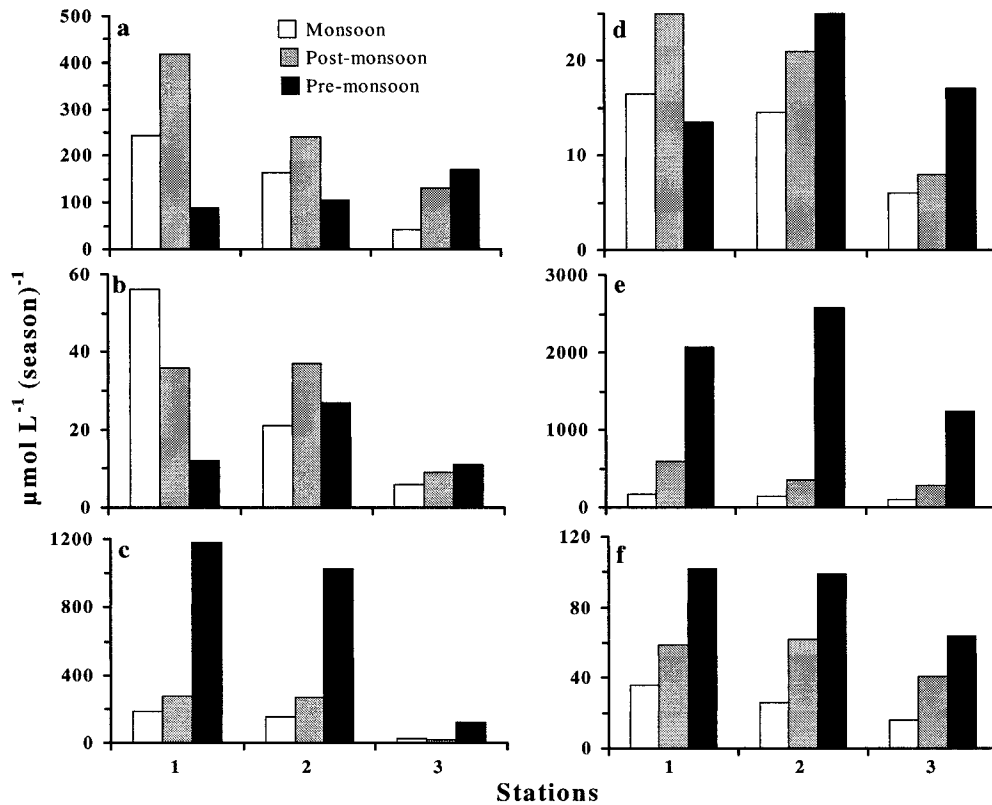


Fig. 16. Seasonally integrated rates of uptake of (a) nitrate, (b) nitrite, (c) ammonium, and (d) urea; (e) ammonium production and (f) nitrite production at the three stations.

tality in summer (Figs. 5a and 9b). A regression analysis of the  $f$ -ratios calculated with and without allowance for in situ nitrification gave a slope of 0.7 (95% CI = 0.46, 0.93,  $p < 0.001$ ). The range and the average extent of overestimate (30%) are substantially of the same order as in coastal waters (Priscu and Downes 1985) or oceanic waters (Dore and Karl 1996) and suggest that even in nearshore waters, where uptake of oxidized forms of N is presumably driven by inputs of allochthonous N, estimation of new production from measurements of  $\text{NO}_3^-$  uptake alone would be of little value if not accompanied by those on nitrification.

The third feature relates to the balance between uptake and production of N. Ammonium regeneration and nitrification provided on average 20% more N than assimilated by plankton. The sinks for this excess dissolved N would be the mangrove vegetation and the benthic algae. Partitioning of dissolved N by these consumers would then explain the concentration-dependant uptake of  $\text{NH}_4^+$  throughout the year and of  $\text{NO}_3^-$  when river flow was weak. In that event, to conform with the high productivity assigned to mangroves (Qasim and Wafar 1990) and the export of organic matter to the sea (Rivera-Monroy et al. 1995), the benthic fluxes of N should be even more important than water column fluxes.

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