

Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment

Erik Kristensen¹

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

Daniel M. Alongi

Australian Institute of Marine Science, PMB No. 3, Townsville M.C., Queensland 4810, Australia

Abstract

The influence of mangrove saplings (*Avicennia marina*) and fiddler crabs (*Uca vocans*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment was studied using outdoor mesocosms with and without plants (21 m⁻²) and crabs (68 m⁻²). Saplings grew more leaves and pneumatophores in the presence of crabs. Dense microalgal mats lead to two to six times higher benthic production and about two times higher benthic respiration in the absence of crabs. Particle mixing by crabs increased the reactive oxidized iron (Fe(III)) in the upper 2 cm of the sediment, whereas oxygen leaching by roots maintained the deeper rhizosphere oxidized and enriched in Fe(III). The highest microbial activity, measured as carbon dioxide production and iron reduction, occurred within the upper 2 cm of ungrazed sediment and was fueled by the large near-surface biomass of microalgae. Leaching of dissolved organic carbon (DOC) from roots stimulated bulk sulfate reduction and caused an upward cascading reduction of the sediment as indicated by low Fe(III) and high Fe(II) between 2-cm and 6-cm depth. The effect DOC was also evident as increased microbial abundance at all depths in the sediment. Fe(III) was the most important electron acceptor for microbial carbon oxidation in ungrazed sediment (63–70%), whereas sulfate reduction was more important in grazed sediment (36–44%), particularly in the presence of plants. Aerobic respiration always accounted for <20%. Fiddler crabs and roots of *A. marina* have complementary effects on the biogeochemistry of mangrove sediment. Their association seems to be mutually beneficial with respect to growth and food availability.

Mangrove forests constitute a highly productive ecosystem along most tropical coastlines. They support abundant benthic communities and high rates of microbial decomposition (Alongi and Sasekumar 1992; Alongi et al. 2001; Holmer et al. 2001). Litter (e.g., leaves, propagules, flowers, etc.) from trees is usually considered the main source of carbon and nutrients for decomposer food webs

in mangrove environments, but the contribution from macroalgae, benthic microalgae, and phytoplankton may in certain areas be of considerable importance (Newell et al. 1995; Alongi 1998). Accordingly, stable carbon isotopic studies have revealed that mangrove-derived litter is directly or indirectly the major food source for many species of benthic macrofauna, whereas others primarily consume algae (e.g., Bouillon et al. 2002). Crabs are generally the key structuring faunal group and the driver of the decomposer food webs in mangrove forest. Whereas sesamid crabs (*Grapsidae*) are remarkable consumers of mangrove litter (Robertson et al. 1992; Thongtham and Kristensen 2005), fiddler crabs (*Ocypodidae*) are efficient consumers of benthic microalgae (France 1998; Reinsel 2004).

Although crabs handle large amounts of detritus in mangrove environments, most of the organic carbon oxidation is usually mediated by anaerobic microbial processes (Alongi et al. 1998; Alongi et al. 2000; Kristensen et al. 2000). The role of specific carbon oxidation pathways

¹ Corresponding author (ebk@biology.sdu.dk).

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is, however, not fully clear and may vary within and among mangrove environments. Denitrification, manganese (Mn) reduction, and iron (Fe) reduction have usually been considered unimportant compared with sulfate reduction (Kristensen et al. 1994; Nedwell et al. 1994). Recent evidence suggests, however, that the role of iron respiration may be comparable to, or higher, than that of sulfate reduction in iron-rich mangrove environments (Kristensen et al. 2000). Besides availability of reactive iron (Thamdrup 2000), the controlling factors involve below-ground plant roots and bioturbating infauna (Gribsholt et al. 2003).

Only a few studies have examined the role of crabs and plant roots for sediment biogeochemistry in mangrove sediments. Nielsen et al. (2003) observed that burrows of fiddler crabs and roots of *Rhizophora apiculata* cause iron reduction to occur down to 7-cm depth. More is known about the role of crabs and plant roots in temperate *Spartina* marshes (Kostka et al. 2002; Gribsholt et al. 2003). Iron reduction may in vegetated and bioturbated marshes comprise up to 100% of the carbon oxidation, whereas sulfate reduction dominates (>70% of carbon oxidation) in areas devoid of plants and animals. The role of iron as electron acceptor in subsurface sediments is primarily driven by rapid oxidative regeneration of reactive Fe(III) by downward translocation of oxygen via irrigated burrows and leaky roots (Thamdrup 2000; Canfield et al. 2005).

The inherent heterogeneity on small and large spatial scales is a major problem in studies of sediment biogeochemistry in mangrove areas and prevents reliable comparisons between various environments and minimizes the chances of discriminating effects of roots and infauna on the biogeochemistry (Holmer et al. 1999; Alongi et al. 2000). This problem can be rectified by establishing large-scale sediment systems (mesocosms) where the experimental conditions are controlled according to the study objectives, e.g., abundance of plants and animals. This approach has proved successful for both ecological and biogeochemical studies in various aquatic environments (e.g., Gribsholt and Kristensen 2002a; Peralta et al. 2003; Orvain et al. 2004), but has until now never been used in studies of mangrove sediment biogeochemistry.

In this study, the effect of mangrove tree saplings (*Avicennia marina*) and fiddler crabs (*Uca vocans*) on sediment metabolism, iron and sulfur biogeochemistry, and microbial activity is assessed in mangrove mesocosms. Four mesocosms with and without crabs and saplings were established and maintained for 6 months before measurements of benthic primary production and respiration, solid phase and pore-water geochemistry, anaerobic carbon oxidation, sulfate reduction, and iron reduction. This approach is not only ideal for evaluating the effects of surface activity of crabs and subsurface activity of roots on sediment biogeochemistry, but also provides indications of ecological links between crabs and plants.

Methods

Sampling site—Samplings were conducted along a wide creek bank approximately 10-km upstream on the man-

grove-vegetated Haughton River Estuary (19°27'S, 147°06'E) at the Coral Sea coast, about 50 km southeast of Townsville, North Queensland, Australia. The climate in the area is dry tropical with monthly average temperatures ranging from 25°C in winter to 31°C in summer. The annual precipitation of 400 mm occurs almost entirely during summer, causing the salinity in the estuary to vary from <10 in summer to >50 in winter. Tides are semidiurnal with amplitude ranging from 0.5 m to 2.5 m.

The gentle slope of the 10-m wide creek bank enabled the occurrence of young mangrove trees (mostly *A. marina*) and fiddler crabs (mostly *U. vocans*). The sediment was composed largely of silt and clay (90% of particles <63 µm) mixed with dead twigs and roots. The highly fluid upper 2 cm of the sediment was oxidized as indicated by a brownish color. Oxidized conditions were maintained to at least 10-cm depth, primarily caused by the presence of numerous highly oxidized burrows of small (<3-cm long) polychaetes and more occasional larger fiddler crabs. The sediment turned gradually black with depth below 10 cm.

Mesocosms—Sediment for mesocosms was collected at low tide in late October 2002 by transferring the upper 10–15 cm of sediment from the creek bank, by digging, into buckets. A total of 1.2 m³ sediment was retrieved and immediately transported to the Australian Institute of Marine Science (AIMS) for further processing. Salinity and temperature of the creek water were 45–50 and approximately 29°C, respectively, during sediment collection. After the return to AIMS, the sediment was homogenized, split into four portions, and transferred to four outdoor tanks (220-cm long, 70-cm wide, and 50-cm deep) to a depth of about 20 cm. Finally, the sediment surface was leveled smooth, allowing an approximate 5-cm downward slope to the drainage end of the tanks. No attempts were made to exclude macroinfauna other than crabs. The following day, tidal simulation was initiated by pumping seawater from underlying 800-liter reservoirs via a timer-controlled pump into each mesocosm tank. Water returned to the reservoirs by passive drainage. No resuspension of surface sediment occurred during flooding. Tidal inundation was semi-diurnal with a maximum water depth of 20 cm and lasted 1.25 h per tide, which is comparable to the average tidal cover at the sampling site. The water in the four reservoirs was replaced every 2 weeks with clean seawater (salinity 36–40) obtained outside the Haughton River Estuary.

