

Transformation and exchange processes in the Bangrong mangrove forest-seagrass bed system, Thailand. Seasonal and spatial variations in benthic metabolism and sulfur biogeochemistry

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ABSTRACT: Sediment cores from 6 stations along a mangrove forest-seagrass bed transect in the Bangrong area, Thailand, were studied for sediment metabolism (TCO₂ production and O₂ uptake) and sulfur cycling (sulfate reduction rates and inorganic sulfur pools) in wet and dry seasons over a 2 yr period. Total sediment metabolism, measured as TCO₂ production, was highest at the mangrove forest sites and decreased along the transect. Sulfate reduction, however, increased along the transect and attained highest values in the seagrass sediments. Sulfate reduction was generally less important in terminal degradation of organic matter (<2 to 44%) in mangrove forests compared to subtidal sediments in general, and redox potentials revealed a relatively high oxidation level of the sediments along the transect (>0 mV), favoring mineralization processes that employed more oxidized electron acceptors than sulfate. The very low sulfate reduction rates at high and mid-intertidal stations in the mangrove forest were probably caused by oxidation of the sediments due to prolonged air exposure during low tide, an abundant crab population with deep burrows and release of oxygen from roots. There were no major differences among seasons in sediment metabolism, whereas the vegetated sites experienced sulfate reduction activity up to 4 times higher during the wet compared to dry season. Sulfur pools were low in the Bangrong mangrove forest compared to other mangrove sites; lowest pools were coincident with high tidal elevation and presence of rooted vegetation, suggesting that the oxidation processes controlled the pool sizes rather than the sulfate reduction rates. There were no major seasonal effects on the sulfur pools along the transect.

KEY WORDS: Sediments · Mangrove forest · Seagrass beds · Sulfur cycling · Sulfate reduction

INTRODUCTION

Mangrove forests and seagrass beds are important coastal ecosystems in tropical areas. The decomposition rate of mangrove and seagrass litter is controlled by a number of factors, e.g. season, tides, nutrient level, litter type and benthic fauna (Robertson & Daniel 1989, Kristensen et al. 1995). Sulfate reduction is generally considered the most important anaerobic decomposition process in mangrove and tidal flat sediments, as alternative anaerobic electron acceptors (e.g. NO₃⁻, Fe) are only present at low concentrations (Holmer et

al. 1994, Kristensen et al. 1995, 1998). Despite the relatively constant temperatures and day length throughout the year in the tropics, changes in other climatic parameters, such as precipitation, wind and solar radiation, may cause significant variability in the physical environment. A distinct seasonal pattern with peak litter fall during the rainy season has been found in many tropical mangrove forests (Woodroffe 1982, Lu & Lin 1990, Tam et al. 1998). However, most studies of benthic metabolism have been conducted during the dry season (Kristensen et al. 1992, 1995), and only a few have examined the wet season (Alongi 1994a,b, Nedwell et al. 1994).

Nutrient concentrations are generally low in mangrove and seagrass ecosystems due to efficient and

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rapid cycling between living pools and detritus (Harrison 1989, Kristensen et al. 1995, Mateo & Romero 1996). Mangrove detritus has high C:N ratios and a significant fraction of the organic matter is considered to be refractory humic compounds and geopolymers (Benner et al. 1990, Kristensen et al. 1994). This is probably an important cause of the observed low rates of mineralization in mangrove ecosystems despite the ambient high temperatures (Kristensen et al. 1992, 1995). Decomposition rates may vary significantly among mangrove plant species, with differences related to anatomy and chemical composition (Benner et al. 1990). Furthermore, the fragmentation and consumption of mangrove leaves by crabs may increase the decay rates by up to 2 orders of magnitude (Robertson 1986, Kristensen & Pilgaard 1999).

The tidal regime has a major influence on the structure and the dynamics of benthic communities. In high intertidal areas the sediment is only inundated for a short period during spring tides and the benthic community appears semi-terrestrial. Aerobic processes dominate due to the penetration of crab burrows and tree roots deep into the sediments (Tomlinson 1986, Eshky et al. 1998). Sulfate reduction may therefore be of minor importance in the mineralization of organic matter (Kristensen et al. 1995). The duration of inundation is longer in low intertidal mangrove forest areas. The benthic community is of more marine origin, but faunal diversity and abundance are low in the unpredictable environment. Surface sediments are usually oxidized, but due to the sparse benthic fauna, anaerobic processes may dominate mineralization in the deeper layers with sulfate reduction being responsible for more than half of the total benthic metabolism (Kristensen et al. 1992, 1995). Seagrasses cannot survive long periods of air exposure and are only found in low intertidal areas, where tidal influence is less pronounced. Enhanced mineralization rates have generally been measured in seagrass areas (Blackburn et al. 1994). Aerobic mineralization is important in these sediments, but enhanced rates of sulfate reduction have also been found, probably due to higher nutrient levels and degradability of detritus pools (Blackburn et al. 1994).

This paper describes a 2 yr study of seasonal variations in particulate organic matter (carbon and nitrogen), sediment metabolism (O_2 , TCO_2) and sulfur cycling (sulfate reduction rates and sulfur pools) along a mangrove forest-seagrass bed transect. The study was conducted at 3 stations within and at 3 stations outside

the Bangrong mangrove forest, Thailand, during 2 dry and 2 wet seasons. The work is part of a larger survey of nutrient dynamics and mineralization processes in the Bangrong mangrove forest-seagrass bed transect (Holmboe et al. unpubl., Holmer et al. unpubl., Kristensen & Pilgaard in press, Kristensen et al. unpubl., Suraswadi et al. unpubl.).

