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Preliminary assessment of benthic community metabolism in a south-east Asian mangrove swamp

Erik Kristensen, Frede Ø. Andersen, Lars H. Kofoed

Institute of Biology, University of Odense, DK-5230 Odense M, Denmark

ABSTRACT: Preliminary data are presented on benthic metabolism, i.e. carbon, oxygen and dissolved inorganic nitrogen (DIN) dynamics in a tropical, south-east Asian mangrove swamp. Primary production by benthic microalgae, measured as ^{14}C assimilation and O_2 production, was low compared to other intertidal areas. Benthic production comprised 4 to 20 % of production estimates obtained from the literature on the mangrove *Rhizophora apiculata*. Factors responsible for the relatively low benthic primary production appeared to be shading by *R. apiculata* and DIN availability. Oxygen penetration into water-covered sediment showed significant differences between light (2.5 mm) and darkness (1.5 mm). In air-exposed sediment, however, O_2 penetration depth was similar in both light and darkness. Oxygen uptake by the sediment obtained from core incubations was 20 to 55 % higher than the rate estimated from vertical O_2 profiles. The estimated O_2 demand needed to support the decay of produced algal cells was ca 73 % of the measured total O_2 uptake by the sediment. Water sampling in a tidal channel indicated that suspended particles transported by incoming tides were trapped in the mangrove system. This tidal import was evident as an upper sedimentary silt-zone (0 to 5 cm) superposing a lower peat containing root-zone (> 5 cm) in the sediment.

INTRODUCTION

Mangrove swamps are usually considered to be areas of high primary productivity which support highly developed detritus-based food webs (e.g. Odum & Heald 1975, Dye & Lasiak 1986, Robertson 1986). It has long been recognized that mangrove trees, e.g. *Rhizophora* spp. and *Avicennia* spp., are the most important primary producers (Christensen 1978, Bunt et al. 1979, Twilley et al. 1986b). During the last decade various studies have been reported on primary production and sessile macroalgae in mangrove swamps (Wium-Andersen 1979, Ricard 1984, Davey & Woelkerling 1985), but the role of benthic microalgae has not yet been addressed. Benthic microalgae, known as important producers of organic matter in intertidal flats all over the world (e.g. Colijn & Jonge 1984), may be of significance for nutrient and detritus dynamics in mangrove swamps.

The decay of organic matter in mangroves has usually been determined as the time dependent weight loss of litter (Boonruang 1978, Cundell et al. 1979, Rice & Tenore 1981). This has provided valuable informations about leaching and microbial attack on intact leaves, but less about the overall microbial activity in mangrove sediments.

Oxygen exchange, generally accepted as a measure of autotrophic and heterotrophic (aerobic as well as anaerobic) activity in sediments (Jørgensen 1983, Andersen & Hargrave 1984, Kristensen & Blackburn 1987), may provide the basis for an estimate of primary production and decomposition by the benthic community. The results can without serious error be converted to carbon flux using a conversion factor of 1 (Andersen & Kristensen 1988).

The present paper is a preliminary study on benthic metabolism, i.e. primary production, O_2 uptake and inorganic nitrogen dynamics, within a south-east Asian mangrove swamp. Benthic metabolism was determined from in situ measurements of $^{14}CO_2$, O_2 and inorganic nitrogen exchange across the sediment-water interface. The influence of light intensity on benthic metabolism and oxygen penetration depth was determined on sediments either being shaded by *Rhizophora apiculata* or exposed to direct sunlight. The role of the benthic community for turnover of organic matter in the present mangrove system is evaluated.

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MATERIALS AND METHODS

Study site. The work was carried out during January 1987 in the Ao Nam Bor mangrove; a small mangrove swamp on the southeast coast of Phuket Island, Thailand (Frith et al. 1976, Christensen 1978). This swamp, which is only about 200 m wide from inland to seaward edge at the study site, is bordered by a ca 500 m wide vegetation free tidal flat. There is no freshwater outflow, other than drainage water from the adjacent mainland during heavy rains. The macrophyte flora is dominated by the mangrove *Rhizophora apiculata* (Bl.) and the benthic macrofauna mainly consist of crabs (Ocypodidae and Grapsidae), snails (Cerithiidae), mudskippers (Gobioidea) and sipunculid worms (Frith et al. 1976).

Tidal range in the area is ca 2 m (1.0 to 2.5 m). The study site, however, is usually not covered by more than 1 m during high tide. On average, the sediment surface is inundated for 4 h per day and exposed to air for 20 h (except for small permanent pools). During high tide, salinity and water temperature are 35 ‰ and 28 °C respectively. However, at low tide during daytime the temperature of exposed sediment surfaces may rise to 35 to 38 °C.