Six days after sediment transfer, two mesocosms were each planted evenly with 29 *A. marina* saplings (19 m⁻² density). The plants had been collected as propagules 3 months earlier from a nearby forest and grown to an average height of 20 cm at the time of transfer to mesocosms. A few dead plants were replaced within the first 2 weeks. Three weeks after sediment transfer, one mesocosm with *A. marina* and one without were each supplied with 96 fiddler crabs (*U. vocans*, 62 m⁻² density) of different size (1–5-cm carapace width) and sex. The crabs were caught by hand along a tidal creek near the sediment sampling site. They immediately started digging burrows and foraged intensively at the sediment surface. The four mesocosms represented the following four treatments:

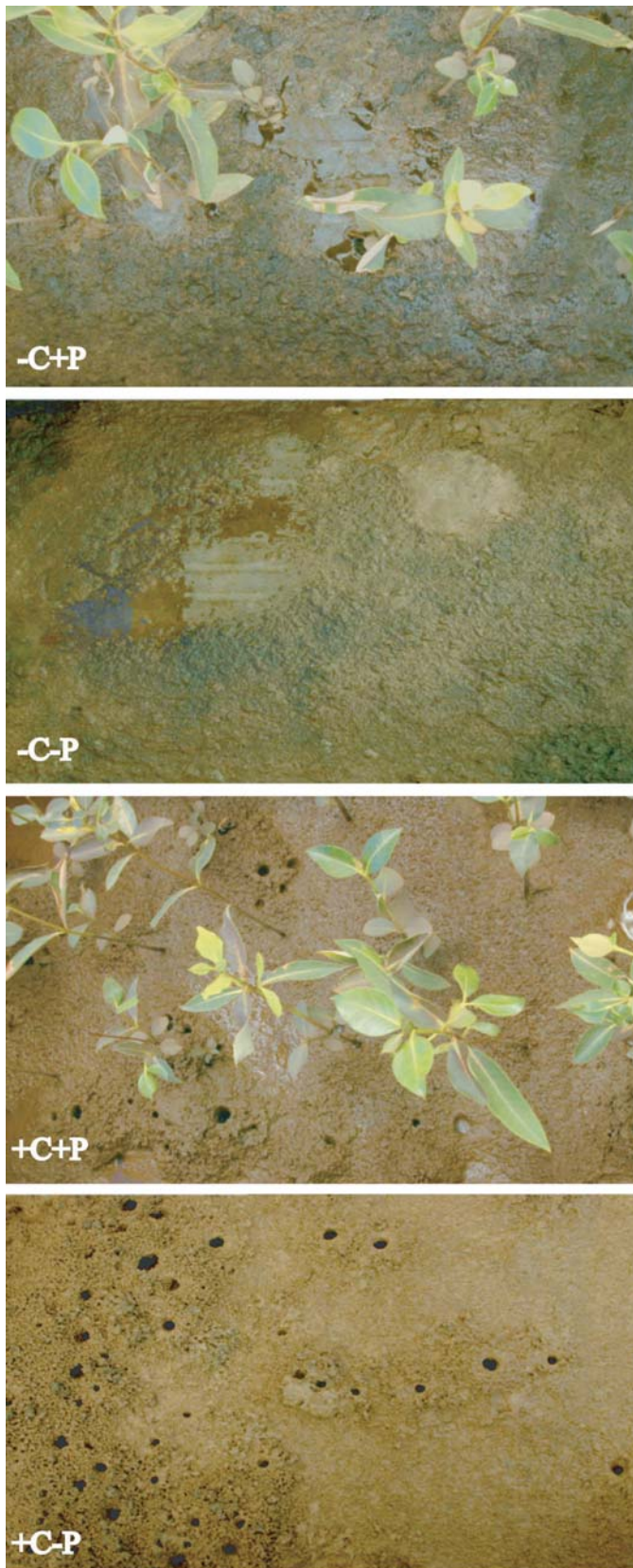


Fig. 1. Photos showing surface section from above each mesocosm treatment 2 months after establishment. $-C+P$, without crabs and with plants; $-C-P$, without crabs and without plants; $+C+P$, with crabs and with plants; $+C-P$, with crabs and without plants.

(1) without crabs and with plants ($-C+P$), (2) without crabs and without plants ($-C-P$), (3) with crabs and with plants ($+C+P$), and (4) with crabs and without plants ($+C-P$) (Fig. 1).

Mesocosms were maintained for 6 months after introduction of crabs at a constant tidal regime and natural day–night cycles. A few dead crabs were replaced at intervals. Air and water temperature ranged from 27°C to 33°C. The growth of plants was monitored by regular measuring of height and counting the number of leaves, branches, and pneumatophores. Nondestructive flux measurements (sediment–water and sediment–air) were conducted during month 5, and destructive sampling for anaerobic sediment incubations, as well as determination of vertical pore water, solid phase parameters, and infaunal abundance, was conducted during month 6.

Flux measurements—Benthic primary production and respiration in mesocosms were determined as carbon dioxide (CO_2) exchange across the sediment–water interface of inundated sediment and across the sediment–air interface of air-exposed sediment, as described by Gribsholt and Kristensen (2002a). Measurements of benthic oxygen (O_2) production in the light and O_2 demand in the dark were conducted simultaneously. During the primary production assay, mesocosms were exposed to natural sunlight around noon, while light was excluded by a frame covered with black plastic during benthic respiration assay. The plastic frame was placed above the selected mesocosms late afternoon the day before and removed immediately after measurements early the following day.

Inundated fluxes were determined using transparent glass chambers (inside diameter [i.d.] 9.4 cm) inserted approximately 7 cm into the sediment, trapping a volume of approximately 650-mL overlying water. For each mesocosm, triplicate chambers were deployed together, with one control chamber having a sealed glass bottom for determination of water phase activity. The tidal pump was started manually about 3 h before placing chambers in the mesocosms, and high tide was maintained until flux incubations were terminated about 4 h later. Care was taken to avoid visible *A. marina* pneumatophores and *U. vocans* burrows inside chambers. The chambers were equipped with an electric-propeller unit at the top for stirring and two lateral sampling ports. One of the ports was sealed with a TPS oxygen electrode, and the other was sealed with a Teflon-coated screw cap, except when water samples were taken for total CO_2 (TCO_2) and dissolved organic carbon (DOC) analysis. O_2 concentration was recorded every 15 min, and O_2 flux was calculated from slope of change over time. Initial O_2 was always around 80% of air saturation, and the linear decrease in the dark never dropped below 60%. Samples for TCO_2 and DOC were taken immediately before the first O_2 reading and after the last O_2 reading. TCO_2 was analyzed within 6 h by

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$+C+P$, with crabs and plants; $+C-P$, with crabs and without plants.

the flow injection/diffusion cell technique (precision <1%) (Hall and Aller 1992). DOC samples were stored frozen in precombusted glass vials and later analyzed on a total organic carbon analyzer (model TOC-5000, Shimadzu) after acidification with 2-mol L⁻¹ hydrochloric acid (HCl) (pH < 3) to remove dissolved inorganic carbon.

