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Preliminary study of benthic metabolism and sulfate reduction in a mangrove swamp of the Indus Delta, Pakistan

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ABSTRACT: Benthic metabolism (sediment O_2 uptake, CO_2 production and sulfate reduction) and nitrogen dynamics were studied in a mangrove swamp of the Indus Delta, Pakistan during fall 1990. The mangrove, which is characterized by large salinity fluctuations, has highly variable concentrations of Cl^- and SO_4^{2-} in the sediment porewater. Vertical profiles of these constituents reflect the historical events of salinity changes in the overlying water. Rates of O_2 uptake (both measured directly and estimated from O_2 profiles) at intertidal creek banks were generally low and about 2 times higher in air-exposed than in water-covered sediment. The high rates found during air exposure was caused by a reduction in the thickness of the diffusive boundary layer and an increased area of oxic-anoxic interfaces due to drainage of water from large sediment interstices (burrows and cracks in the surface). The frequency and duration of water cover were important determinants for microbial respiration in the sediment. Highest rates during water cover were measured subtidally in creek sediment and lowest rates at intertidal creek bank sites. Desiccation may reduce overall microbial respiration at the creek banks. About half of the CO_2 production measured during water cover could be accounted for by sulfate reduction in intertidal sediments, whereas only 18 % of the CO_2 production in subtidal creek sediments could be ascribed to sulfate reduction. The remainder may be produced by other respiration processes. The low metabolic activity in the mangrove sediment was partly caused by the refractory nature of sediment detritus (mostly remains from tree leaves and roots). The generally low fluxes of dissolved inorganic nitrogen combined with the low nitrogen content in sediment detritus (C:N ≈ 20) also indicated that nitrogen was a limiting factor for microbial activity in this mangrove swamp.

INTRODUCTION

Our present understanding of benthic metabolism and nutrient dynamics in mangrove swamps is invariably based on a few studies from North America, Australia and Southeast Asia (Odum & Heald 1975, Kristensen et al. 1988, 1991, Alongi 1989). These investigations have shown that results obtained from one location are not necessarily representative of other areas, since mangrove community structure and dynamics depends on a variety of physical and chemical factors besides tree dominance, e.g. tidal range, freshwater input, and seasonality (temperature and precipitation) (Alongi 1989). This great variability found within and between mangroves, emphasizes the need for more detailed investigations on spatial and temporal patterns of sediment processes in different mangrove systems.

Decomposition of mangrove detritus is essentially a microbially mediated process, although large organisms such as crabs may contribute significantly in the initial stages of decomposition (Odum & Heald 1975, Robertson 1986). The role of anaerobic processes in mangrove element cycling, however, is largely unresolved. Only few studies have dealt with anaerobic decomposition (Benner & Hodson 1985, Benner et al. 1986) and sulfate reduction (Kristensen et al. 1991) in mangrove sediments. Results from these studies indicate that decomposition of many organic compounds can be orders of magnitudes faster in aerobic than anaerobic mangrove sediment, but they also indicate that sulfate reduction may account for up to 100 % of

the total sediment metabolism (measured as CO_2 efflux).

The purpose of the present preliminary study was to examine benthic metabolism and nutrient dynamics in a mangrove swamp of the Indus Delta, Pakistan. Three different techniques were used to determine fluxes of O_2 across the sediment surface: (1) estimates from microprofiles; (2) direct measurement in systems with water cover; and (3) direct measurements in systems without water cover. The O_2 flux analysis, supplemented with measured fluxes of CO_2 and dissolved inorganic nitrogen (water-covered), provided insight to the temporal and spatial complexity of benthic metabolism in the mangrove swamp. Information on anaerobic respiration in the sediment was obtained as sulfate reduction.

MATERIALS AND METHODS

Study site. Work was carried out in a riverine mangrove swamp at the western part of the Indus Delta, Pakistan, during September and October 1990. The Indus Delta is characterized by strong seasonal variations in salinity; high in summer (>70 ‰) and low in winter (ca 30 ‰). The summer maximum is caused by evaporation and low freshwater input from the Indus River due to intensive agricultural irrigation. The vast majority of the mangrove stands in the Indus Delta is *Avicennia marina*, because this species has the highest reported salt tolerance among mangrove trees (Ahmed 1992). However, in large areas the mangrove community is a 'scrub-type' forest with reduced growth due to water and salt stress (Lugo & Snedaker 1974, Lin & Sternberg 1992).

The study site was located in a 100 m wide and 5 to 7 m deep side branch of the Isaro Creek, close to the deep-sea port Port Qasim (Fig. 1). Tidal range during the study period was 1 to 3 m. The mangrove forest in the area was open and dominated by shrubs of *Avicennia marina*. The prevailing burrowing benthic macrofauna in the intertidal zone were Sesarmid and Ocypodid crabs. Water temperature and salinity during the study were 30 ± 2 °C and 30 ± 2 ‰, respectively.

Three representative stations were chosen in the Isaro Creek branch (2 intertidal and 1 subtidal; Fig. 1). Stn 1 ('dry' site) was situated 15 m from the creek bank close to a group of *Avicennia marina* shrubs. This station appeared mostly dry with cracks in the sediment surface as a result of infrequent inundations (5 to 10 tides mo^{-1}). Pneumatophores of mangrove trees were abundant at this site (452 ± 43 m^{-2} sediment surface). Stn 2 ('wet' site) was located on a non-vegetated, intertidal creek bank. The sediment surface at this station appeared wet at any time due to inundation during every tide. Pneumatophores were less frequent here (244 ± 48 m^{-2}) and a green algal mat (unknown species) was clearly visible at the sediment surface. At both intertidal stations the benthic macrofauna was dominated by <50 burrowing crabs m^{-2}. Stn 3 ('creek' site) was located in the middle of the creek at ca 5 m water depth. No evidence of macro-biological life was found in or on the sediment.