Measurements were made at 2 stations ca 30 m from the seaward fringe of the mangrove forest and ca 15 m from a tidal creek (subzone 3b in Frith et al. 1976). The 2 stations, named SUN and SDW, were ca 5 m apart. The SUN station was exposed to direct sunlight 6 to 8 h a day (at noon: 2700 μE m^{-2} s^{-1}), whereas the SDW station was permanently shadowed by 'prop' roots and dense growth of *Rhizophora apiculata* (at noon: 288 μE m^{-2} s^{-1}).

Sediment handling. Cores for determination of sediment characteristics were sampled by hand with 5.6 cm i.d. plexiglass corers. Sediment cores were processed within 2 h after sampling. Those used for determination of density, porosity, organic content and dissolved inorganic nitrogen (DIN) were cut into 0–1, 1–2, 2–3, 3–4, 4–6, 6–8, 8–10 cm sections.

Sediment density was determined from the weight and volume of wet sediment samples. Porosity was calculated from the water loss at 100 °C for 12 h. Sediment organic content was measured by weight as (1) loss-on-ignition (LOI) at 500 °C for 12 h; (2) particulate organic carbon (POC); (3) particulate organic nitrogen (PON) as described by Kristensen & Andersen (1987). POC and PON were analysed by a Hewlett-Packard 185 B CHN-analyzer.

Pore water was obtained from sediment samples by centrifugation for 10 min at 580 *g* in double centrifuge tubes (Andersen & Kristensen 1988). The supernatant was stored frozen until analysis in duplicates by the standard autoanalyzer methods of Solórzano (1969) for NH_4^+ and of Armstrong et al. (1967) for NO_2^- and NO_3^-. Since the measured NO_2^- concentrations generally were less than 10 % of the NO_3^- results, NO_2^- will be included with the presented NO_3^- data.

Chlorophyll *a* content of surface sediment was determined in 3 replicates from each station. Each replicate (ca 2 g wet wt) consisted of 6 pooled samples, taken to a depth of 3 mm by a 7 mm i.d. glass tube. After sampling, replicates were added 1 to 2 drops of saturated $MgCO_3$ solution and extracted in 12 ml 90 % acetone. The mixture was vortexed for 1 min and kept in darkness at 5 °C overnight. The next day, after vortexing again, the supernatant was centrifuged for 5 min at 580 g. Absorbance at 665 and 750 nm was measured before and after acidification by one drop of 2 *N* HCl. Subsequent extractions, which revealed no detectable pigment absorbance, indicated a 100 % extraction efficiency. The chlorophyll *a* content was calculated according to the method of Parsons et al. (1984a).

Oxygen measurements by mini-electrodes. Depth of O_2 penetration inhto the sediment was measured by a membrane-coated polarographic 760 O_2 needle electrode (Diamond Electro-Tech, Inc.) with a platinum tip diameter of 35 to 40 μm (outer diameter 700 μm). Spatial resolution was less than 0.5 mm (Helder & Bakker 1985). The electrode was mounted on a manually driven micromanipulator, connected to an ammeter (Keithly 480 digital picoammeter) and recorded on a Minigor RE 501 (Goerz Electro) recorder.

Light and dark O_2 profiles from the 2 stations were obtained at in situ conditions. Profiles were measured in steps of 0.5 mm on cores both with and without a nonstirred water column (10 mm water depth). Light intensity was SUN: 1154 to 1538 μE m^{-2} s^{-1} and SDW: 115 to 346 μE m^{-2} s^{-1}.

The diffusive flux of O_2 into the sediment was estimated from the steepest gradient below the sediment surface (0.5 to 1.0 mm) by the one-dimensional version of Fick's first law of diffusion (Berner 1980):

$$J = -\phi D_s \Delta[O_2]/\Delta z \quad (1)$$

Where J = flux of O_2 into the sediment (μmol m^{-2} h^{-1}); D_s = apparent diffusion coefficient of O_2 in the sediment; ϕ = porosity; $\Delta[O_2]$ = O_2 gradient in the Δz = 0.5 to 1.0 mm layer of sediment. D_s was calculated from the porosity (ϕ) data and the temperature corrected (Li & Gregory 1974) diffusion coefficient (D) of O_2 in sea water ($D = 2.0 \times 10^{-5}$ cm^2 s^{-1} at 20 °C and 35 ‰ S; Broecker & Peng 1974) by the method of Iversen & Jørgensen (unpubl.).

^{14}C incubations. Carbon assimilation by benthic microalgae was determined in situ using a modified version of the ^{14}C-CO_2 technique described by Leach (1970). Surface sediment was sampled to a depth of ca 5 mm with a 7 mm i.d. piston equipped plastic tube.