MATERIALS AND METHODS

Study site. The examined locations were situated in the Bangrong mangrove forest ($8^{\circ} 03' N$, $98^{\circ} 25' E$) and in the adjacent seagrass beds on the northeastern coast of Phuket Island, Thailand (Fig. 1). The climate in the area is monsoonal with an annual precipitation of about 2300 mm. The dry season extends from December to April and the wet season from May to November. The annual average temperature and salinity are $28^{\circ}C$ and 35 PSU, respectively. The tidal range is 3 and 1 m at spring and neap tide, respectively.

The study was conducted in 1996-97 with a total of 4 sampling periods, 2 during the dry season (January 1996 and 1997) and 2 during the wet season (August 1996 and 1997). Six stations were established along the mangrove forest-seagrass bed transect. Three stations were selected in the mangrove forest: Stn MA was situated close to the landward edge of the mangrove forest at an elevation of about 0.9 m above mean water

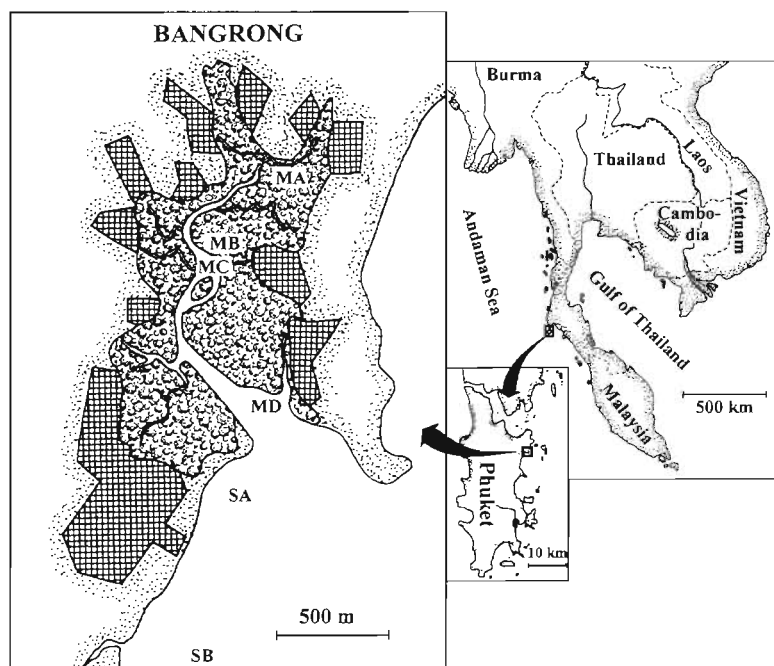


Fig. 1. Sampling stations in the Bangrong mangrove area on the east coast of Phuket Island in southern Thailand. Hatched area represents shrimp farming locations

level (MWL). The vegetation was dominated by *Rhizophora apiculata*, *R. mucronata* and *Ceriops tagal*, and the sediment was intensively bioturbated by sesarimid and ocypodid crabs. Stn MB was situated in the mid-intertidal zone between stilt roots of *R. apiculata* and *R. mucronata*, about 10 m from the main channel at an elevation of about 0.6 m above MWL. Stn MC was established about 0.2 m above MWL adjacent to Stn MB at a non-vegetated mudflat in the main channel. Three stations were established outside the mangrove forest: Stn MD was situated about 50 m outside the forest at a non-vegetated low-intertidal mud- and sandflat at 0.1 m below MWL. Two seagrass stations were situated about 500 (Stn SA) and 800 m (Stn SB) from the mangrove forest. Both stations were established in a low-intertidal sandy sediment at 1.4 and 1.3 m below MWL, respectively. Stn SA was sparsely vegetated with *Enhalus acoroides* (L.f.) Royle in the turbid water from the mangrove forest, and Stn SB was densely vegetated with *E. acoroides* in water turbid from wave action.

Collection of samples. For determination of sediment-water fluxes (O_2 , TCO_2) and pore water sulfate (SO_4^{2-}), 3 sediment cores (8 cm i.d., length 20 cm) were sampled per station during low tide. At the same time 2 sediment cores (8 cm i.d., length 15 cm) were sampled to determine O_2 uptake by air-exposed sediment, 3 cores (2.6 cm i.d., 20 cm length) for determination of sulfate reduction rates and sulfide pools, 3 cores (5 cm i.d., 20 cm length) to determine solid phase characteristics (organic content) and 3 cores (5 cm i.d., 20 cm length) for redox measurements. Cores were collected close to the vegetation, but if possible without cutting roots and rhizomes to prevent leakage of root exudates. Attempts were made to sample cores without visible traces of benthic macrofauna to limit any bioturbation effect.

Sediment fluxes. The sediment cores were brought to the laboratory while still air exposed. Seawater was added from the location to a height of 9 cm and the cores were pre-incubated for 3 to 5 h at *in situ* temperature in darkness. Flux measurements of O_2 and TCO_2 used 3 to 4 h closed-core incubations in darkness. The cores were placed in a thermostatted (28 to 29°C) seawater tank and supplied with a stirring magnet driven by an external rotating magnet (60 rpm). The water phase in the cores was replaced 1 h before initiating the incubation. An additional core containing only seawater from the location was included to determine the water phase contribution to the measured concentration changes. Water samples were taken at the start and end of incubation, assuming constant concentration change with time. This was occasionally verified by sequential samplings (data not shown). The sampled water was filtered through pre-

combusted GF/F filters and subsamples for O_2 and TCO_2 were analyzed immediately. The standard Winkler technique was used for O_2 analysis. TCO_2 was analyzed by the flow injection/diffusion cell technique of Hall & Aller (1992).