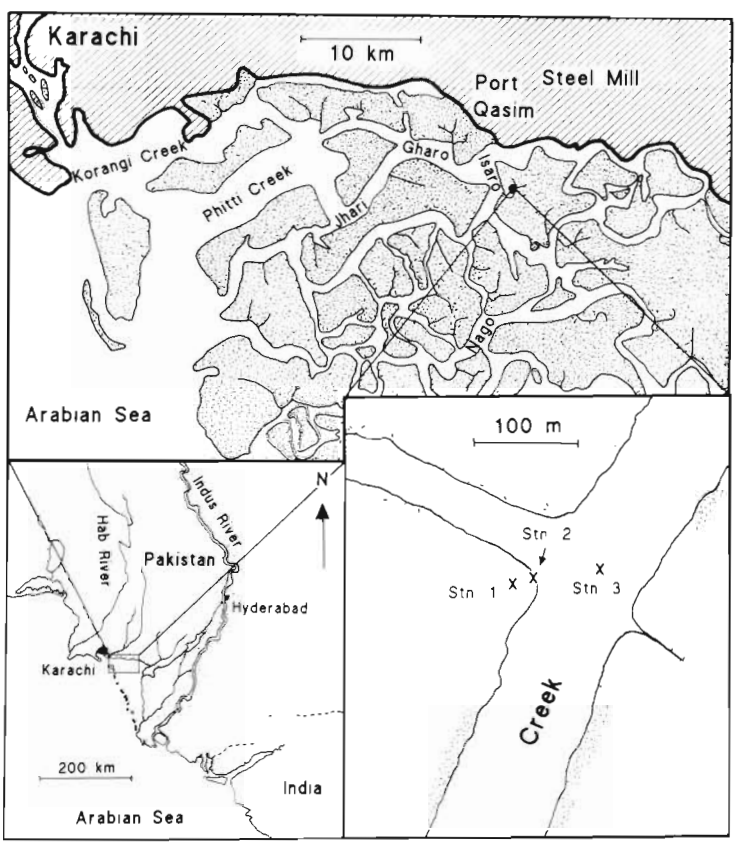

Fig. 1 Location of the 3 stations examined in the Isaro Creek branch, Indus Delta, Pakistan

The sediment at all 3 stations was composed of non-sulfidic fine-grained silt. At the 'dry' and 'wet' sites dead and living roots were visible as peat-like zones in the sediment.

Flux measurements. Total sediment metabolism was determined as O_2 (Stns 1 to 3) and CO_2 (Stns 1 & 2) exchange across the sediment-water interface and supplemented with DIN (NO_2^- + NO_3^- and NH_4^+) flux measurements. Cores for flux incubations on inundated sediment ('+w-cores') at Stns 1 and 2 were collected by hand during low tide using

8 cm i.d. × 25 cm long acrylic core liners. A total of 3 cores were taken per station on each of 3 sampling occasions. After return to the laboratory all cores were adjusted to ca 20 cm sediment depth. Subsequently, seawater from Isaro Creek was added and the cores were allowed to 'rest' at constant temperature (29 °C) in darkness for 4 to 6 h. The water phase was renewed 0.5 h before incubations. During incubation, cores were sealed with lids containing stirrer motors, which maintained a continuous water circulation at a rate less than the resuspension limit. Stirring rate was similar at all 3 stations. By assuming constant solute exchange rate with time, all fluxes were determined from the concentration difference between initial and final samples during incubation periods of 2 to 4 h. Measurements of sediment respiration were performed in darkness on the day of sampling and benthic primary production was determined the next day in daylight (around noon). Oxygen was analyzed by the standard Winkler technique (Parsons et al. 1984), and total carbon dioxide (TCO_2) was quantified by potentiometric Gran titrations (Talling 1973).

Oxygen uptake by air-exposed sediment ('−w-cores', Stns 1 & 2) in the dark was determined on 3 separate cores (similar core liners as used for '+w-cores') taken at low tide. Initially the cores were adjusted to 23 to 24 cm sediment depth, allowing only 1 to 2 cm air space (ca 60 ml). After 1 to 2 h acclimation a rubber stopper, with a polarographic oxygen electrode (Radiometer, Denmark) inserted through a hole, was fitted to the core liner. The oxygen electrode protruded into the air space above the sediment. Pressure changes in the enclosed head space during stopper emplacement were equilibrated through a hypodermic needle in the side. Incubation was started when the needle was removed. After 10 to 15 h the electrode was connected to a Keithly 480 digital picoammeter and the final O_2 reading was noted. Temperature was maintained constant at 30 ± 1 °C during the incubation. Subsequently, the stopper and oxygen electrode was transferred to a core liner half filled with distilled water and the O_2 reading at air saturation (equivalent to the start value) was noted after 10 to 15 min equilibration. O_2 consumption was calculated using the concentration change and air volume trapped below the stopper.

Benthic fluxes of O_2 and DIN at the subtidal Stn 3 ('creek' site) were determined in situ using a benthic flux chamber covering a sediment area of 412 cm^2. The chamber had a hinged lid and was open at the bottom. The lid contained a magnetically coupled stirring motor and 4 ports connected to spring-actuated syringes for sampling of water inside the flux chamber. Chamber, lid and stirring motor were identical to those described by Devol (1987). The flux chamber was lowered to the creek bottom with a hand line, which was tied to a free-floating buoy during deployment. When initially placed on the bottom, the lid was electronically closed entrapping a volume of water (ca 2 l) over the sediment. At 4 pre-programmed time intervals samples of the entrapped water were taken using the spring-actuated syringes. Lid closure and syringe sampling operations were accomplished using electrodeplating dissolving links. Also at pre-programmed time intervals the O_2 content of the entrapped water was measured using a pulsed, polarographic oxygen electrode (Langdon 1984). All electronic operations, including polarization of the oxygen electrode and storage of electrode readings were controlled by a programmable microprocessor. Deployment times were typically 3 to 4 h.