The samples were gently transferred to the bottom of 7 mm i.d. Durham glass tubes. Subsequently, the Durham tubes were placed in the sediment securing that the sediment surface inside the tubes were at the level of the outside sediment. At each station 4 tubes were handled. Fixation rates in light (not corrected for dark uptake of ^{14}C) were assumed to reflect the net assimilation rates (Colijn & Jonge 1984). To each tube was added 1 ml GF/C filtered sea water containing 2 m*M* TCO_2 and 0.1 µCi ^{14}C-CO_2 (1.85 MBq $mmol^{-1}$). After 30 min the water phase was removed and the incubation was stopped by adding 4 % formalin. The content of each Durham tube was transferred to CO_2 permeable plastic scintillation vials. The samples were acidified with 2.5 ml 0.5 *N* HCl, and added 7.5 ml water and 10 ml gelforming scintillation liquid (Hydrocount, J. T. Baker Chemicals). After vortexing the samples were counted for 40 000 counts or 20 min in a Searle, Mark III, scintillation counter with a dpm correction option. The samples were counted twice over a period of 1 mo to assure that no labeled TCO_2 remained.

Flux measurements. Exchanges of O_2 and DIN at the 2 stations were determined from concentration changes during light and dark in situ incubations. At each station 4 transparent Plexiglass corers (25 cm long and 5.6 cm i.d.) were pushed 15 to 20 cm into the sediment, leaving 5 to 10 cm of the corer above the sediment surface. The water phase of the inserted corers were gently replaced with GF/C filtered sea water. The upper end of each corer was closed with a battery driven magnetic stirrer fitted to the opening, providing a water circulation well below the resuspension limit. During dark incubations the corers were wrapped in alu-foil. To prevent evolution of O_2 bubbles during light incubations, and thus an underestimate of photosynthesis, the added water was vacuum-boiled to an O_2 concentration of 28 to 59 % of full air saturation. The water added initially during dark incubations was close to O_2 saturation (73 to 93 %). Durations of light and dark incubations were 1.0 and 1.5 h respectively. Oxygen concentration in light never exceeded saturation, and in darkness never fell below 56 % saturation. Oxygen was determined by the Winkler titration technique (Parsons et al. 1984a). DIN (NH_4^+, NO_2^-, NO_3^-) was analysed and presented as earlier described.

Import-export samplings. The concentration of particulate carbon (PC) and nitrogen (PN) and DIN in the water of a tidal channel adjacent to the study site was determined at daytime during one tidal cycle. A sampling site was chosen at the channel outlet near the seaward fringe of the mangrove forest. Representative water samples (sampling depth: 10 to 30 cm) were taken at hourly intervals with a 60 ml syringe. The water was immediately filtered through GF/C filters using a swinnex-25 filter holder (Millipore Corp.), and stored in vials at −20 °C until analysis for DIN (NH_4^+, NO_2^-, NO_3^-). The filters were air dried and the content of PC and PN were determined on a CHN-analyzer.

Statistical analysis. The Student-Newman-Keuls (SNK) multiple comparisons test of means was used to determine significant factors within the various vertical sediment profiles. Differences in pairs of means, e.g. between the 2 stations, were tested using a 1-way ANOVA (Model I) analysis of variance.

RESULTS

Sediment characteristics

Since no spatial difference was observed, sediment characteristics are presented as pooled data from the 2 stations.

Profiles of density, porosity, organic content and DIN in the Ao Nam Bor mangrove sediment showed 2 horizontal zones. The upper 4 cm was composed of fine grained silty sediment (density: 1.66 to 1.71 g cm^{-3}; porosity: 0.63 to 0.70) (Table 1). Below this depth density and porosity decreased to 1.59 to 1.63 g cm^{-3} and 0.60 to 0.62 respectively, indicating a more densely packed lower strata composed of lighter peat material. Visual inspection confirmed the 2 layered structure; an upper ca 5 cm grey-brown zone of well sorted silty material (silt-zone) superposing a grey-black fibrous peat zone dominated by living and dead roots of *Rhizophora apiculata* (root-zone).

The organic content (measured as LOI, POC and PON) showed no significant changes with depth in the sediment (Table 1). However, a slight difference between the upper part of the silt-zone and the root-zone was evident for all 3 parameters. Thus, the C:N molar ratio of the organic matter increased from 24 to 27 with depth in the silt-zone ($p < 0.05$), and remained constantly high (28 to 29) in the root-zone. The contribution of POC to the LOI values (24.3 to 25.6 %) appeared relatively low, but it was close to the range usually found for other sediments, i.e. 30 to 35 % (Kristensen unpubl.). A fraction of the non-carbon LOI may, however, be clay or lattice bound water (Mook & Hoskin 1982). Inorganic carbon (carbonates) generally accounted for ca 1 % of the total carbon content at all depths.