Sediment O_2 uptake was measured during air exposure in 2 campaigns (January and August 1996). The darkened sediment cores were sealed with a rubber stopper, in which a polarographic oxygen electrode (Radiometer, Denmark) was inserted leaving an air space of 1 to 2 cm above the sediment surface. The O_2 consumption was determined from concentration changes over a 12 h incubation period (Kristensen et al. 1992).

Sulfate reduction rates and sulfur pools. Sulfate reduction rates were determined by the core injection technique of Jørgensen (1978). A volume of 2 to 10 μ l of $^{35}SO_4$ solution (70 to 110 kBq) was injected at 1 cm intervals down to 18 cm in the 2.6 cm i.d. cores. After incubation with air-exposed sediment surface for 12 h in darkness, cores were sectioned into 1 cm (0 to 4 cm) and 2 cm intervals (6 to 16 cm) and preserved in 1 M zinc acetate. Short-time incubations (1 to 2 h) revealed sulfate reduction rates in the same range, emphasizing that reoxidation of the label was not a significant methodological problem in sediments where the penetration of oxygen and pools of reoxidants (Fe, Mn) were low (data not shown). Samples were stored frozen until distillation according to the 1-step procedure of Fossing & Jørgensen (1989). Pools of total reduced sulfides were determined by the spectrophotometric method of Cline (1969).

Pore water extractions. One day after incubations, the flux cores were sectioned into 1 cm (0 to 4 cm) and 2 cm intervals (6 to 20 cm). Pore water from the sandy sediment (Stns MD, SA and SB) was obtained by centrifugation in double centrifuge tubes (10 min at 1500 rpm) and from the silty stations (Stns MA, MB and MC) (10 min at 3000 rpm) in single centrifuge tubes. The supernatant was filtered by use of GF/F filters, and samples were taken for analysis of SO_4^{2-} by ion-chromatography on a Dionex autosuppressed anion system with carbonate/bicarbonate as eluent.

Solid phase measurements. Sediment cores for solid phase characteristics were sectioned into the same depth intervals as those used for pore water extractions. Sediment density was determined as the weight of a known sediment volume. Water content was determined as weight loss after drying at 105°C for 12 h, and particulate organic carbon (POC) and nitrogen (PON) were measured according to the method of Kristensen & Andersen (1987).

Redox measurements. Redox potential (E_h) was measured in the overlying water and at 1 (0 to 5 cm) and 2 cm intervals (5 to 16 cm) according to Hargrave

(1972), using a platinum electrode with a calomel electrode as reference. A stabilization time of 2 min was used before each reading.

Statistical analysis. A 2-way factorial analysis of variance (ANOVA) was used to test the main effect of season (Wet and Dry) and the different stations along the transect (6 stations).

RESULTS

Sediment characteristics along the transect

Sediment characteristics were only determined once (dry season in 1996) during the study period (Table 1). Organic content was 40 to 50% higher at Stn MB than at Stns MA and MC. The C:N ratio, on the other hand, was similar at the 3 mangrove forest sites (22 to 25). The organic carbon and nitrogen content at Stn MD and the seagrass stations (Stns SA and SB) only accounted for 17 to 48% and 3 to 20% of the level at Stn MB, with much higher C:N ratios (51 to 101).

The sediment at the high intertidal site (Stn MA) was inundated for about 5 h during spring tides and remained continuously air exposed during neap tides. There were only minor physical tidal effects on the sediment, which was characterised by a high silt and clay content (around 80%, Holmer et al. unpubl.) and an extensive root system below an upper silt layer (0 to 2 cm). The benthic fauna was abundant and consisted of burrow-dwelling ocypodid and sesarmid crabs (72 to 117 m⁻²). The *Rhizophora*-vegetated station (Stn MB) was also characterized by high silt and clay content (around 70%, Holmer et al. unpubl.) and an extensive root system below an upper silt layer (0 to 1 cm). Benthic fauna was almost absent except for a scattered occurrence of sipunculids and sesarmid crabs. Stn MB was submerged for 7 h during spring tides and remained air exposed at neap tides. The

unvegetated mangrove creek station (Stn MC) can be characterised as a tidal flat within the mangrove forest. This station was physically disturbed during tidal inundation and had a lower silt and clay content (about 50%, Holmer et al. unpubl.) than the other mangrove forest sites. Stn MC was water covered for 11 and 13 h at spring and neap tides, respectively. There was a considerable abundance of burrowing fiddler crabs *Uca* sp. (55 m⁻²), and mudskippers *Periophthalmus* sp. and *Scartelaos* sp. The silt and clay content decreased further along the transect to 5–20% (Holmer et al. unpubl.) at the stations outside the mangrove forest, which were exposed to strong tidal currents and waves. The unvegetated site (Stn MD) was inundated for 12 and 17 h at spring and neap tides, respectively. The seagrass stations were only air

Table 1. Characteristics of sediments along the examined transect in the Bangrong mangrove forest. Particulate organic carbon (POC) and nitrogen (PON) and C:N ratio of the organic matter represent depth average (0 to 20 cm) of 2 sediment cores (\pm range) sampled during the dry season in January 1996