Nitrate was determined by cadmium-copper reduction of nitrate to nitrite and subsequent colorimetric analysis for nitrite using an automated non-segmented flow version (Lambourn et al. 1991) of the method described by Armstrong et al. (1967). Ammonium was determined by the standard autoanalyzer method of Solorzano (1969).

Oxygen distribution in sediment. The depth of O_2 penetration into the sediments of Stns 1 ('dry' site) and 2 ('wet' site) was measured using a membrane-coated polarographic 760 O_2 needle electrode (Diamond Electro-Tech, Inc.) with a platinum tip diameter of 35 to 40 µm. Spatial resolution was less than 0.2 mm. The electrode was mounted on a manually driven micromanipulator, connected to a Keithly picoammeter and recorded on a Minigor RE501 recorder.

Light (approximately noon) and dark O_2 profiles from the dry and wet sites were obtained at *in situ* conditions. Oxygen was monitored in steps of 0.2 to 0.5 mm on cores both with ('+w-profile') and without ('−w-profile') a 2 mm deep non-stirred water column.

The diffusive flux of O_2 into and out of the sediment (J_{O_2}, µmol m^{-2} d^{-1}) was estimated from the gradient at the sediment-water interface by the 1-dimensional version of Fick's first law of diffusion: $J_{O_2} = -\phi D_s \Delta[O_2]/\Delta z$, where D_s = apparent diffusion coefficient of O_2 at the sediment-water interface; ϕ = porosity; $\Delta[O_2]$ = O_2 concentration gradient in the Δz depth interval. D_s was calculated from porosity and the temperature-corrected diffusion coefficient of O_2 in seawater (D = 2.6 × 10^{-5} cm^2 s^{-1} at 30 °C and 30 ‰ S) (Broecker & Peng 1974, Li & Gregory 1974)

Sulfate reduction assay. Sediment samples for the determination of sulfate reduction rate were collected at all 3 stations with 5 cm i.d. × 40 cm long acrylic core liners that had pre-drilled 2 cm holes along their length. These holes were covered with black electrical tape during the coring procedure, after which the tape was carefully cut away and small subcores were taken horizontally with 5 ml glass syringes cut off at the 1 ml

mark and fitted with plastic plungers. Samples were taken down to ca 20 cm depth. A 1-hole rubber stopper was immediately inserted into the open end of the sample in a manner such that no air was trapped. The hole in the stopper had been previously plugged with silicon cement. Using a microliter syringe, 100 µl of carrier free ^{35}S-SO_4^{2-} (7.4 MBq ml^{-1}) was then injected through the silicone septum and the samples were incubated 34 to 36 h at *in situ* temperature. The incubation was terminated by fixing the sample with 1 ml of formalin plus 5 ml of 5 % ZnAc. Both the acid volatile (AVS) and chromium reducible (CRS) fractions of the sulfide produced during incubation were recovered. AVS was extracted as described by Devol & Ahmed (1981). The sample was then washed 3 times with artificial seawater and CRS was extracted using the distillation procedure of Fossing & Jørgensen (1989).

Sediment characteristics and porewater extraction. Sediment cores for determination of water content, organic content, and pore water solutes (alkalinity, Cl^- and SO_4^{2-}) were collected by the use of 5 cm i.d. × 30 cm long acrylic core liners. Cores were sectioned into 1 cm (0 to 4 cm) and 2 cm (4 to 10 or 20 cm) intervals. Subsamples of known volume were dried at 100 °C for 12 h for determination of porosity. Subsequently, the STG procedure of Kristensen (1990) was performed. Briefly, the 100 °C pre-dried sediment samples were further dried at 130 °C to remove adsorbed water (typically 2 to 4 %). These samples were then combusted in 2 steps, at 280 and 520 °C for 6 h, respectively. After both combustions samples were cooled in a desiccator and weighed. The weight loss in the range 280 to 520 °C (PII) was related to the total loss on ignition (LOI) in the range 130 to 520 °C (PI + PII) to obtain the *Rp* (ratio between peaks) index, as follows: *Rp* = PII/(PI + PII). Low *Rp*'s (around 0.2) are typical for materials rich in aliphatic compounds (lipids, carbohydrates), whereas high *Rp*'s (> 0.5) represent aromatic compounds and materials rich in nitrogen (humates, proteins). Particulate organic carbon (POC) and nitrogen (PON) of 130 °C pre-dried subsamples were analyzed on a Hewlett-Packard 185B CHN-analyzer.

Porewater was extracted by centrifugation and analyzed for alkalinity, SO_4^{2-} and Cl^-. Alkalinity was determined by micro-Gran titration of 0.4 to 1.0 ml samples using 0.1000 M HCl in 0.53 M NaCl. Analysis for SO_4^{2-} and Cl^- were performed on acidified samples by ion liquid chromatography.