Pore water NH_4^+ and NO_3^- showed maximum concentrations (75 and 21 µ*M*, respectively) in the upper 2 to 3 cm (Fig. 1). For NH_4^+ a slight, but not significant, decrease occurred below 3 cm depth. The profile of NO_3^- in Fig. 1 B, which unfortunately is based on only 1 sediment core (malfunction of the analytical equipment), showed a significantly higher concentration

Table 1 Vertical profiles of wet density, porosity, loss-on-ignition (LOI), particulate organic carbon (POC), particulate organic nitrogen (PON) and C:N molar ratio in sediments from the Ao Nam Bor mangrove. Mean values ± SE of 4 measurements

Depth (cm)	Density (g cm^{-3})	Porosity (cm^3 cm^{-3})	LOI (%)	POC (%)	PON (10^{-2} %)	C:N
0–1	1.66 ± 0.02	0.64 ± 0.01	7.36 ± 0.43	1.84 ± 0.14	9.2 ± 0.5	24.0 ± 0.8
1–2	1.71 ± 0.04	0.70 ± 0.03	8.21 ± 0.70	2.07 ± 0.21	9.7 ± 0.7	24.8 ± 1.0
2–3	1.68 ± 0.05	0.65 ± 0.02	8.22 ± 0.61	2.23 ± 0.32	9.9 ± 0.5	26.5 ± 2.0
3–4	1.69 ± 0.06	0.63 ± 0.03	8.46 ± 0.88	2.30 ± 0.59	9.6 ± 1.2	26.7 ± 3.3
4–6	1.59 ± 0.05	0.62 ± 0.04	9.24 ± 0.93	2.32 ± 0.30	9.7 ± 1.1	27.7 ± 0.9
6–8	1.63 ± 0.02	0.60 ± 0.03	8.24 ± 0.60	2.15 ± 0.18	8.5 ± 0.6	29.4 ± 0.5
8–10	1.64 ± 0.02	0.60 ± 0.01	8.40 ± 0.39	2.23 ± 0.10	9.0 ± 0.6	29.0 ± 1.3

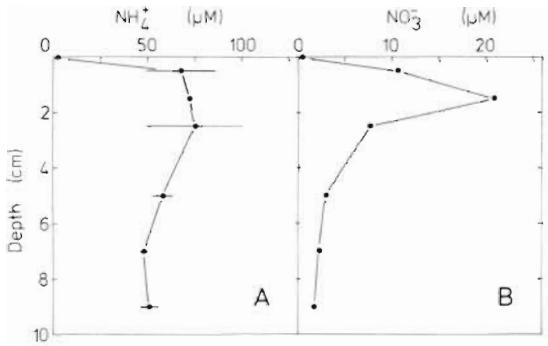

Fig. 1 Vertical profiles of (A) porewater NH_4^+ concentrations (means ± SE of 3 cores) and (B) porewater NO_3^- concentration. (Values based on 1 core)

above 4 cm depth than below ($p < 0.05$). However, this does not necessarily represent the average NO_3^- pattern in this mangrove sediment. The presence of NO_3^- deep in the sediment may be caused by nitrification associated to oxidized burrow structures and root-sediment interfaces.

Benthic oxygen uptake

Oxygen generally penetrated ca 2 mm into sediments of the Ao Nam Bor mangrove (Fig. 2). The effect of light/dark cycles on O_2 penetration were most dramatic when the sediment was covered with a stagnant water column. At the SUN station O_2 penetrated 2.5 mm into the inundated sediment when exposed to sunlight, but only 1.5 mm in darkness. A similar but less dramatic pattern was observed at the SDW station, i.e. 2.0 to 2.5 and 2.0 mm penetration depth respectively. At both stations the O_2 concentration at the sediment-water interface was undersaturated in darkness: 67 % (SUN) and 57 % (SDW) of full air saturation. In daylight, however, the interface became supersaturated with O_2 (SUN: 136 %; SDW: 103 %) due to microalgal photosynthesis. In air-exposed sediment O_2 penetration depth was similar in both light and darkness. Thus, at the SUN station O_2 penetrated constantly 1.5 mm into the sediment, whereas the SDW station exhibited a stable 2 mm oxic zone. The effect of light on O_2 concentration in air exposed sediment was detectable as supersaturation close to the surface; 146 % (SUN) and 128 % (SDW).

The estimated diffusive O_2 uptake was influenced by both water cover and sediment-type. Highest rates were obtained for sediments exposed to air in both light and darkness (SUN: 0.77 ± 0.09 mmol m^{-2} h^{-1} and SDW: 0.59 ± 0.05 mmol m^{-2} h^{-1}, Table 2), whereas the lowest rates were found for water covered sediments in darkness (SUN: 0.36 ± 0.07 mmol m^{-2} h^{-1} and SDW: 0.33 ± 0.02 mmol m^{-2} h^{-1}). The latter values, which are significantly lower than those obtained from exposed sediments ($p < 0.05$), apparently underestimate the true diffusive O_2 flux by ca 50 % due to undersaturation at the sediment surface. Average diffusive O_2 uptake was 1.29 times higher in exposed SUN than in exposed SDW sediment ($p \sim 0.05$) (Table 2). Rates of O_2 uptake measured directly by dark core incubations were 1.56 (SUN, $p < 0.01$) and 1.19 (SDW, $p \sim 0.10$) times higher than the estimated diffusive flux (Table 2). Thus, the directly measured flux in SUN sediment was 1.68 times higher than in SDW sediment ($p < 0.01$).