Stn	POC (mmol g dw ⁻¹)	PON (μ mol g dw ⁻¹)	C:N (mol)
MA	2.45 \pm 0.37	111.0 \pm 24.0	22.6 \pm 3.7
MB	3.65 \pm 0.23	167.0 \pm 13.0	21.9 \pm 1.5
MC	2.67 \pm 0.30	109.0 \pm 25.0	25.3 \pm 4.8
MD	1.77 \pm 0.47	33.0 \pm 8.0	55.5 \pm 14.3
SA	0.64 \pm 0.11	5.0 \pm 7.0	101.1 \pm 47.5
SB	0.62 \pm 0.14	15.0 \pm 8.0	50.5 \pm 21.8

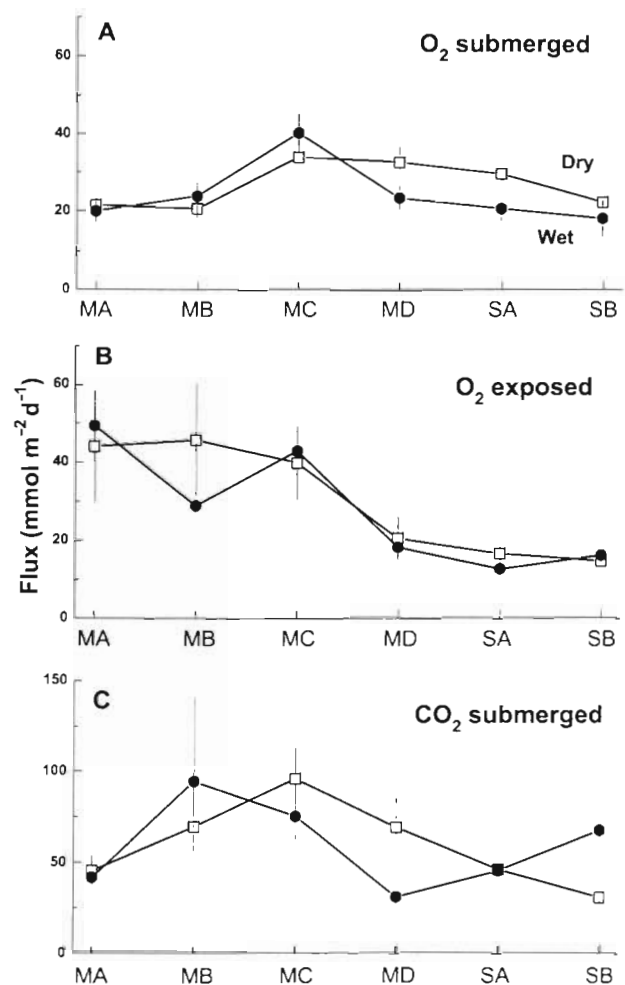


Fig. 2. (A,B) Rates of O₂ uptake and (C) CO₂ release (mmol m⁻² d⁻¹) across the sediment-water interface in darkness. O₂ uptake is measured both on (A) submerged and (B) air-exposed sediments. Rates are given for dry (n = 6) and wet (n = 3) seasons (\pm SEM) for the submerged fluxes, and for air-exposed fluxes (only measured in 1996) (n = 2, \pm range)

Table 2. Community respiratory quotient (CRQ) in dry and wet seasons at the 6 examined stations. Values represent mean (\pm SEM, $n = 3$ to 6)

Stn	CRQ dry	CRQ wet
MA	2.09 \pm 0.32	2.21 \pm 0.40
MB	3.24 \pm 0.42	3.54 \pm 1.16
MC	2.87 \pm 0.64	1.85 \pm 0.11
MD	1.99 \pm 0.28	1.39 \pm 0.22
SA	1.60 \pm 0.16	2.32 \pm 0.45
SB	1.36 \pm 0.16	4.05 \pm 0.74

exposed for short periods (~ 1 h) during spring tides. The benthic fauna was sparse at the 3 stations outside the mangrove forest. We observed a few polychaete burrows and brittle stars among the seagrasses, whereas mobile epifauna (cerithidic snails and hermit crabs) was quite abundant at the unvegetated site.

Sediment fluxes: oxygen and TCO_2

Rates of sediment O_2 uptake during submerged conditions increased along the transect within the mangrove forest, attaining highest rates at Stn MC, and decreased with distance from the mangrove forest, with 33 to 55% lower rates at Stn SB (Fig. 2A). There was no significant seasonal variation in sediment O_2 uptake during submerged conditions at the mangrove forest sites (Wet vs Dry, $p > 0.2$, $n = 6$), whereas it was lower at Stn SA (18 to 31%) during the wet season (Wet vs Dry, $p < 0.01$, $n = 6$). The air-exposed sediment O_2 uptake was up to 2 times higher compared to sediment O_2 uptake during submerged conditions within the mangrove forest, particularly at the vegetated sites, whereas it was up to 50% lower than sediment O_2 uptake during submerged conditions outside (Fig. 2B). There was no major seasonal variation in air-exposed sediment O_2 uptake. CO_2 production was up to 3 times higher at Stns MB and MC than at the other stations (Fig. 2C). The seasonal effect on CO_2 production varied among stations. At Stn SB CO_2 production was highest during the wet season (Wet vs Dry, $p < 0.003$, $n = 6$), whereas the CO_2 production was similar during the 2 seasons (Stns MA, MB, MC, SA) or highest during the dry season (Stn MD) (Wet vs Dry, $p = 0.07$, $n = 6$).

The community respiratory quotient was calculated as the ratio between CO_2 production and sediment O_2 uptake during submerged conditions, and was highest (>2.1) within the vegetated mangrove forest and lowest at the seagrass stations (<1.6) during the dry season (Table 2). The community respiratory quotient was also highest at Stn MB (3.9) during the wet season, but also attained high values at the seagrass stations (2.3 to 4.1).