Air-exposed fluxes were conducted roughly 2 h after onset of low tide. Triplicate cylindrical Plexiglas tubes (8-cm i.d. and 12-cm length) were inserted 10 cm into the sediment between pneumatophores and burrow openings in each mesocosm, trapping about 100-mL headspace. The tubes were capped airtight with transparent lids, and O₂ was measured before and after a 4-h incubation period with a Radiometer oxygen electrode inserted through the lids (Kristensen et al. 1992). After termination of O₂ measurements, a gas flowthrough system was established by a peristaltic pump via polyethylene tubing through two ports in the lid for determination of CO₂ changes. Moistened atmospheric air was continuously pulled into the headspace of the core tube at a rate of 10–12 mL min⁻¹. When steady state was reached after 30–60 min, 50-mL samples of incurrent (atmospheric air) and excurrent gas were collected in syringes and immediately analyzed for CO₂ in an MTI Analytical Instruments P200 gas analyzer equipped with a HayeSep A column and a thermal conductivity detector.

Anoxic sediment incubations—Anaerobic carbon oxidation and iron respiration were quantified at 0–2-cm, 2–4-cm, 6–8-cm, and 10–12-cm depth in the sediment. Four sediment cores (8-cm i.d. and 16-cm deep) were sampled from each mesocosm using acrylic core tubes. After sectioning, the four sediment slices from each depth interval were pooled, and the pore water SO₄²⁻ concentration was increased by 10 mmol L⁻¹ to avoid depletion during incubation and mixed thoroughly under nitrogen (N₂) in a glove bag. The homogeneous sediment mixtures from each depth interval (~200 mL) were transferred into eight 20-mL glass scintillation vials (jars), which were capped with no headspace, taped to prevent oxygen intrusion, and incubated in the dark at 25°C. Two jars from each depth were sacrificed at 2–4-day (0–2-cm depth) and 7-day (below 2-cm depth) intervals for determination of pore-water TCO₂, DOC, and Fe²⁺ concentrations. Pore water was extracted from the jars by centrifugation at 2,700 rpm for 10 min, returned to the glove bag, and filtered through Whatman GF/F filters. Subsamples for TCO₂ and DOC were handled and analyzed as described above, whereas those for Fe²⁺ were acidified (20 μL of 0.5 mol L⁻¹ HCl per 1 mL) and stored at 5°C in polyethylene vials until analysis by the spectrophotometric ferrozine technique [50-μL sample transferred to 2 mL of 0.02% ferrozine in 50-mmol L⁻¹ 4-(2-hydroxyethyl)-1-piperazine ethanesulfonic acid buffer, pH = 7] (Stookey 1970).

The sediment remaining after pore-water extraction was homogenized under N₂ for reactive Fe(II) extraction by a modified version of the HCl technique of Lovley and Phillips (1987b). Briefly, 100–300-mg subsamples were extracted in 5 mL of 0.5-mol L⁻¹ HCl for 30 minutes on a shaking platform at 25°C and centrifuged (5,000 rpm for

10 min). The supernatant was GF/F filtered and stored at 5°C until analysis as described above for Fe²⁺.

Reaction rates in jars were calculated from a linear fit of concentration changes in the time series of samples. Iron reduction (corrected for compaction during pore-water extraction) was determined as reactive Fe(II) accumulation assuming limited precipitation of iron into non-acid extractable phases (Canfield et al. 1993).

Sulfate reduction assay—Sulfate reduction was measured by the core injection technique of Jørgensen (1978). Three 16-cm-long cores were retrieved from each mesocosm using 20-cm long and 2.6-cm i.d. core tubes with silicone-filled injection ports. Carrier-free ³⁵S-SO₄²⁻ was injected at 1-cm intervals to 13-cm depth, and the cores were incubated at 25°C with dry surface in darkness for 4–6 h. Subsequently, each core was sliced under N₂ at 2-cm intervals and fixed in 20% zinc acetate. Samples were stored frozen until distillation by the procedure of Fossing and Jørgensen (1989) to quantify the fraction of reduced radiolabel converted into sulfides.

Sediment characteristics and pore-water solutes—Triplicate sediment cores (5-cm i.d.) were taken from each mesocosm to determine vertical profiles of porosity, organic content, solid-phase reactive iron [Fe(II) and Fe(III)], and reduced inorganic sulfur. The cores were sectioned into 0–1-cm, 1–2-cm, 2–3-cm, 3–4-cm, 4–6-cm, 6–8-cm, 10–12-cm, and 14–16-cm intervals. Porosity was estimated from water loss upon drying of sediment subsamples at 100°C and wet density (weight of a known volume). The dried sediments were subsequently used for determination of particulate organic carbon (POC) and particulate organic nitrogen (PON) by a Carlo Erba model EA1108 CHNS analyzer using the difference-on-ignition method (Kristensen and Andersen 1987). Sediment subsamples for solid-phase reactive iron determination were extracted as described above for jar incubations. For Fe(II) analysis, 50 μL of the supernatant was transferred to 2-mL ferrozine solution, and total Fe [Fe(II) + Fe(III)] was determined similarly after reducing the supernatant with 1.5-mol L⁻¹ hydroxylamine hydrochloride in 0.25-mol L⁻¹ HCl (volume ratio 5:1). The reactive amorphous Fe(III) oxyhydroxide concentration was operationally defined as the difference between total Fe and Fe(II) (Kostka and Luther 1994). Separate sediment subsamples for reduced inorganic sulfur were distilled by the two-step procedure to quantify acid-volatile sulfides (AVS ~ hydrogen sulfide [H₂S] and mackinawite [FeS]) and chromium-reducible sulfur (CRS ~ elemental sulfur [S⁰] and pyrite [FeS₂]). Sulfide was analyzed by the methylene blue method (Cline 1969).

Separate sets of triplicate cores from each mesocosm were sectioned as mentioned above for analysis of pore-water TCO₂, DOC, SO₄²⁻, and Fe²⁺. Pore water was extracted by transferring the sediment slices to 50-mL tubes followed by centrifugation at 5,000 rpm for 10 min. The supernatant pore water was handled and analyzed as described for anaerobic sediment incubations.

Abundance of infauna, microphytobenthos, and bacteria—The abundance of macroinfauna was determined by sieving three sediment cores (8-cm i.d.) from each mesocosm through a 1-mm mesh. The material retained was carefully examined for fauna, and the recovered animals were identified to lowest taxonomic level and counted. The abundance of crabs at the end was not quantified because this would require a careful and extremely elaborate examination of all remaining sediment in mesocosms.

Chlorophyll *a* (Chl *a*) concentrations were used as a measure of microalgal abundance. Sediment samples of about 0.5 g wet weight from cores taken for solid-phase parameters were extracted in 5 mL of 96% ethanol for 24 h at 5°C. After centrifugation at 5,000 rpm for 5 min, the supernatant was decanted and analyzed for Chl *a* by the spectrophotometric method of Parsons et al. (1984).

Samples for enumeration of bacterial populations were taken in parallel to those for Chl *a*. About 100 mg of sediment was transferred to 1.5-mL Eppendorf tubes containing 1 mL of 5 vol% glutaraldehyde in 35% seawater. Samples were stored at 5°C and enumerated by epifluorescence microscopy on 4',6-diamidino-2-phenylindole (DAPI)-stained subsamples (Porter and Feig 1980; Andresen and Kristensen 2002).

Statistical analysis—Only one replicate of each mesocosm treatment was established because of logistic and resource limitations. We are, however, confident that samples taken within each mesocosm represent true replicates for the following reasons: (1) all mesocosms were identical before the experiment was initiated, and they were maintained similarly throughout and (2) the studied interactions and effects were examined at a small scale (centimeter to millimeter) with a level of variation within each mesocosm that is greater than between mesocosms.

Differences in fluxes and faunal abundance were tested using one-way analysis of variance (ANOVA). Data for plant parameters and depth profiles of reaction rates, pore-water solutes, and solid-phase parameters were evaluated by two-way repeated measures ANOVA. In some cases the ANOVAs were followed by a Bonferroni-adjusted Fisher's least significant difference test to resolve which treatment differed. The fraction of plants with pneumatophores was compared using z-test of proportions. A significance level of $\alpha = 0.05$ was used in all tests. Data were analyzed using SAS (version 8).