Benthic primary production

Primary production by the benthic microalgae appeared negatively affected by shading of *Rhizophora*

Table 2. Comparison of sediment O_2 uptake determined either from core incubations in darkness or estimated from O_2 profiles. Results from SUN and SDW station. Profile data are from measurements on cores without water cover. Means ± SE of 3 and 8 measurements respectively. Values are in mmol m^{-2} h^{-1}

Method	O_2 uptake	
	SUN	SDW
Incubation	1.19 ± 0.05	0.71 ± 0.13
Profile	0.77 ± 0.09	0.59 ± 0.05

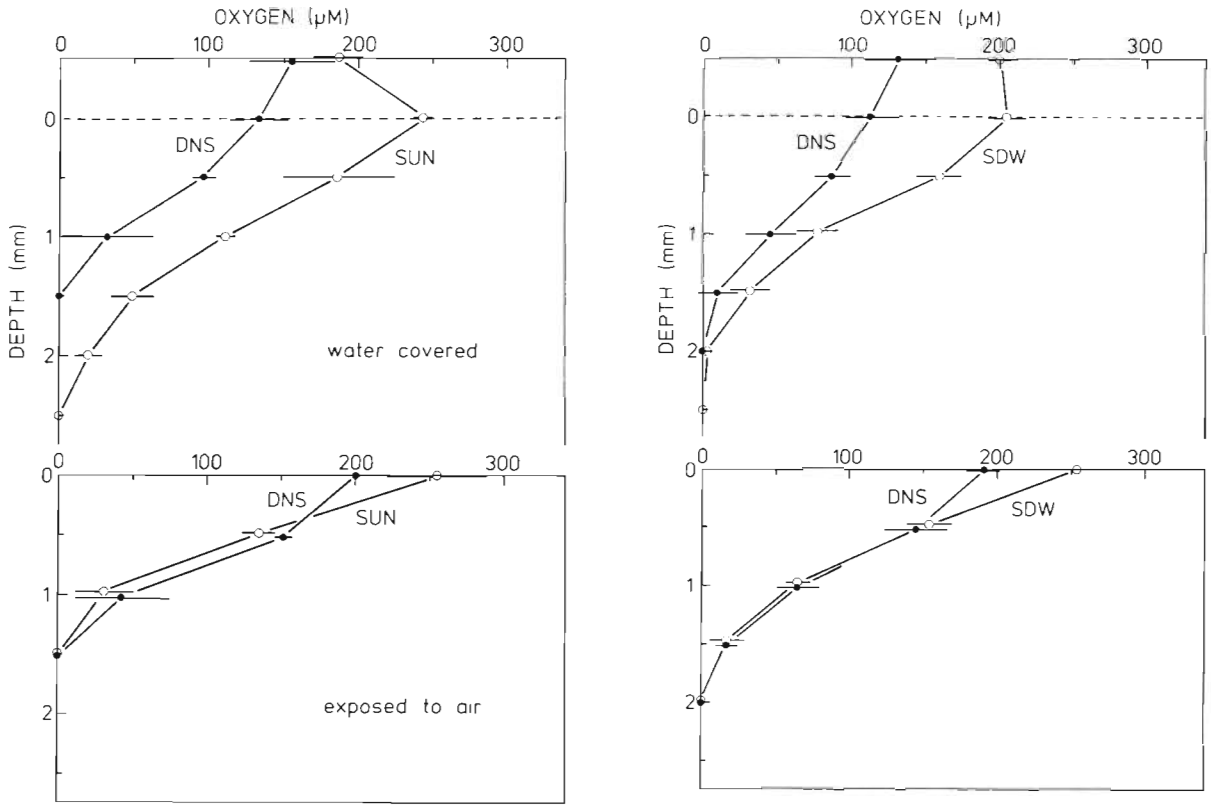

Fig. 2. Vertical profiles of O_2 in the surface layer of mangrove sediments. Left: sun-exposed sediment in light (SUN) and darkness (DNS). Right: sediment shaded by *Rhizophora apiculata* in light (SDW) and darkness (DNS). Profiles shown for water covered (upper) and air exposed (lower) sediments. Means ± SE of 4 measurements

apiculata (Table 3). The assimilation of ^{14}C and gross O_2 production (production in light + uptake in darkness) were 1.4 ($p < 0.05$) and 1.7 ($p < 0.025$) times higher at the SUN station than at the SDW station. However, the community photosynthetic quotient (CPQ) at the 2 stations (SUN: 1.47; SDW: 1.26 mol O_2/mol C) was not significantly different from 1 ($p > 0.05$).

Net O_2 production in light was, SUN: 0.87 and SDW: 0.51 mmol m^{-2} h^{-1}. On a daily basis (12 h light, 12 h darkness), however, O_2 uptake by the heterotrophic community exceeded the production by the benthic microalgae, i.e. a net O_2 uptake of 7.6 and 4.7 mmol $m^{-2}d^{-1}$ respectively.