Sulfate reduction rates

Sulfate reduction rates were generally low within the mangrove forest and increased towards the seagrass stations (Fig. 3). At the 2 vegetated mangrove sites (Stns MA and MB) rates increased with depth, whereas the unvegetated tidal flats (Stns MC and MD) had a subsurface maximum at 2 to 3 cm depth, with constant or decreasing rates below. At the seagrass stations maximum rates were also found in a subsurface layer (2 to 5 cm), with significantly higher rates during the wet season.

The depth-integrated sulfate reduction rates were low within the mangrove forest (<8 $\text{mmol m}^{-2} \text{d}^{-1}$) and

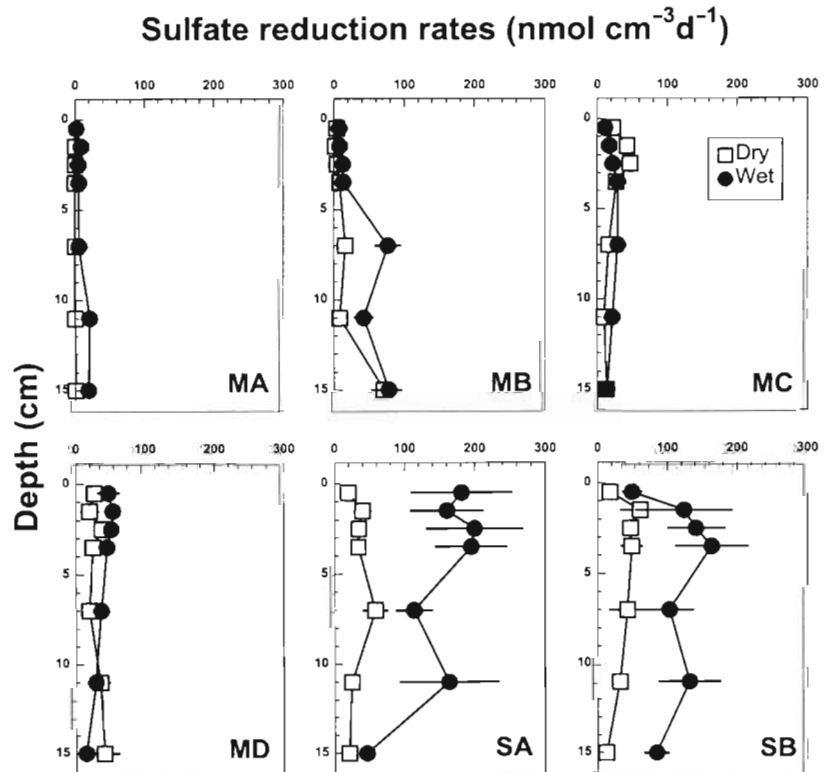


Fig. 3. Depth profiles of sulfate reduction rates ($\text{nmol cm}^{-3} \text{d}^{-1}$) in the upper 15 cm of the sediments at the 6 examined stations during the dry and wet season. Data symbols represent mean ($n = 3$ to 6, \pm SEM)

significantly higher in the seagrass beds (6 to 22 $\text{mmol m}^{-2} \text{d}^{-1}$) (Stns MA, MB and MC vs Stns MD, SA and SB, $p < 0.014$) (Fig. 4A). Rates were generally higher during the wet season, especially at the seagrass stations (up to 4 times) (Wet vs Dry, $p < 0.05$ at Stns MA, MB, SA and SB, $n = 6$). The contribution of sulfate reduction to sediment metabolism (CO_2 production) also increased along the transect, accounting for <2% at Stn MA during the dry season to ~32 to 44% at the seagrass stations during the wet season (Fig. 4B).

Total reducible sulfide pools

The total reducible sulfide pools were low throughout the examined depth interval at Stn MA, whereas

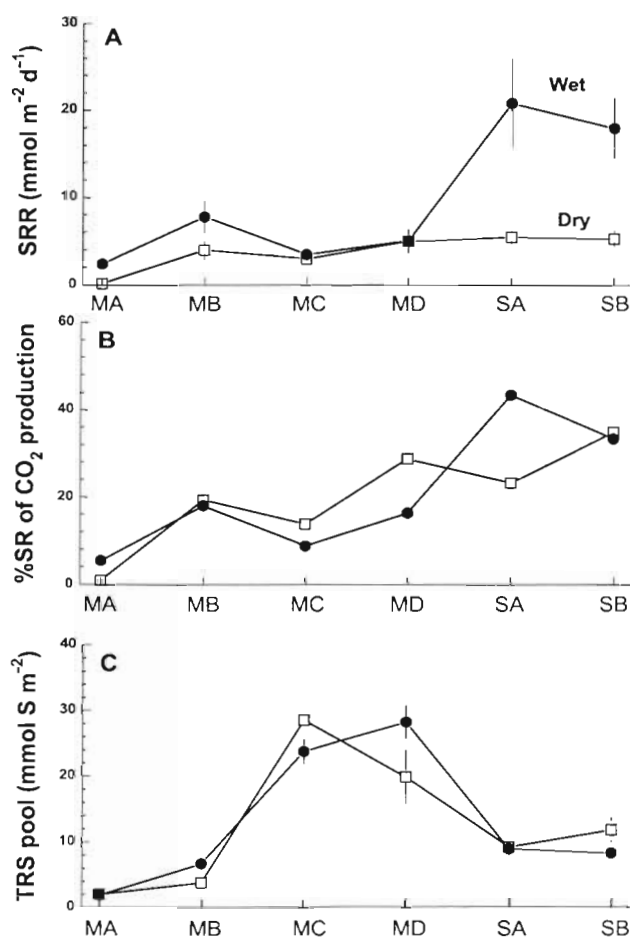


Fig. 4. (A) Depth-integrated sulfate reduction rates (SRR) (0 to 16 cm, $\text{mmol m}^{-2} \text{d}^{-1}$) along the transect in dry ($n = 3$) and wet seasons ($n = 6$) (\pm SEM). (B) Sulfate reduction rates converted to carbon equivalents ($2 \times$ SRR) as percentage of the total sediment metabolism (CO_2 production) along the transect. (C) Depth-integrated pools of total chromium reducible sulfides (TRS) (0 to 16 cm, mmol S m^{-2}) along the transect in dry ($n = 3$) and wet seasons ($n = 6$) (\pm SEM)