Table 1. Sediment characteristics: porosity, loss-on-ignition (LOI), particulate organic carbon (POC), particulate organic nitrogen (PON), molar C : N ratio, and *Rp* index at the 3 stations in the Isaro Creek branch. Values are mean of 3 measurements (± SD), except at the 'creek' site where only 1 core was examined

Depth (cm)	Porosity × 10^{-2}	LOI (%)	POC (µmol g^{-1} dry wt)	PON (µmol g^{-1} dry wt)	C : N (mol)	*Rp* × 10^{-2}
'Dry' site						
0–1	50 (2)	5.3 (0.0)	892 (28)	41 (6)	22 (4)	83 (1)
1–2	48 (1)	4.8 (0.1)	802 (47)	39 (1)	21 (1)	84 (1)
2–3	48 (2)	4.5 (0.3)	730 (38)	24 (17)	21 (1)	84 (1)
3–4	47 (0)	4.3 (0.1)	661 (63)	37 (5)	18 (2)	82 (1)
4–6	46 (1)	3.7 (0.1)	588 (29)	37 (1)	16 (1)	79 (2)
6–8	45 (3)	3.1 (0.3)	452 (4)	35 (0)	14 (0)	77 (0)
8–10	45 (1)	2.9 (0.1)	402 (67)	37 (2)	11 (2)	78 (1)
'Wet' site						
0–1	56 (4)	4.8 (0.2)	779 (85)	42 (4)	19 (2)	82 (1)
1–2	54 (2)	4.9 (0.2)	847 (36)	34 (1)	25 (2)	84 (1)
2–3	54 (2)	4.5 (0.1)	703 (42)	37 (3)	19 (2)	84 (1)
3–4	53 (3)	4.4 (0.1)	753 (73)	37 (1)	21 (1)	83 (0)
4–6	54 (2)	4.7 (0.2)	766 (39)	39 (1)	20 (2)	83 (1)
6–8	55 (1)	4.5 (0.1)	707 (53)	35 (3)	20 (1)	82 (1)
8–10	53 (2)	3.7 (0.1)	672 (53)	32 (3)	20 (1)	80 (1)
'Creek' site						
0–1	68	5.4	957	50	19	81
1–2	–	5.0	837	–	–	85
2–3	66	4.9	862	–	–	84
3–4	–	4.6	709	33	22	84
4–6	68	4.2	809	38	21	82
6–8	–	4.3	707	34	21	79
8–10	65	4.7	798	35	23	82
12–14	55	4.9	747	33	23	84
16–18	41	5.3	727	–	–	82

RESULTS

Sediment characteristics

The sediment characteristics indicated a high degree of similarity between the 3 stations examined (Table 1). Differences in porosity reflected the elevation and inundation frequency of the respective stations. Highest values were found in the upper part of the 'creek' site (0.65 to 0.68) and lowest values at the 'dry' site (0.45 to 0.50) (ANOVA: $p < 0.01$). LOI was generally between 4 and 5 %, POC between 700 and 900 µmol C g^{-1}, and PON between 30 and 40 µmol N g^{-1}, with no significant differences between stations and with depth in the sediment, except at the 'dry' site where LOI and POC decreased below 4 cm reaching 50 % of the surface value at 8 to 10 cm depth ($p < 0.05$). Accordingly, C:N also decreased with depth from ca 21 at 0 to 4 cm to 11 at 8 to 10 cm ($p < 0.01$). At the other stations C:N ratios around 20 predominated at all depths. The depth dependent decrease in POC and C : N with depth at the 'dry site', which was accompanied by a 5 to 10 % drop in *Rp* ($p < 0.05$), reflected changes in the biochemical composition of the sediment detritus. The generally high *Rp* and C:N values, however, indicate that most of the organic matter at the 3 stations was composed of relatively refractory 'humic'-like heterocyclic compounds (ca 80 % was combusted only at temperatures above 280 °C).

Oxygen and carbon dioxide exchange

Oxygen penetrated from 1 to 3 mm into the surface sediment at the 'dry' and the 'wet' site (Fig. 2). Deepest penetration was observed in light-exposed sediment: 2 mm at the 'dry' and 3 mm at the 'wet' site, which was associated with a 140 and 160 % surface supersaturation at the 2 sites, respectively. Oxygen penetration in the dark was similar at the 2 stations (0.8 to 1.2 mm); deepest in air-exposed sediment ('−w-profile'). No O_2 profiles were obtained from the creek site.

Oxygen exchange across the sediment-water interface was highest at the 'creek' site and lowest at the 'dry' site ($p < 0.05$), but the individual estimates were highly dependent on the method used (Table 2). Highest rates of O_2 uptake in the dark at both the 'dry' and the 'wet' site were obtained on air-exposed sediment using the '−w-core' technique ($p < 0.05$). The rates were 2 to 3 times higher than found by the traditional '+w-core' method. No '−w-core' measurements

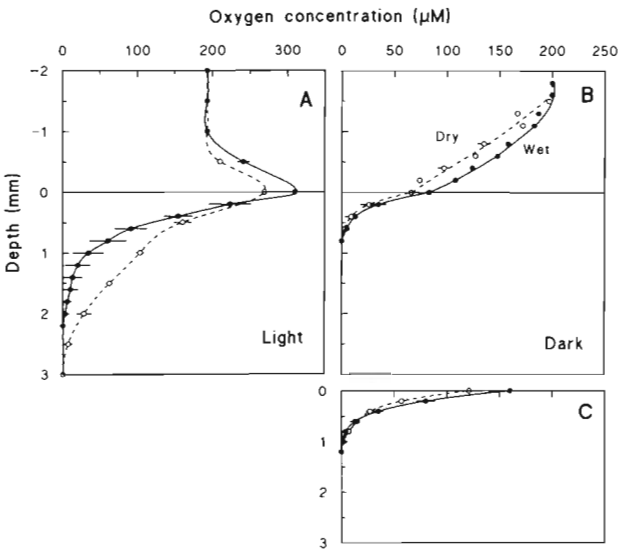

Fig. 2. Vertical profiles of O_2 in the surface layer of the 2 intertidal 'dry' and 'wet' sediments. (A) Sun-exposed; (B) inundated in darkness (+w-profile); and (C) exposed to air in darkness (−w-profile). Values are given as mean ± SE of 6 determinations

Table 2. Fluxes of oxygen, carbon dioxide, ammonium and nitrate across the sediment-water interface at the 3 Isaro Creek sites. Results obtained in light and dark are shown. Oxygen fluxes determined by 3 methods are given: core incubation with water cover ('+w-core'); core incubation without water cover ('−w-core'); and estimated as diffusion based on the vertical oxygen profile obtained with ('+w-profile') and without ('−w-profile') water cover. All values are in mmol m^{-2} d^{-1} (± SD, n = 3 to 6)