Results

Macrofauna and macroflora—After introduction of fiddler crabs, the surface topography of +C+P and +C-P mesocosms changed dramatically. The crabs dug numerous burrows with up to 5-cm-high mounds and chimneys around openings, creating depressions away from burrows (Fig. 1). Burrows were primarily constructed near solid surfaces, such as tank walls and, in the case of +C+P, around *A. marina* stems and roots, and were most numerous near the water inlet/exit end of the tanks. The constant movement and feeding by crabs at low tide created 1–2-cm-deep tracks in the sediment lined with

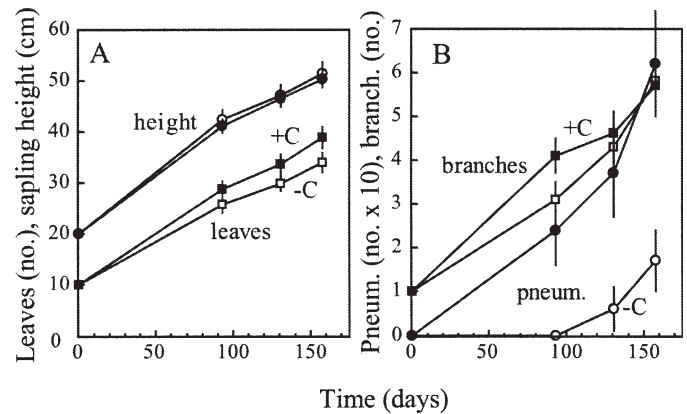


Fig. 2. Development of *A. marina* morphology through time in mesocosms with (+C, solid symbols) and without (-C, open symbols) crabs. (A) Sapling height and number of leaves per plant; (B) number of branches and visible pneumatophores per plant. Error bars indicate SEM ($n = 29$).

deposits of handled sediment pellets and feces. All crabs returned to their burrows at high tide and plugged the opening with sediment until next low tide.

Both mesocosms without grazing crabs (-C+P and -C-P) developed a homogeneous green microalgal mat (likely a mix of diatoms, green algae, and cyanobacteria) within the first month. The mats became patchier and turned gradually darker green through time. No visible signs of microalgae were evident in the mesocosms with crabs. A high abundance of burrow-dwelling chironomid larvae feeding on the microalgal mat developed in mesocosms without crabs during the first month after establishment (not quantified). Subsequently, the abundance of larvae gradually declined and was 70 ± 115 (-C+P) and 870 ± 808 (-C-P) m^{-2} at the end (\pm SD, $n = 3$). No larvae were noticed at any time in mesocosms with crabs. In these grazed systems, the abundance of polychaetes (e.g., nereidids), on the other hand, reached a significantly higher level at the end ($530 \pm 115 m^{-2}$ in +C+P and $670 \pm 305 m^{-2}$ in +C-P) than in the ungrazed mesocosms ($270 \pm 115 m^{-2}$ in -C+P and $70 \pm 115 m^{-2}$ in -C-P) (\pm SD, $n = 3$).

The *A. marina* saplings grew with an almost constant rate of about $0.2 cm d^{-1}$, irrespective of the presence of crabs, reaching a maximum height of $51 \pm 11 cm$ with 5.7 ± 3.0 (\pm SD, $n = 58$) branches per plant at the end (Fig. 2A,B). They developed more leaves, and a significantly larger fraction of plants grew pneumatophores in the presence of crabs (39 ± 2 leaves and 0.6 ± 0.1 pneumatophores per plant, \pm SD, $n = 29$) than in the absence of crabs (34 ± 2 leaves and 0.2 ± 0.1 pneumatophores). Root biomass accounted for about 60% and 40% of the total plant biomass on wet and dry weight basis, respectively, with no apparent influence of crabs.

Sediment characteristics—The sediment was visibly oxidized to 0.5–1-cm and 2–3-cm depth in mesocosms without and with crabs, respectively. Below, the sediment turned grey and, with depth, gradually more blackish.

Table 1. Characteristics of sediment from the four mesocosms. Values are given as mean (\pm SD) for the depth interval 0–1 cm and as the range for the interval 1–16 cm.

Location	Porosity (vol/vol)	Organic content (LOI, %)	POC (mmol (g dry wt) ⁻¹)	POC : PON (mol)
0–1 cm				
–C+P	0.77 \pm 0.02	12.0 \pm 0.4	1.83 \pm 0.12	27.2
–C–P	0.70 \pm 0.01	11.2 \pm 0.2	1.66 \pm 0.04	16.3
+C+P	0.74 \pm 0.01	10.3 \pm 0.0	1.51 \pm 0.05	17.7
+C–P	0.71 \pm 0.01	10.4 \pm 0.4	1.48 \pm 0.02	20.1
1–16 cm				
–C+P	0.68–0.71	10.5–10.9	1.58–1.69	21.5–26.8
–C–P	0.69–0.70	10.7–10.8	1.48–1.56	17.7–19.0
+C+P	0.67–0.72	10.1–10.7	1.49–1.61	18.7–20.3
+C–P	0.69–0.71	10.2–10.4	1.47–1.60	18.9–21.9

Burrows of chironomid larvae and polychaetes were evident as numerous oxidized traces in the upper 10–12 cm. Live roots were always surrounded by an oxidized halo at all depths.

Porosity and organic content was almost constant with depth from 1 cm to 16 cm in mesocosms, whereas the upper centimeters in many cases showed some deviation (Table 1). Porosity ranged from 0.67 to 0.72, except for higher values near the surface when plants were present. Organic content measured as loss-on-ignition and POC ranged from 10.1% to 10.9% and 1.47 mmol (g dry wt)⁻¹ to 1.69 mmol (g dry wt)⁻¹, respectively, except for somewhat higher values near the surface when crabs were absent. The POC : PON ratio was variable and ranged between 16.3 and 27.2 with no consistent pattern.

Microorganisms—Microalgal biomass (as Chl *a*) near the sediment surface was strongly affected by the presence of crabs (Fig. 3A,B). Chl *a* concentration in the upper 0–1 cm of mesocosms without crabs was significantly (four to five times) higher than the background level of about 2 μ g (g wet wt)⁻¹, whereas the corresponding difference in mesocosms with grazing crabs was negligible. There was no significant effect of plants on the abundance of microalgae.

Bacterial abundance decreased significantly with depth in all the examined sediments (Fig. 3C,D). The most pronounced difference between mesocosms was caused by the presence of plant roots. They were responsible for a significantly increased bacterial abundance of 30–190% (mean 85%) in the absence of crab and 8–97% (mean 42%) in the presence of crabs. Grazing by crabs decreased the number of bacteria in the upper 0–1 cm of the sediment by 63% in the absence of plants and 30% in the presence of plants. The effect was only significant in the absence of plants.

Solid-phase iron and reduced inorganic sulfur—All sediments showed a solid-phase reactive iron content of 100–150 μ mol cm⁻³. Fe(III) dominated near the sediment surface with a concentration of 90–130 μ mol cm⁻³ at 0–1 cm and declined rapidly with depth to 0–20 μ mol cm⁻³ below 5 cm (Fig. 4A,B). The decrease in Fe(III) with depth was significantly faster in mesocosms with plants, reaching

a level of about 20 μ mol cm⁻³ at 2 cm with no further change deeper down. This level was first reached at 5–7 cm in mesocosms without plants, but here the concentration continued to decrease to almost zero below 10-cm depth. The effect of crabs on Fe(III) was evident as a significant enrichment in the upper 1–2-cm depth interval in the presence of plants.