the pools at Stn MB were highest in the surface layer and decreased with depth, especially during the dry season (Fig. 5). At the non-vegetated stations total reducible sulfide pools increased with depth (up to 250 nmol cm^{-3}). Highest values at Stn MC were found in the dry season, and at Stn MD in the wet season. The total reducible sulfide pools increased slightly with depth at the seagrass beds (up to 132 nmol cm^{-3}). At Stn SA highest values were found in the wet season, whereas there were no significant differences between seasons at Stn SB.

The depth-integrated total reducible sulfide pools were low at the vegetated mangrove and seagrass sites (2 to 12 mmol S m^{-2}), and highest at the non-vegetated stations (22 to 27 mmol S m^{-2}) (Fig. 4C). There was no clear seasonal trend in the total reducible sulfide pools along the transect (Wet vs Dry, $p > 0.05$).

Pore water sulfate

Sulfate concentrations were high (>26 mM) and almost constant with depth at the stations outside the mangrove forest, whereas a considerable change with depth and a large difference between seasons were observed at the mangrove forest sites (Fig. 6). Stns MA, MB and MC showed high sulfate concentrations in the surface layers during the dry season (>30 mM), and low concentrations in the wet season (down to 11 mM). High concentrations were coincident with high chloride and low values with low chloride concentrations (data not shown), indicating that the pore waters were concentrated due to evaporation during the dry season and diluted with rainwater during the wet season.

Redox profiles

The pattern of redox profiles (E_h) were similar at all sites with a high value (+350 to 400 mV) in the overlying water column and rapidly decreasing potentials until 2 cm depth. From 2 to 15 cm E_h was almost constant with highest values at Stn MA (> +110 mV) and lower values at the other sites (from +80 to -120 mV) (Fig. 7). Redox potentials were generally higher below 2 to 5 cm in the wet than the dry season at all stations (except for Stn MB).

DISCUSSION

Higher oxygen uptake during air exposure at low tide compared to submerged fluxes at the vegetated mangrove sites emphasizes the importance of including air-exposed fluxes into diel budgets of mangrove

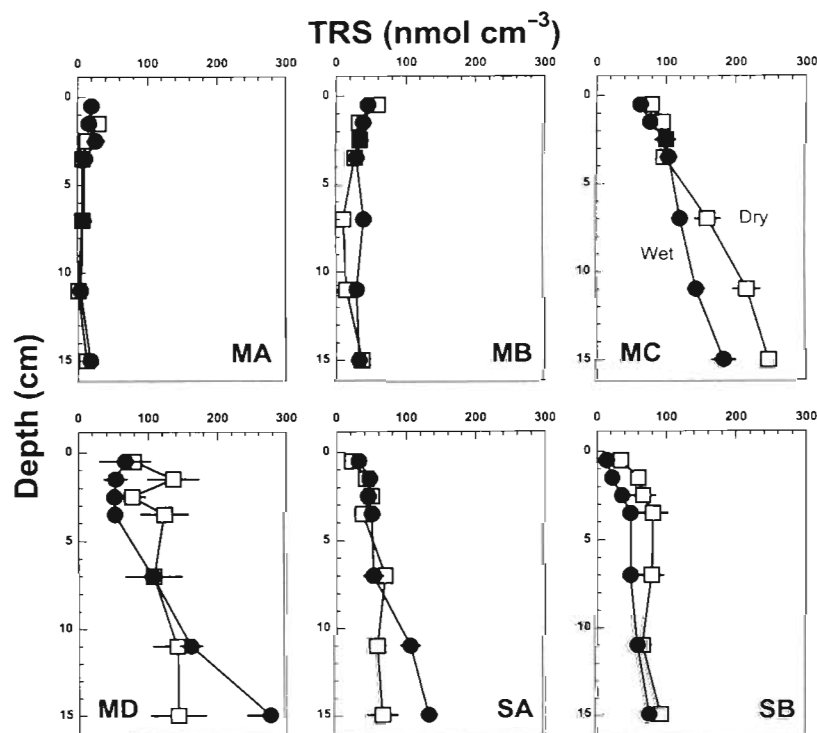


Fig. 5. Depth profiles of total chromium reducible sulfides (TRS, nmol cm⁻³) at the 6 examined stations during the dry and wet season in the upper 15 cm of the sediments. Data points represent mean (n = 3 to 6, ±SEM)