The biomass of benthic microalgae at the 2 stations, measured as chlorophyll *a* in the upper 0 to 3 mm sediment layer, is shown in Table 3. The chlorophyll *a* content at the 2 stations was not significantly different ($p > 0.05$), although the value for the SUN station appeared 24 % higher than that for the SDW station. The assimilation number (mg C [mg Chl *a*]$^{-1}$ h^{-1}) was 0.75 (SDW) – 0.88 (SUN) from ^{14}C assimilation data and 0.95 (SDW) – 1.28 (SUN) from gross O_2 production data based on a CPQ of 1.0 (Andersen & Kristensen 1988).

Table 3. Chlorophyll *a* content (mg m^{-2}; 0 to 3 mm), gross O_2 production (mmol m^{-2} h^{-1}) and ^{14}C-CO_2 assimilation in mangrove sediments, exposed to direct sunlight (SUN) or shaded by trees (SDW). Mean ± SE of 3, 4 and 4 measurements respectively

Station	Chlorophyll *a*	Gross O_2 production	CO_2 assimilation
SUN	19.2 ± 2.2	2.06 ± 0.18	1.40 ± 0.15
SDW	15.5 ± 2.3	1.22 ± 0.21	0.97 ± 0.10

Dissolved inorganic nitrogen flux

Vertical gradients of pore water NH_4^+ and NO_3^- close to the sediment surface indicated an upward flux of DIN (Fig. 1). The directly measured DIN flux, however, was always directed towards the sediment-water interface (Table 4). No consistent relationship between DIN uptake by the sediment and light/dark cycles was found. The scatter in the data, especially for NH_4^+, may have blurred any particular relation.

Import-export

The tidal samplings indicated a substantial import of suspended particulate carbon (PC) and nitrogen (PN)

Table 4. Fluxes of DIN (NH_4^+, NO_3^-) from overlying water into sediment. Means ± SE of 3 measurements for SUN and SDW stations in light and darkness. Values are in μmol m^{-2} h^{-1}

Station	NH_4^+ flux	NO_3^- flux	Total DIN flux
SUN			
light	38.7 ± 63.9	43.9 ± 23.4	82.6
dark	29.2 ± 22.9	30.6 ± 2.7	59.8
SDW			
light	72.7 ± 33.4	29.7 ± 12.0	102.4
dark	103.5 ± 78.5	50.7 ± 4.3	154.2

during rising tides (Fig. 3). When water entered the channel at high velocity, the concentration of suspended material almost doubled within 1 h (Fig. 3C); subsequently a decrease occurred in proportion to water velocity. Water leaving the channel during receding tide was low in suspended particles. The C:N ratio of the particulate matter was lowest at low tide (115), but increased when water entered the channel at rising tide (Fig. 3D). Maximum C:N was reached at the highest water level (175).

Ammonium in the channel water was almost depleted at high tide (Fig. 3B). However, the decrease from 2.8 to 0.1 μ*M* commenced more than 2 h before any water water entered the channel. This indicates that factors other than tides may be responsible for NH_4^+ removal. The concentration of NO_3^- was low throughout the tidal cycle, 0.3 to 0.5 μ*M*. The highest concentration was observed at the end of the high tide period.

DISCUSSION

The biomass of benthic microalgae in the tropical Ao Nam Bor mangrove agrees with data from 5 Australian mangroves (Alongi 1988). However, estimates of both biomass and primary production (Table 3) are low compared to values from intertidal flats of the temperate zone (e.g. Colijn & Jonge 1984). The assimilation number of the mangrove algae (0.75 to 1.28 mg C [mg Chl *a*]$^{-1}$h^{-1}), on the other hand, is in the upper range of that previously found in situ for benthic microalgae (Cadee & Hegeman 1974, Admiraal & Peletier 1980, Rasmussen et al. 1983, Calijn & Jonge 1984). Such high assimilation numbers, indicating high photosynthetic efficiencies, are characteristic of microalgae from tropical waters (Parsons et al. 1984b).

Shading by macrophytes is a well-known limiting factor for benthic primary production in intertidal areas (Van Raalte et al. 1976). The reduction of both microalgal biomass (20 %) and primary production (31 to 41 %) beneath the canopy of *Rhizophora apiculata* (SDW) relative to the sun exposed sediment (SUN) indicate that light limitation may occur at the former station. Thus, the shadow effect of *R. apiculata* explains the observed difference in microalgal biomass and production between the 2 stations, but the overall low benthic primary production in the Ao Nam Bor mangrove is caused by other factors.