Fe(II) showed a pattern opposite to that of Fe(III), with a rapid increase from low concentration near the sediment surface (0–20 μ mol cm⁻³ at 0–1-cm depth) to high concen-

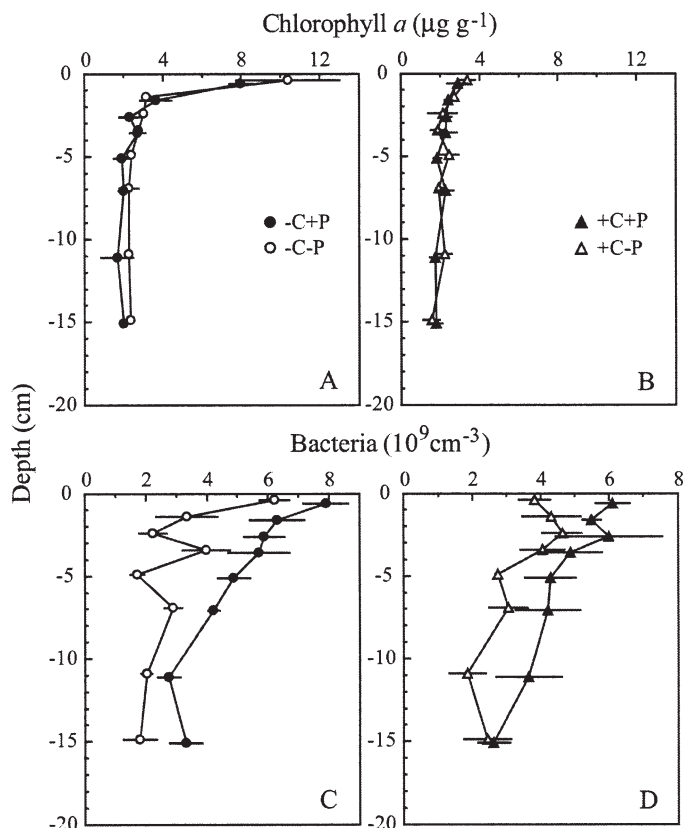


Fig. 3. Vertical distribution of (A, B) Chl *a* content and (C, D) bacterial abundance in sediment of the four mesocosms. Error bars indicate SEM ($n = 3$).

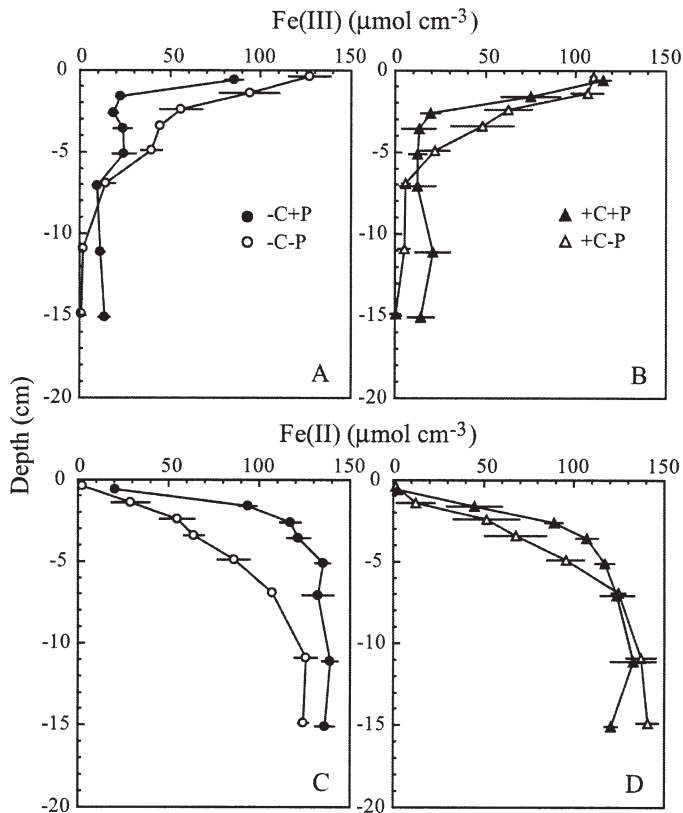


Fig. 4. Vertical distribution of (A, B) 0.5 mol L^{-1} HCl extractable solid-phase Fe(III) and (C, D) Fe(II) in sediment of the four mesocosms. Error bars indicate SEM ($n = 3$).

trations deeper in the sediment ($130\text{--}140 \mu\text{mol cm}^{-3}$ below 10-cm depth) (Fig. 4C,D). The steepness of increase was significantly higher and the maximum approached at shallower depth (4–5 cm) in mesocosms with plants than without plants (7–10 cm). The profiles were displaced slightly downward in the upper 2 cm in mesocosms with crabs.

Depth profiles of CRS varied among mesocosms in a pattern similar to that of Fe(II). CRS increased with depth from $35\text{--}60 \mu\text{mol cm}^{-3}$ at 0–1 cm to $60\text{--}90 \mu\text{mol cm}^{-3}$ below 2–4 cm depth (Fig. 5A,B). The CRS content was highest in mesocosms with plants—a trend that was significant only in the absence of crabs. AVS was almost zero in the upper 2–5 cm and increased linearly further down in the sediment. However, the concentration was generally low and only exceeded 1% of CRS in a few instances. AVS was significantly higher in mesocosms with plants than without plants below 5-cm depth only in the absence of crabs (Fig. 5C,D).

Pore-water solutes— TCO_2 generally increased with sediment depth in all mesocosms (Fig. 6A,B). The increase was most pronounced from 5 cm to 10 cm, reaching higher concentrations in the presence ($15\text{--}19 \text{ mmol L}^{-1}$) than the absence ($10\text{--}11 \text{ mmol L}^{-1}$) of plants, with an effect of crabs only in the presence of plants. The profiles of DOC showed the same significant pattern as TCO_2 , increasing from $<0.5 \text{ mmol L}^{-1}$ near the surface to $2.5\text{--}3 \text{ mmol L}^{-1}$ in the absence of plants and $4\text{--}4.5 \text{ mmol L}^{-1}$ in the

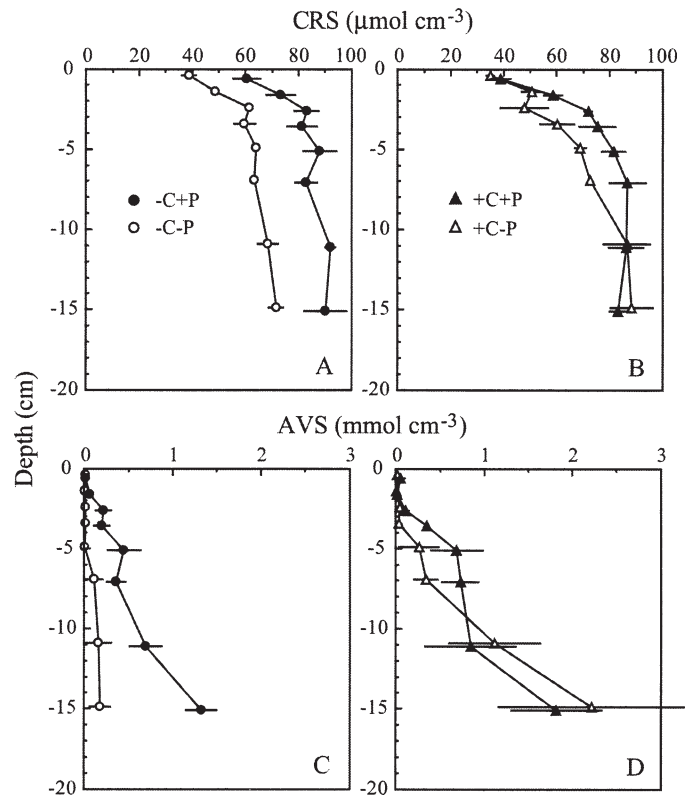


Fig. 5. Vertical distribution of (A, B) CRS and (C, D) AVS in sediment of the four mesocosms. Error bars indicate SEM ($n = 3$).

presence of plants (Fig. 6C,D). The influence of crabs on DOC was only evident as a trend for lowered level in the 1–2 cm-depth interval.