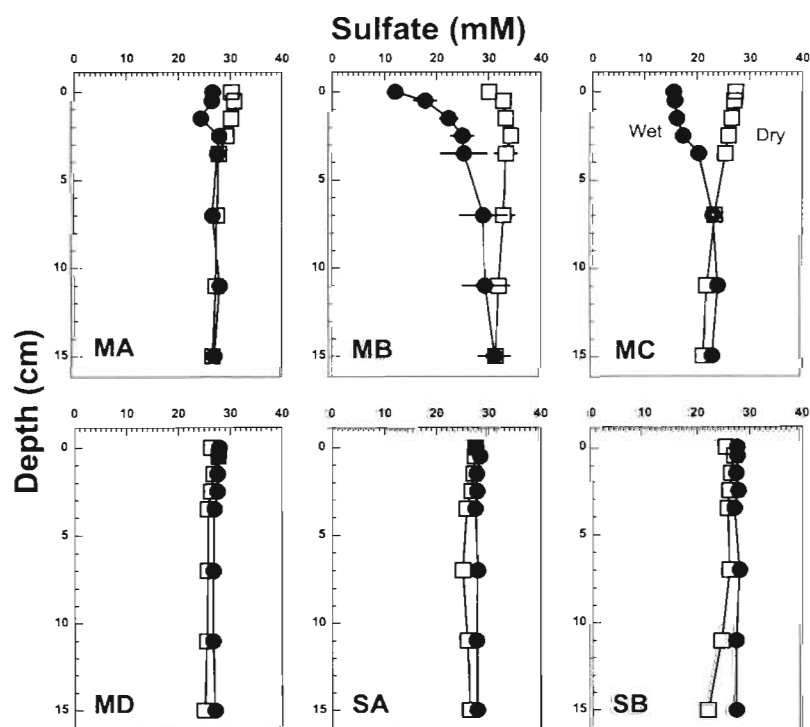


Fig. 6. Concentration (mM) of sulfate in the pore water in the upper 15 cm of the sediment at the 6 examined stations in the dry and wet seasons. Symbols represent the mean (n = 3 to 6, ±SEM)

forest sediment metabolism. Enhanced sediment oxygen uptake is likely due to the increased area of oxic-anoxic interfaces due to the rough surface topography, which results in reduced thickness of the diffusive boundary layer during air exposure (Kristensen et al. 1992). There were no distinct differences between submerged and air-exposed fluxes at the non-vegetated and seagrass sites. These areas are characterized by a smooth surface topography due to currents and waves.

Variation in benthic metabolism along the transect was controlled by a combination of detritus availability, tidal elevation, vegetation cover and bioturbation. All sediments had high redox potentials, indicating that the mangrove forest-seagrass bed transition zone is more oxidized and that sulfate reduction is of less importance compared to 'classic' subtidal coastal sediments (Thode-Andersen & Jørgensen 1989). Benthic metabolism along the transect was generally lower than that found in other mangrove environments (Alongi 1994b, Kristensen et al. 1995). The refractory nature of detritus and the low pool sizes outside the mangrove forest suggest that the organic matter is difficult to access by benthic organisms and may contribute to the low sediment metabolism compared to temperate environments (Kristensen et al. 1995).

The presence of mangrove trees was expected to stimulate microbial activity in the sediment (Kristensen et al. 1992, 1994, Holmer et al. 1994). Sulfate reduction attained relatively high rates at Stn MB with dense cover of *Rhizophora*, although rates were low compared to other *Rhizophora* sites (Kristensen et al. 1992, 1994, Holmer et al. 1994, Nedwell et al. 1994). Sulfate reduction accounted for ~20% of total sediment metabolism, and highest rates were primarily found in the rooted depths, suggesting that root exudates or fresh *Rhizophora* detritus stimulate the microbial activity. On the other hand the high intertidal Stn MA, which experiences long daily air exposure (>19 h) and has a large number of

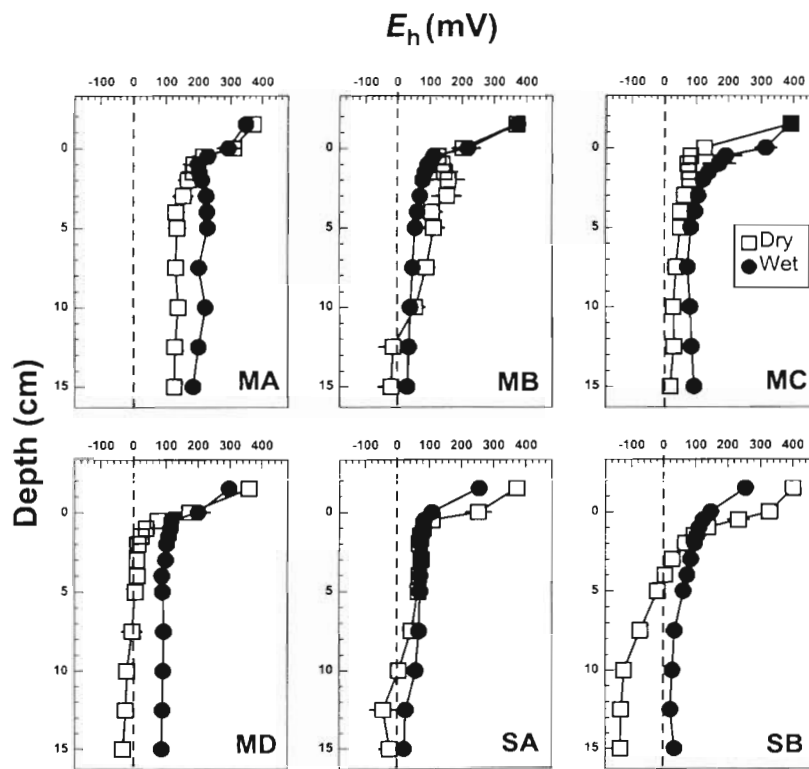


Fig. 7. Redox potentials (E_h , mV) in the upper 15 cm of the sediments at the 6 examined stations in the dry and wet season. Symbols represent the mean ($n = 3$ to 6, \pm SEM), and 0 the sediment-water interface