Nutrient availability (i.e. inorganic nitrogen) may limit benthic microalgal production in intertidal areas (van Raalte et al. 1976, Darley et al. 1981, Rutgers van der Loeff et al. 1981). The pools of dissolved inorganic nitrogen (DIN = $NO_3^- + NH_4^+$) in the Ao Nam Bor mangrove (overlying water, 0.4 to 3.0 μ*M*; sediment pore water, 50 to 90 μ*M*; Figs. 1 and 3B) are several times smaller than those usually found in intertidal areas (Hartwig 1978, Rutgers van der Loeff et al. 1981). Accordingly, the dichotomy between the expected DIN flux across the sediment-water interface, deduced from the vertical profiles of NH_4^+ and NO_3^- (Fig. 1), and the directly measured DIN flux (Table 4) suggests that microalgae at the sediment surface may be DIN starved. The algae assimilates DIN both from below and above the sediment-water interface, despite low concentration in the overlying water, thereby acting as a 'filter' for the DIN flux from the sediment (Henriksen et al. 1980, Andersen & Kristensen 1988). The sediment DIN uptake observed in darkness may partially be caused by continued algal (and root) assimilation during nonphotosynthetic periods as observed by Andersen & Kristensen (1988). Microalgae that become nitrogen deficient during the day are known to make up for the deficiency by assimilation of DIN in the dark (Dugdale & Goering 1967, Kristensen unpubl.). This may particularly be true in the present study because the dark incubations were initiated less than ½ h after the light incubations.

The DIN dynamics within a mangrove swamp should be reflected in the water of the adjacent tidal channels (Fig. 3B). The gradually decreasing NH_4^+ concentration observed in the morning before the tide enters the channel may representsediment uptake due to increasing photosynthesis of the mangrove flora. When the tide reaches the channel, the concentration of NH_4^+ in the channel water and incoming seawater are similar. At low tide in the afternoon the concentration of NH_4^+ returns to a higher level due to ceased plant uptake and percolation from the channel banks. The tidal concentration pattern of NO_3^- suggests that higher nitrification occurs at high tide than low tide. However, the exact influence of nitrification and plant uptake on the DIN dynamics in channel waters needs to be assessed by following the concentration pattern during several tidal cycles; both during day and night.

Oxygen penetration depth found for the present mangrove sediment (Fig. 2) is within the range usually

found in silty intertidal sediments (Revsbech et al. 1980, Revsbech & Jørgensen 1986). The estimates of O_2 uptake by the mangrove sediment, derived from the profiles in air exposed sediment cores, only account for 64 to 84 % of the measured total O_2 uptake (Table 2). Similarly, Revsbech & Jørgensen (1986) and Andersen & Helder (1987) noted that O_2 uptake rates estimated from profiles generally are in the range of 30 to 90 % of measured total rates. Estimated rates represent a balance between diffusional supply of O_2 to the sediment and rate of O_2 consumption in the sediment. Oxygen profiles therefore only reflect microbial and chemical O_2 demand, whereas the directly measured total rates, in addition, include the demand from the macro- and meiofauna present. Some of the difference may also be caused by the irregular topography of the sediment surface.

The present study provides, although with spatial and temporal limitations, the basis for a preliminary quantitative evaluation of benthic community metabolism in the Ao Nam Bor mangrove. Gross and net daily benthic primary production are 12 to 25 and 6 to 10 mmol C m^{-2} d^{-1} respectively, when extrapolated to 12 h daylight. Estimates of tree production in the Ao Nam Bor mangrove forest, based on litterfall data corrected for production of twigs, trunks and roots (Bunt et al. 1979), are 118 to 172 mmol C m^{-2} d^{-1} (S. Poovachiranon pers. comm.). Accordingly, benthic primary production may account for 4 to 20 % of the tree production in this mangrove (exclusive of epiphytic micro- and macroalgae on mangrove roots).

Rate of O_2 uptake, which usually measures the oxidation of organic matter by both aerobic and anaerobic heterotrophs (Andersen & Hargrave 1984, Kristensen & Blackburn 1987, Andersen & Kristensen 1988) indicates a relatively low rate of decay in this mangrove sediment. However, this approach should be taken with caution, because the motile benthic fauna (e.g. sesarmid crabs) will not be included in assays of benthic O_2 uptake. These animals may consume a large fraction of the litterfall (Robertson 1986, Kofoed unpubl.). Organic matter originating from *Rhizophora apiculata*, except for the leachable fraction, is known as refractory to microbial decay in the sediment (Rice & Tenore 1981, Benner & Hodson 1985). Dead algal cells, on the other hand, generally decompose 5 to 10 times faster than leaf tissues (Boonruang 1978, Rice & Tenore 1981, Twilley et al. 1986a). Benthic algae may therefore represent an essential input of labile organic matter to the microbial detritus food chain, as stressed by the close correlation between benthic primary production and O_2 uptake at the 2 stations (Tables 2 and 3). The diurnal O_2 uptake, corrected for algal decay (O_2 demand during organic carbon decay equals O_2 evolution during organic carbon production), provides 4.7 to 7.6 mmol O_2 m^{-2} d^{-1} (i.e. 27 % of total dark O_2 uptake) for the decomposition of tree material (including epiphytic algae) in the sediment. This is much less than needed for a total mineralization of all the tree material produced, even when leaching and assimilation by leaf