	O_2				CO_2	NH_4^+	$NO_2^- + NO_3^-$
	Core		Profile				
	+w	−w	+w	−w			
Dark							
Dry	−16 (3)	−34 (9)	−11 (2)	−17 (2)	47 (21)	–	–
Wet	−17 (1)	−45 (16)	−17 (2)	−26 (4)	50 (18)	0.21 (0.13)	0.46 (0.10)
Creek	−28 (12)	–	–	–	–	–	−0.55 (–)
Light							
Dry	−3 (1)	–	27 (15)	–	−14 (5)	0.24 (0.58)	−0.56 (0.33)
Wet	59 (30)	–	31 (10)	–	−104 (71)	−0.23 (0.89)	−0.69 (0.72)
Creek	–	–	–	–	–	–	–

were performed on 'creek' site sediment, but the '+w-core' rates measured at this station was almost 2 times higher than rates obtained by the same technique from the other 2 stations ($p < 0.05$). Dark O_2 uptake estimates from O_2 profiles in air exposed 'dry' site and 'wet' site sediment ('−w-profile') were ca 2 times higher than those obtained from '+w-profile' flux estimates ($p < 0.001$). The '+w-core' dark O_2 uptake was similar to or slightly higher ($p = 0.07$) than the '+w-profile' estimates, whereas '−w-core' dark O_2 exchange was 55 to 70 % higher than the '−w-profile' flux estimate ($p < 0.05$). Dark CO_2 exchange, which was only determined by the '+w-core' incubation technique, was significantly higher than any measured or estimated '+w' O_2 flux ($p < 0.01$). The CRQ (Community Respiration Quotient) = (CO_2 flux)/(O_2 flux) in the core incubations was 2.9 when '+w-core' O_2 uptake was used and 1.1 ('wet') to 1.4 ('dry') when '−w-core' O_2 uptake was used.

The O_2 and CO_2 exchange in light exposed sediment changed direction compared to those obtained in the dark with highest O_2 production and CO_2 consumption at the 'wet' site ($p < 0.05$). The only exception was for O_2 from '+w-core' incubation of 'dry' site sediment, where a slight net uptake occurred. Exchange estimates based on profile measurements in light-exposed sediment, on the other hand, were not significantly higher at the 'wet' site than at the 'dry' site. Gross primary production determined on a daily basis from '+w-core' fluxes by assuming a 12 h light : 12 h dark cycle, was 6 and 31 mmol m^{-2} d^{-1} for O_2 and CO_2 at the 'dry' site, and 38 and 71 mmol m^{-2} d^{-1} for O_2 and CO_2 at the 'wet' site. The CPQ (Community Production Quotient) = (gross O_2 production)/(gross CO_2 consumption) was 0.21 ('dry') and 0.49 ('wet').

DIN exchange

DIN flux pattern was complicated by the general lack of data (lost samples). Results from both light and dark incubations are only available from the 'wet' site (Table 2). The DIN exchange at this station followed the commonly observed pattern with a net release in darkness and a net uptake in light. 'Dry' site DIN fluxes from light incubations (no data available from dark incubations) showed an uptake of $NO_2^- + NO_3^-$ of almost the same magnitude as found at the 'wet' site and a release of NH_4^+ similar to that found for the 'wet' site in the dark. The 'creek' site exhibited a considerable uptake of $NO_2^- + NO_3^-$ in darkness (no other DIN data available from this station).

Sulfate reduction

The depth pattern and absolute rates of sulfate reduction (SRR) were significantly different at the 3 stations ($p < 0.01$, Fig. 3). At the 'dry' site SRR was highest in the uppermost cm (150 nmol cm^{-3} d^{-1}). Below SRR decreased abruptly to about ⅓ of the maximum rate ($p < 0.01$) and remained at this level down to 19 cm depth. Most of the label at this station was recovered in the CRS pool with only 1 to 15 % recovered as AVS. The SRR depth profile at the 'wet' site showed an opposite pattern, with low rates in the uppermost cm (20 nmol cm^{-3} d^{-1}), a subsurface peak at 3 to 7 cm (50 to 130 nmol cm^{-3} d^{-1}) followed by a depression around 10 cm depth and again increasing rates in the deeper layers (130 to 180 nmol cm^{-3} d^{-1}). CRS was also the

Table 3. Integrated sulfate reduction (ΣSRR) in the upper 20 cm of the sediment. Values are given as mmol S m^{-2} d^{-1}; in units of carbon mineralized, mmol C m^{-2} d^{-1} (2ΣSRR); and as % of CO_2 flux in the dark [(2ΣSRR/CO_2 flux) 100]

	ΣSRR	C mineralized	% of CO_2 flux
Dry	11.7	23.4	50
Wet	16.1	32.2	64
Creek	2.5	5.0	18[a]

[a] This value is estimated from O_2 uptake based on a CRQ of 1

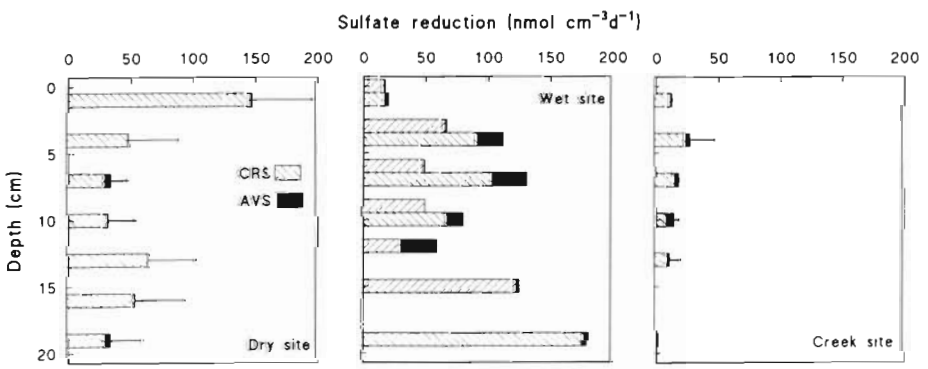

Fig. 3. Vertical distribution of sulfate reduction rates (SRR) at the 3 stations. Recoveries of ^{35}S in the chromium reducible sulfur (CRS) and the acid volatile sulfur (AVS) pools are indicated. Values from the 'dry' and 'creek' sites are presented as mean (+ range) of 2 determinations. Values from the 'wet' site represent 2 determinations at different depth intervals