Dissolved Fe^{2+} was low or absent in the upper 4–5 cm and lowest in the presence of crabs (Fig. 7A,B). Below this depth, Fe^{2+} increased rapidly to a significantly higher concentration in the presence of plants (1 mmol L^{-1}) than in the absence ($0.5\text{--}0.6 \text{ mmol L}^{-1}$) of plants followed by a less steep increase to a similar level of 1.3 mmol L^{-1} to 1.8 mmol L^{-1} irrespective of treatment at 16-cm depth. Dissolved Fe^{2+} only appeared when Fe(III) decreased below a level of about $20 \mu\text{mol cm}^{-3}$.

Fluxes across the sediment–water/air interface—The exchange of O_2 and CO_2 across the sediment–water/air interface was always significantly highest in mesocosms devoid of crabs, irrespective of water cover and light regime (Fig. 8). Microphytobenthic net primary production (NPP) was of comparable magnitude in the two treatments without crabs, showing significantly higher rates during inundation ($-123 \text{ CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ to $-98 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) than during air exposure ($-73 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ to $-58 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). Benthic respiration (RSP) during darkness in these mesocosms was also significantly higher during inundation ($78\text{--}91 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) than during air exposure ($56\text{--}61 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), providing gross primary production ($\text{GPP} = \text{NPP} + \text{RSP}$) that was considerably higher during in-

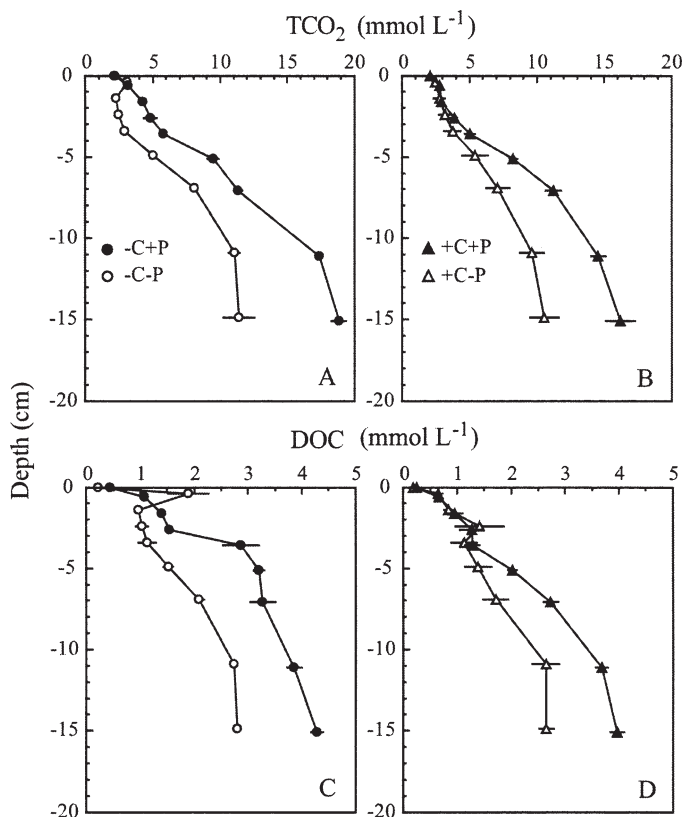


Fig. 6. Vertical distribution of (A, B) pore-water TCO_2 and (C, D) DOC in sediment of the four mesocosms. Error bars indicate SEM ($n = 3$).

undation ($189\text{--}200 \text{ mmol m}^{-2} \text{ d}^{-1}$) than during air exposure ($114\text{--}134 \text{ mmol m}^{-2} \text{ d}^{-1}$). It must be noted that benthic O_2 demand in the dark showed the opposite pattern of CO_2 release, with significantly higher rates during air exposure than during inundation. The community respiration quotients ($\text{CRQ} = \text{CO}_2 \text{ flux}/\text{O}_2 \text{ flux}$) of $0.6\text{--}0.7$ during air exposure compared with 2.1 during inundation suggest that the measured O_2 uptake probably was excessive and/or CO_2 release was deficient for exposed sediment.

Fluxes in mesocosms with crabs generally showed the same response to water cover as those without crabs, but the rates were considerably lower and more erratic. NPP during inundation ($-21 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ to $13 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and air exposure ($-17 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ to $-1 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) were of comparable magnitude. RSP showed no significant difference between treatments and ranged from $41 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ to $47 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ during inundation and $32\text{--}34 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ during air exposure. As a consequence, GPP showed no specific pattern and ranged between $34 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ and $63 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. Also here, the low CRQ of 0.7 of exposed sediment compared with 3.3 during inundation indicated an apparent excessive uptake of O_2 and/or deficient CO_2 release across the sediment-air interface.

The flux of DOC during inundation was always directed out of the sediment with no significant differences among

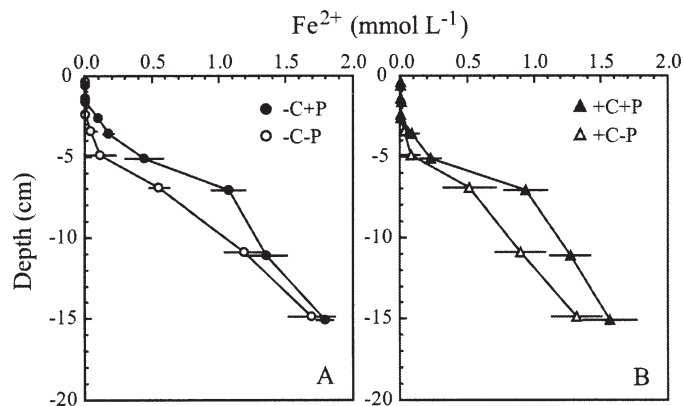


Fig. 7. Vertical distribution of pore-water Fe^{2+} (A, B) in sediment of the four mesocosms. Error bars indicate SEM ($n = 3$).

treatments (data not shown), but with somewhat lower rates in the light ($6.1\text{--}7.9 \text{ mmol DOC m}^{-2} \text{ d}^{-1}$) than in the dark ($8.8\text{--}16.3 \text{ mmol DOC m}^{-2} \text{ d}^{-1}$).

Reaction profiles—Anaerobic carbon oxidation (measured as CO_2 production) was very high in the upper centimeters of mesocosms devoid of crabs ($1,400\text{--}2,300 \text{ nmol cm}^{-3} \text{ d}^{-1}$, Fig. 9A,B). Otherwise, the rates were modest and ranged between $150 \text{ nmol cm}^{-3} \text{ d}^{-1}$ and $400 \text{ nmol cm}^{-3} \text{ d}^{-1}$ with no significant trend among mesocosms and with depth in the sediment. As a consequence of the high rates in the microalgal mat, the depth-integrated ($0\text{--}16 \text{ cm}$) CO_2 production in mesocosms without crabs was higher (43% for +P and 138% for -P) than in those with active crabs (Table 2). There was no significant effect of plants on the CO_2 production. The depth-integrated CO_2 rates corresponded well with the time-weighted dark O_2 uptake across the sediment-water/air interface (based on 10% inundation and 90% air exposure time), but was 15–60% higher than the time-weighted dark CO_2 release.

The net generation of DOC within the anoxic sediment showed no specific depth pattern (Fig. 9C,D) and was negligible, showing rates less than 10% of the CO_2 production. The depth-integrated net DOC production ($0.2\text{--}5.5 \text{ mmol m}^{-2} \text{ d}^{-1}$) was comparable to the time-weighted dark release of DOC across the sediment-water interface ($0.9\text{--}1.7 \text{ mmol m}^{-2} \text{ d}^{-1}$).