permanent crab burrows, showed low sulfate reduction rates. The oxidizing capacity of crab bioturbation lowered the role of sulfate reduction to account for only 2 to 6% of the total sediment metabolism. The high mineralization activity found at the tidal flat within the mangrove forest was associated with intense benthic primary production (Holmer et al. unpubl.). Benthic microalgae may be an important source of labile organic matter in the uppermost layers at this station as indicated by high rates of sulfate reduction near the surface. A similar relationship between benthic microalgae and sulfate reduction has been found in temperate intertidal sediments (Lomstein et al. 1998). The rates of benthic metabolism at the seagrass stations were similar to those in the mangrove forest despite the low pools of detritus. Root exudates or a rapid burial of seagrass detritus may stimulate organic matter decomposition, as sulfate reduction rates were highest in the depths where roots were found at the field sites, which is consistent with results from other seagrass beds (Blackburn et al. 1994, Isaksen & Finster 1996, Holmer & Nielsen 1997, Blaabjerg et al. 1998). Studies of eelgrass beds have shown a diurnal variation in sulfate reduction rates with high activity in the photosynthetic period (Isaksen & Finster 1996, Blaabjerg et al. 1998).

Unfortunately, we were only able to sample at low tide and could not coordinate with the photosynthetic period. The heterogeneity between replicates may therefore be caused by the differences in sampling time. Leakage of root exudates during the incubations which may stimulate microbial activity (Isaksen & Finster 1996) was largely avoided in this study by incubating sediment with a minimum of roots.

The pools of sulfides appear to be controlled by a number of factors in addition to sulfate reduction. Pools were generally low compared to subtidal sediments (Thode-Andersen & Jørgensen 1989), but varied significantly along the transect with maximum concentrations in the deeper parts of unvegetated sediments. This is in contrast to the low sulfate reduction rates found at these sites, but as macrophytes were absent and burrowing benthic fauna were scarce, the reoxidation is probably low compared to the vegetated and bioturbated sites. The community respiratory quotients were high at the vegetated stations, indicating a significant burial of sulfides. This was not consistent with the

low pools of sulfides found in these sediments. Seagrasses are adapted to survive in reduced and sulfidic sediments by excretion of oxygen from roots to oxidize the rhizosphere and reoxidize toxic sulfide (Pedersen et al. 1998). This leads to low pools of sulfides despite the relatively high rates of sulfate reduction. The same mechanism has been found in *Avicennia* trees (Andersen & Kristensen 1988), although the oxic layer around the roots was narrow. As pools of sulfides were also low in the rooted depths of *Rhizophora*-vegetated sediments, oxygen excretion from roots may also occur for this species. Very low pools of sulfides were found at the high intertidal site consistent with the low sulfate reduction rates and the large degree of aeration by bioturbation, particularly during low tide.

Seasonal variations in benthic metabolism along the mangrove forest-seagrass bed transect

There was no major seasonality in sediment oxygen uptake and TCO_2 production, indicating that the oxygen-consuming processes and the overall mineralization were not affected by the seasonal variations between wet and dry periods. The lack of seasonal

response in mineralization is considered to be due to the fairly constant environmental conditions in the tropics with minor seasonality in the parameters that control mineralization, e.g. temperature, organic matter pools and other edaphic characteristics (Alongi 1994b). Despite the minor changes in overall mineralization, sulfate reduction rates showed some seasonality. Several processes may affect sulfate reduction rates, e.g. organic matter supply, sulfate concentration and redox conditions. However, the seasonality in sulfate reduction did not follow the benthic primary production along the transect (Holmer unpubl.), indicating that the relationship between benthic microalgae dynamics and anaerobic processes was generally weak. Benthic microalgae were only considered to be a significant source for sulfate reduction at the tidal flats, and the seasonal variation in sulfate reduction at these stations showed a correlation with the variation in benthic primary production (Holmer et al. unpubl.).

Sulfate reduction was 2 to 4 times higher at the high- and mid-intertidal sites during the wet season compared to the dry season. Sulfate concentrations were lower in the surface layers at these sites during the wet season due to dilution with rainwater, but sulfate (>11 mM) was never limiting (Boudreau & Westrich 1984). A lower photosynthetic activity by the mangrove trees during the wet season may lower the oxidation of the sediments and thereby increase the importance of anaerobic processes (Nedwell et al. 1994). Changes in redox potentials, however, did not correlate with sulfate reduction in the vegetated sediments, as redox potentials remained high despite increasing sulfate reduction rates. It is most likely that the rates were stimulated by increased pools of available organic matter. Rates were primarily stimulated in the deeper layers, where the production of root exudates or labile detritus from the vegetation may be enhanced during the wet season (Tam et al. 1998).

There was no major seasonal variation in sulfate concentration and redox potentials at the seagrass stations, whereas sulfate reduction rates were up to 4 times higher during the wet season. Stimulation of sulfate reduction may be due to enhanced release of organic exudates from the roots or a higher detritus production (Blackburn et al. 1994, Stapel & Hemminga 1997). The controlling parameters for the seasonal variation in vegetated sediments, however, need to be examined further. The enhanced rates of sulfate reduction were not followed by changes in pools of sulfides, suggesting that the reoxidation was rapid and continuous in the seagrass sediments. The seasonal variation in pools of sulfides was generally low along the mangrove forest-seagrass bed transect, which is most likely due to the rapid reoxidation and minor burial at all sites. This diminishes the seasonal variation in pool sizes.

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