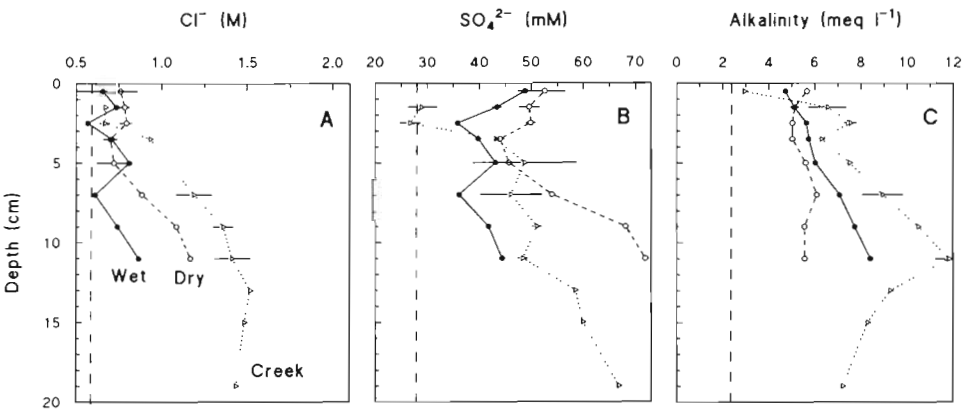

Fig. 4. Vertical distribution of (A) Cl^-, (B) SO_4^{2-}, and (C) alkalinity at the 3 stations. Vertical dashed line indicates the overlying water concentration at the time of sampling. Values are presented as mean ± range of 2 determinations

most important reduced sulfur product at this station, but less pronounced and more variable than observed at the 'dry' site. Thus, in 1 core 1 to 6 % of the label was recovered as AVS (except at 12 cm depth where AVS accounted for 49 %) while in another 16 to 22 % was recovered as AVS (except at 19 cm where AVS accounted for 2 %). At the 'creek' site SRR was generally much lower than at the other 2 stations ($p < 0.001$). SRR increased from ca 15 nmol cm^{-3} d^{-1} in the upper cm to ca 30 nmol cm^{-3} d^{-1} at 4 cm, followed by a gradual decrease to ca 1 nmol cm^{-3} d^{-1} at 19 cm depth. Recovery of the label into AVS and CRS was variable and AVS accounted for 10 to 59 % of the total label with an increasing trend with depth in the sediment.

The depth integrated SRR (ΣSRR, 0 to 20 cm) was 11.7, 16.1 and 2.5 mmol m^{-2} d^{-1} at the 'dry', 'wet', and 'creek' sites, respectively (Table 3). Sulfate reduction converted to carbon mineralization units (2ΣSRR) was equivalent to 50, 64 and 18 % of the measured CO_2 flux (O_2 flux at the 'creek' site) across the sediment-water interface at the 3 sites, respectively.

Pore water chemistry

The concentration of Cl^- and SO_4^{2-} in the pore water increased irregularly with depth at the 'dry' ($p < 0.01$) and the 'creek' site ($p < 0.001$), reaching values in the 10 to 20 cm layer that was 1.5 to 2.5 times higher than the overlying water (Fig. 4A, B). No significant increase was found at the 'wet' site. Based on SO_4^{2-}/Cl^- ratios (0.05 in overlying water), there was a distinct SO_4^{2-} enrichment in the 'dry' and 'wet' site sediments (Fig. 5). The relative surplus of SO_4^{2-} declined with depth as indicated by decreasing SO_4^{2-}/Cl^- ratios ($p = 0.05$). The decrease was most rapid in the upper 2 cm. At the 'creek' site a marked SO_4^{2-} deficit was apparent with no significant trend down to 19 cm depth.

The depth profile of alkalinity in the pore water of the 'wet' and 'creek' site increased significantly with depth down to 12 cm ($p < 0.0001$, Fig. 4C). Alkalinity at 12 cm depth was 1.1, 1.8 and 4.0 times higher than in the uppermost cm for 'dry', 'wet' and 'creek' sites, respectively. The 0 to 1 cm value was 5.7, 4.7 and 2.9 meq l^{-1}, respectively. At the 'creek' site a 50 % decrease in alkalinity was apparent from 12 to 20 cm depth ($p < 0.001$).