Iron reduction (FeR) determined from the anoxic jars showed a depth pattern similar to CO_2 production with rates in the upper cm of mesocosms devoid of crabs ($6,600\text{--}8,900 \text{ nmol cm}^{-3} \text{ d}^{-1}$) one to two orders of magnitude higher than deeper in the sediment and near the surface of mesocosms with crabs ($100\text{--}1,500 \text{ nmol cm}^{-3} \text{ d}^{-1}$) (Fig. 10A,B). There was no significant effect of plants.

Sulfate reduction rates (SRR) ranged from $30\text{--}70 \text{ nmol cm}^{-3} \text{ d}^{-1}$ in an irregular pattern from top to bottom in sediment devoid of crabs, whereas the rate in sediment with crabs increased from virtually zero near the surface to $60\text{--}110 \text{ nmol cm}^{-3} \text{ d}^{-1}$ below 7-cm depth. The presence of roots apparently increased SRR, particularly in sediment with crabs where the rates were significantly higher than in sediment without plants.

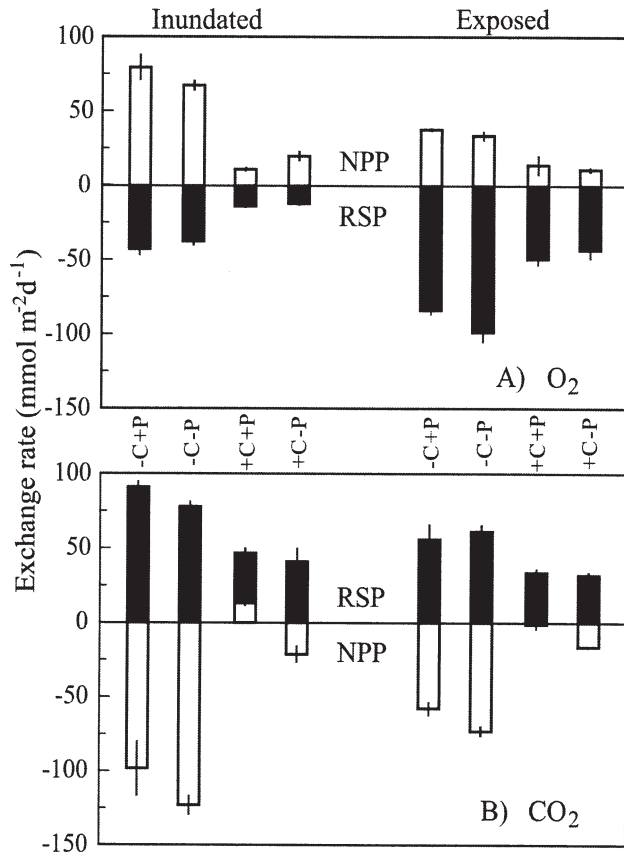


Fig. 8. Exchange of (A) O_2 and (B) CO_2 across the sediment–water (left) and sediment–air (right) interface in light (open bars) and darkness (closed bars). Error bars indicate SEM ($n = 3$).

Discussion

Tidal mesocosms are well suited for studying the influence of plants and animals on the biogeochemistry of intertidal sediments (Gribsholt and Kristensen 2002a). The present mangrove mesocosms mimic in situ conditions well as evidenced by the similarity in basic sediment parameters to those previously observed in mangrove forests from the same area (Alongi et al. 1999). The pretreatment, i.e.,

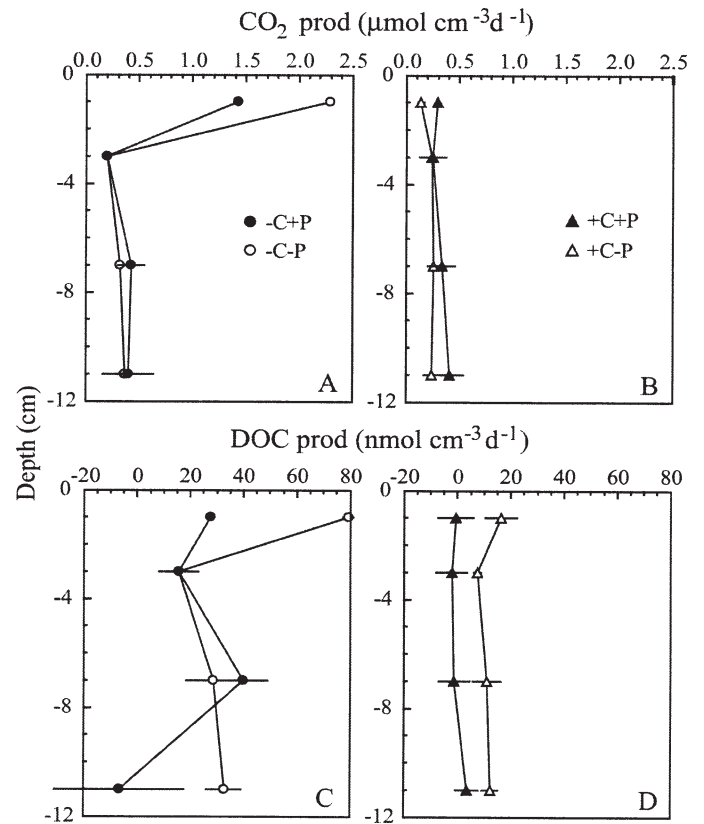


Fig. 9. Vertical distribution of (A, B) anaerobic CO_2 production and (C, D) DOC production in sediment of the four mesocosms. Error bars indicate range ($n = 2$).

mixing and homogenization, of the sediment used in mesocosms may, however, have displaced reactive organic matter and microbial reactions from the surface and into deeper sediment layers. The burrowing and feeding behavior of fiddler crabs (*U. vocans*) in the mesocosms was similar to that observed for this and related species under natural conditions (de la Iglesia et al. 1994; Weis and Weis 2004). *A. marina* also behaved well in mesocosms exhibiting a growth rate (0.2 cm d^{-1}) and a below-ground :

Table 2. Sediment metabolism in darkness given as measured O_2 uptake and CO_2 release across the sediment–water/air interface. Fluxes are weighed according to 10% inundation and 90% air exposure time. Depth-integrated (0–16 cm) total carbon oxidation is determined as CO_2 accumulation in anaerobic jars. The fraction derived from measured Fe(III) reduction is estimated using a Fe : C conversion factor of four, while carbon oxidation from sulfate reduction is derived from measured ^{35}S -sulfate reduction with a S : C conversion factor of 0.5. All rates are given as $\text{mmol C m}^{-2} \text{ d}^{-1}$ (\pm SD) and negative values indicate uptake. Values in parenthesis indicate the percentage contribution of FeR and SRR to the total jar CO_2 production.