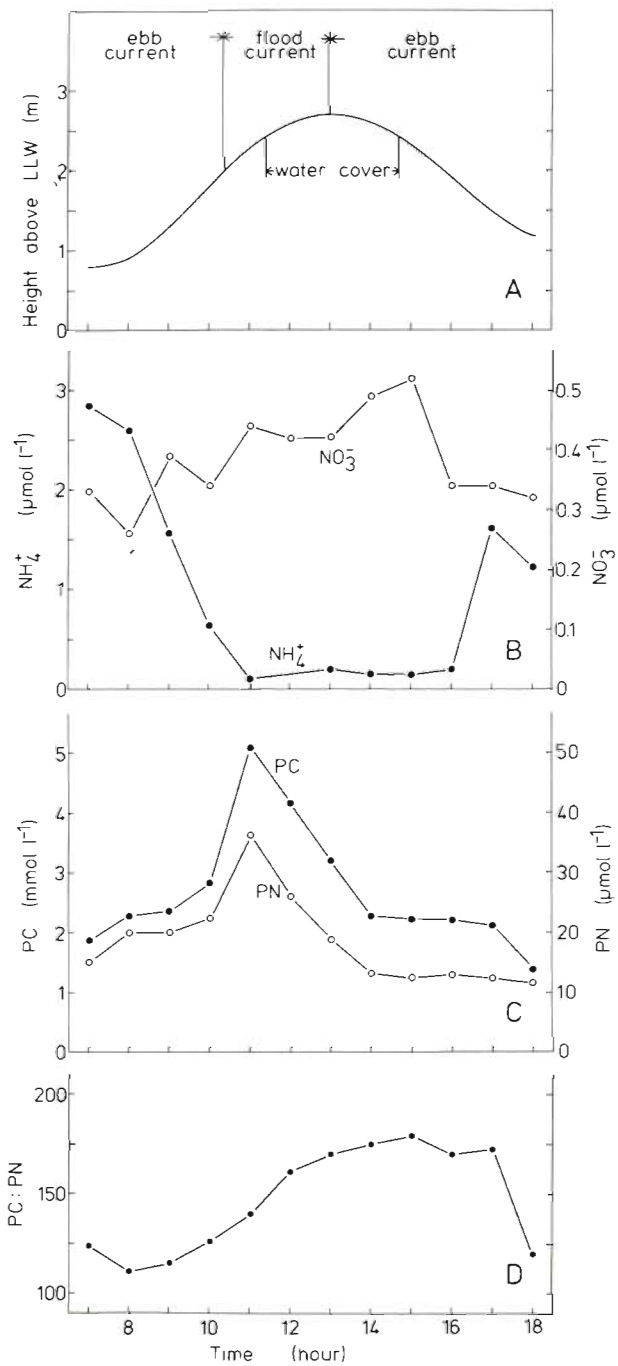

Fig. 3. Load of dissolved and suspended material in water samples from a tidal channel adjacent to the study site. One tidal period was followed. (A) Water level above LLW with indication of water current direction and inundation time at study site. (B) NH_4^+ and NO_3^- concentration. (C) Particulate carbon and nitrogen. (D) C:N ratio of suspended particles

eating crabs are considered. The low mineralization rate of tree material indicates a net accumulation of low degradable organic matter in the Ao Nam Bor mangrove; in accordance with the commonly observed rapid accretion of mangrove forests in south-east Asia (Macnae 1968).

The 2-layered structure of the mangrove sediment is probably the combined result of sedimentation during high tides, faecal pellet deposition and root growth (Table 1). The high concentration of suspended particles in the water entering during high tides apparently originates from the tidal mudflat outside the mangrove forest (Fig. 3 C). When the flood reaches the mudflat, material that has been loosened by wave action is flushed into the mangrove swamp. Later at high tide, when the water current ceases, the material is deposited as a silt layer on the sediment surface. Sedimentation may be of considerable magnitude, since the difference in concentration of suspended particles in water entering and leaving the mangrove swamp is as high as 3 mmol C l^{-1} and 25 µmol N l^{-1}. The high C:N ratio of the suspended material suggests that a major fraction is carbonates probably of coral origin (Fig. 3 D). This is in contrast to the mangrove sediment that hardly contains any carbonates.

This study suggests that the benthic community in mangrove forests is an important site for organic matter production and decomposition. However, more work is needed to elucidate the following points: (1) temporal and spatial variations in benthic metabolism; (2) exact causes for the low benthic primary production; (3) quantitative significance of aerobic and anaerobic microbial decay of intact leaves, leaf detritus and microalgae; (4) role of tidal transport in organic matter dynamics in mangrove systems.

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