DISCUSSION

The sediment profiles of SO_4^{2-}, Cl^- and alkalinity found in the Indus Delta (Fig. 4) indicate non steady-state conditions or the presence of saline porewater deep in the sediment. During warm summer months when most of the Indus River water is used for irrigation purposes, there is no or only limited freshwater input to the delta area. Evapotranspiration thus causes a rapid salinity increase of the standing water mass (Ahmed 1992, Harrison, P. J., Snedaker, S. C., Ahmed, S. I., unpubl.). Ions from this saline water (70 to 100 ‰)

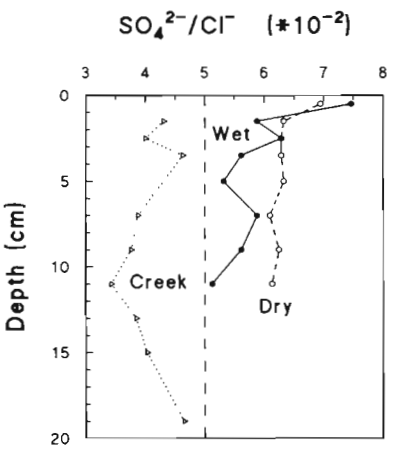

Fig. 5. Vertical distribution of SO_4^{2-}/Cl^- ratios at the 3 stations. Vertical dashed line indicates the SO_4^{2-}/Cl^- ratio of the overlying water at the time of sampling

are subsequently transported into the sediment by diffusion and advection (e.g. crab bioturbation). Exclusion of SO_4^{2-} and Cl^- in transpiration by the trees is most important in densely vegetated mangroves (Carlson & Yarbro 1985). The profiles of SO_4^{2-} and Cl^- obtained in the sparsely vegetated Indus mangrove during fall (September-October) may largely reflect the historical events of salinity changes in the overlying water, rather than changes in sediment processes. Lord & Church (1983) have found a similar pattern in salt marsh sediments. The high SO_4^{2-}/Cl^- ratio observed in the sediment at the intertidal 'dry' and 'wet' sites (up to 40 % higher than in seawater) indicates that significant production of SO_4^{2-} by oxidation of reduced sulfur has occurred at the time of sampling. In accordance with the observation of Lord & Church (1983) and Hines et al. (1989), the oxidation rate appears to be highest where desiccation is most pronounced, i.e. near the surface and at the 'dry' site. The low SO_4^{2-}/Cl^- ratio at the subtidal 'creek' site, on the other hand, reflects the consumption of SO_4^{2-} by sulfate reducers.

Solute exchange

The rates of O_2 and CO_2 exchange across the sediment surface in the Indus mangrove are in the lower range of previously reported rates from intertidal sediments of both tropical and temperate environments (Dye 1983, King et al. 1985, Mackin & Swider 1989, Kristensen et al. 1991). The different techniques used here to quantify sediment O_2 uptake at the 'dry' and 'wet' sites, however, provide contrasting results. The methods can be ranked quantitatively in the following order: '−w-core': '−w-profile': '+w-core': '+w-profile' for the 'dry' site as 3.1:1.8:1.5:1 and for the 'wet' site as 2.6:1.7:1:1 (Table 2).

The ratio between direct measurements and profile estimates of O_2 at the 2 intertidal sites, '+w-core': '+w-profile' = 1.0 to 1.5; and '−w-core': '−w-profile' = 1.5 to 1.7, are in agreement with previous studies on coastal sediments (Revsbech & Jørgensen 1986, Andersen & Helder 1987, Hofman et al. 1991). Profile measurements reflect aerobic microbial respiration and reoxidation of reduced compounds, whereas directly measured rates, in addition, include the impact of macro- and meiofauna. Benthic animals are known to increase solute flux across the sediment-water interface up to 3 times (Aller 1982, Andersen & Kristensen 1988, Kristensen 1988). The irregular surface topography of the sediment, however, may also contribute to the general discrepancy found between the 2 methods (Revsbech & Jørgensen 1986).

Both the directly measured and the profile estimated rates of O_2 uptake are higher in air exposed than in water-covered sediment. Previous studies have shown a similar pattern of O_2 uptake in other intertidal areas. Dye (1983) found that O_2 was consumed ca 2 times faster in air exposed than water-covered mangrove sediments in South Africa using benthic chambers (2.0 to 2.6 times in the present study), and Brotas et al. (1990) found a difference of 1.5 in intertidal sediments of Ria Formosa, Portugal, using microelectrodes (1.7 to 1.8 in the present study). The primary cause for these variations may be diffusive boundary layer differences. The diffusive boundary layer generally constitutes a 0.2 to 1.0 mm thick barrier to mass transfer across the sediment-water interface in inundated sediments (Jørgensen & Des Marais 1990). The boundary layer in darkened cores from the Indus mangrove is about 1.5 mm thick when the sediment is covered with a stagnant water mass, whereas no or only a very narrow boundary layer is evident in the air-exposed sediment (Fig. 2B). As a consequence, the O_2 concentration at the sediment-water interface is only 70 to 80 µM when covered with water compared to 120 to 160 µM when exposed to air.

Another cause for the different O_2 uptake between air-exposed and inundated sediment could be the increased area of oxic-anoxic interfaces during air exposure. Drainage of water from large sediment interstices, such as burrows and cracks in the surface are likely to occur in rooted mangrove sediments. During water-cover these interstices act as anoxic macropores with no significant impact on O_2 flux (Jørgensen & Revsbech 1985). Air-filled interstices, on the other hand, increase the area of oxic-anoxic interfaces and provide sites of rapid O_2 consumption (both aerobic respiration and reoxidation of reduced metabolites) and thus increase overall O_2 uptake by the entire sediment system.

The higher flux of O_2 at the 'wet' site compared to the more elevated 'dry' site suggests that the frequency and duration of water cover is an important determinant for microbial respiration in the sediment. The pattern is consistent for both respiration and primary production. The high O_2 uptake found at the subtidal 'creek' site compared to the '+w-core' rates at the intertidal stations further substantiates this trend. Dye (1983) observed the same pattern in a South African mangrove. Based on the quality and quantity of organic matter at all 3 stations no difference should be expected (Table 1). Desiccation apparently reduces the metabolic activity of both microheterotrophic respirers and microalgal communities at the sediment surface in the intertidal zone, with a progressively greater impact at the higher intertidal levels. The mechanisms responsible for this decrease are not fully understood, but increased mortality and downward migration of the

microorganisms during desiccation have been suggested (Holmes & Mahall 1982, West et al. 1989).

The low DIN fluxes found in the present study agree with the generally low nitrogen content of the sediment (C : N ≈ 20). The dark flux C : N ratio of 75 (CO_2 : DIN) found at the 'wet' site indicates that nitrification-denitrification and nitrogen assimilation by microalgae and bacteria close to the sediment surface may act as a filter for DIN diffusing from deeper layers. Assimilation by bacteria during decay of nitrogen-poor leaf material may consume substantial amounts of DIN. These proportions are only true when carbon and nitrogen are mineralized in a ratio close to that found in the particulate organic pool, which may or may not be the case (Burdige 1991). In accordance with Kristensen et al. (1988), however, the present study indicates that nitrogen is a limiting factor for microbial activity in mangrove swamp sediments.

Sulfate reduction

The depth-integrated rates of sulfate reduction found in the present study (Table 3) are low compared to most salt marshes (Howarth 1984, Howes et al. 1984, King 1988) and mangrove swamps (Kristensen et al. 1991). The low sulfate reduction rates, however, are associated with relatively low fluxes of O_2 and CO_2 across the sediment-water interface. The community respiratory quotient (CRQ) of 1 to 3 for fluxes at the 2 intertidal stations indicates that only a fraction of the produced sulfide is reoxidized by oxygen at the time of sampling. The remainder is precipitated as iron-sulfides within the sediment. About half of the measured CO_2 flux at the 2 intertidal sites can be accounted for by sulfate reduction (equivalent to CRQ of 2 when no sulfide is oxidized). A similar contribution of sulfate reduction to total sediment metabolism has previously been observed in other coastal areas (Jørgensen 1983, Howarth 1984, A. H. Devol unpubl.). Kristensen et al. (1991), on the other hand, found that sulfate reduction in a mangrove from Thailand may be responsible for nearly 100 % of the measured CO_2 production.

The very low sulfate reduction in the 'creek' site is puzzling, since only 18 % of the CO_2 produced (based on CRQ of 1) can be ascribed to sulfate reduction. Most of the respiratory processes therefore appears to be due to electron acceptors other than SO_4^{2-}. The present study offers no specific explanation for the large difference in sulfate reduction between the subtidal and intertidal sites, but possible causes may include: (1) higher availability of alternative electron acceptors (NO_3^-, Mn^{4+}, Fe^{3+}) deep in the sediment caused by strong tidal water currents; (2) inhibition of sulfate reduction due to accumulated degradation products originating from e.g. tannin-rich leaf material; and (3) hitherto unknown carbon pathways in mangrove creek sediments.

The distinct difference in vertical profiles of SRR at the 2 intertidal stations is probably caused by the availability of labile organic substrates. Bulk organic matter in the sediment is generally of low degradable nature (based on the high C : N ratios and *Rp* values), being largely composed of humic like (lignin) material originating from the trees (Benner & Hodson 1985, Kristensen 1990). The 'dry' site exhibits a depth dependent change to more nitrogen rich (low C : N) aliphatic (low *Rp*) materials in deeper layers (Table 1). Although this change is correlated with decreasing SRR (C : N, $r = 0.83$; *Rp*, $r = 0.84$, $n = 4$), the relationship appears to be fortuitous, since no other correlation was observed between organic matter quality and SRR both within and between the 3 stations. Variability in SRR is more likely controlled by the availability of small, but dynamic pools of labile, dissolved compounds (i.e. acetate) (King 1991). The SRR surface (0 to 1 cm) maximum observed at the 'dry' site may be driven by labile organic carbon released from benthic organisms being killed by the frequent desiccation of the uppermost sediment surface (West et al. 1989). Desiccation may therefore diminish aerobic respiration at the surface and stimulate anaerobic respiration immediately below the dry surface layer. The subsurface maximum at the 'wet' site, on the other hand, indicates a vertical translocation of metabolizable organic substrates within the sediment (Howarth & Teal 1979), either due to subsurface root growth or due to downward transport of newly deposited organic matter from the surface by bioturbation (e.g. burrowing crabs).

At both intertidal sites a subsurface depression of sulfate reduction is evident just below the zone of maximum rates. A similar depression found in a mangrove sediment in Thailand (Kristensen et al. 1991) was ascribed to the oxidizing activity of *Rhizophora apiculata* roots. Oxygen diffusing from live roots increases redox conditions in the surrounding sediment and thereby suppresses sulfate reduction (Howes et al. 1981, Boto & Wellington 1984).

The very high recovery of reduced ^{35}S-label found in the CRS (chromium reducible sulfur, FeS_2 and S^0) pool is in accordance with previous studies on vegetated sediments, i.e. *Spartina* marshes (Howarth & Giblin 1983, Howarth & Merkel 1984) and mangrove sediments (Kristensen et al. 1991). The oxidizing activity of roots and relatively low pH in these types of sediments usually favours a rapid formation of FeS_2 (Berner 1964, Giblin 1988). However, due to the potential role of isotopic exchange involving S^0 and other reduced sulfur pools (Fossing & Jørgensen 1990) and to the fact that AVS (HS^- and FeS) and CRS are opera-

tionally defined fractions, the segregation of sulfate reduction into 2 pools is only indicative of the tracer distribution and not of the differential formation rates of the compounds.

The low benthic respiration in the present mangrove system, measured as O_2 and CO_2 fluxes and sulfate reduction, is primarily caused by the recalcitrant nature of sediment detritus (mainly remains from tree leaves). Exposure of intertidal sediment to air increases the O_2 uptake due to an increased area of oxic-anoxic interfaces and a decreased diffusive boundary layer. Prolonged air exposure, however, lowers benthic respiration due to desiccation. In comparison with previous studies on sediment metabolism in mangroves from other parts of the world the Indus Delta mangrove is a very saline system. The periodically high salt content in water and sediments impairs the mangrove flora and fauna and creates a poor system with low biological activity.

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