	–C+P	–C–P	+C+P	+C–P
Fluxes				
O_2 uptake	-79.8 ± 5.4	-92.6 ± 10.5	-45.8 ± 6.8	-40.4 ± 9.2
CO_2 release	59.4 ± 16.2	63.0 ± 7.2	34.8 ± 4.6	32.8 ± 4.0
Depth integrated				
Jar CO_2 production	79.5 ± 21.8	90.1 ± 11.7	55.7 ± 17.9	37.8 ± 7.3
Jar Fe(III) reduction	49.7 ± 17.6 (63)	63.4 ± 28.4 (70)	20.6 ± 7.4 (37)	23.6 ± 4.8 (62)
^{35}S -sulfate reduction	18.6 ± 4.4 (23)	16.3 ± 5.5 (18)	24.4 ± 5.0 (44)	13.5 ± 2.0 (36)

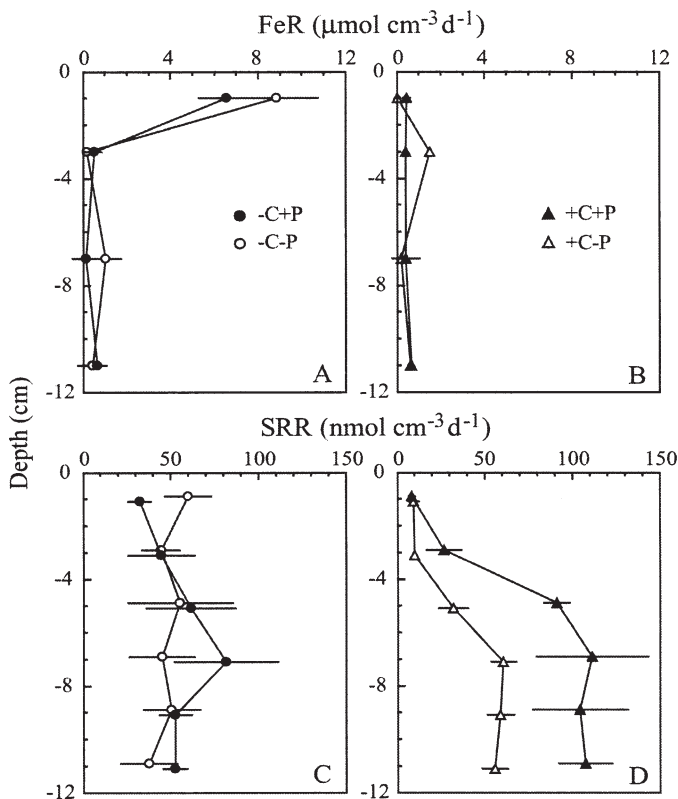


Fig. 10. Vertical distribution of (A, B) anaerobic iron reduction (FeR measured as Fe(II) generation) and (C, D) sulfate reduction (SRR measured by the ^{35}S technique) in sediment of the four mesocosms. Error bars indicate range ($n = 2$) in A, B and SEM ($n = 3$) in C, D.

above-ground ratio (~ 0.7) similar to those reported for natural mangrove settings (Liao et al. 2004). It must be emphasized, however, that 20-cm-tall mangrove saplings cannot develop into a mature forest in 6 months. The results obtained here should therefore be extrapolated with care to mature forest systems.

Fiddler crabs (*U. vocans*) and roots of *A. marina* have complementary effects on the biogeochemistry of mangrove sediment. While the role of crabs is largely confined to the upper 2 cm, roots have the largest effect below this depth in the sediment. Crabs increase the availability of Fe(III) for iron reducers near the sediment surface, but simultaneously their grazing efficiently removes microphytobenthos that otherwise supply the heterotrophic microbial community with labile organic carbon. As a consequence, near-surface sulfate reducers are competitively inhibited by more efficient iron reducers. Plant roots translocate O_2 into rhizospheres deep in the sediment and potentially provide Fe(III) for iron reducers. At the same time, exudation of labile DOC from roots stimulates sulfate reducers and causes a cascading effect that forces reduced conditions upward in the sediment.

Fiddler crabs and sediment biogeochemistry—The conspicuous removal of particularly Chl *a* but also bacteria near the sediment–water interface (Fig. 3) and the absence of chironomid larvae in mesocosms with crabs substanti-

ates the efficient grazing by *U. vocans*. Most species of fiddler crabs are known primarily to ingest benthic microalgae and bacteria (France 1998; Bouillon et al. 2002), although it is less clear how they handle meiofauna and small macrobenthos (Reinsel 2004). The commonly observed reduction of meiofaunal density (Hoffman et al. 1984) and, in the present case, absence of chironomid larvae by fiddler crabs can be a direct effect through predation or an indirect effect through disturbance or competition for food (Alongi 1989; Reinsel 2004; Weis and Weis 2004).

Foraging by fiddler crabs is generally confined to the upper few millimeters of the sediment (Dye and Lasiak 1986), but the activities of *U. vocans* affect redox sensitive elements (Fe and S, Figs. 4, 5, 7), down to at least 2-cm depth. The higher content of oxidized forms [Fe(III)] and lower content of reduced forms [Fe(II), Fe^{2+} , AVS, and CRS] in the upper 2 cm must be caused by continuous mixing and oxidation of surface sediment by the intense activities of the crabs (Hoffman et al. 1984). Mixing occurs not only during feeding but also when the dactyls of the legs sink into the sediment during crawling, and visual observations revealed crawling tracks everywhere on the sediment surface in mesocosms with crabs. Deposition at the surface of pseudofeces during feeding and subsurface sediment during burrow construction and maintenance, combined with the smoothening and oxidation effect of crawling crabs, augments the effective mixing depth.

The low rates of FeR in oxidized near-surface sediment inhabited by *U. vocans* (Fig. 10B) is caused by a lack of reactive organic carbon and not availability of Fe(III). This is substantiated by the one to two orders of magnitude higher FeR in the surface of ungrazed mesocosms (Fig. 10A) that are poorer in Fe(III) but much richer in labile organic carbon from the microalgal mat. The lower, but still sufficient, Fe(III) content driving FeR near the surface of ungrazed mesocosms must be maintained by burrowing and irrigation of the abundant chironomid larvae. Thus, Matisoff and Wang (1998) found that irrigation by various species of burrow-dwelling chironomid larvae strongly enhance fluxes of solutes to >4 cm into sediments. The associated downward transport of O_2 and oxidation of Fe(II), combined with frequent abandoning of old and construction of new burrows, must sustain the Fe redox cycle and enhance FeR in near-surface sediment of mesocosms devoid of crabs. The parallel, but much less dramatic, pattern with three to six times higher SRR near the sediment surface in ungrazed mesocosms compare with grazed mesocosms (Fig. 10C,D) is probably also caused by the higher organic matter availability. Nevertheless, most probable number (MPN) counts near the sediment surface reveal that sulfate-reducing bacteria (SRB) are two to four times more abundant in grazed than ungrazed mesocosms, while the latter contains one order of magnitude more iron-reducing bacteria (FeRB) than the former (Kostka unpubl. data). Thus, the cell-specific activity of FeRB is apparently unaffected by treatment, while the cell-specific activity of SRB is up to 20 times higher in ungrazed than grazed treatments. Despite their higher abundance, the activity of SRB may be competitively hampered by FeRB when the

availability of labile organic carbon is low (e.g., grazed situation), whereas such interaction is less likely when labile organic matter is in surplus (e.g., ungrazed situation) (Lovley and Phillips 1987a; Canfield et al. 2005).

Crab burrows were deliberately avoided during sampling to assure that only the effect of surface activities by the crabs was detected. This approach may, however, have biased the estimated average sediment biogeochemistry as crab burrows are potential sites for intense microbial activity and redox cycling driven by alternating oxic–anoxic conditions (Gribsholt et al. 2003; Nielsen et al. 2003). Nevertheless, Nielsen et al. (2003) estimated that the Fe(III) enrichment driving FeR and the impeded SRR is limited to a few mm zone around fiddler crab burrows and therefore is of minor influence on the averaged carbon oxidation pathways because of the relatively low abundance of burrows ($<100\text{ m}^{-2}$). According to their calculations, FeR around burrows in the present mesocosms does not exceed 2.5% of the total anaerobic carbon oxidation. The error introduced in overall budgets by ignoring burrows is in this case small and insignificant.

Roots and sediment biogeochemistry—Roots of many aquatic macrophytes are efficient conduits for oxygen to the interior of sediments because their well developed aerenchymatic tissues enable rapid downward O_2 diffusion (Sorrell and Armstrong 1994; Holmer et al. 2002). For example, Andersen and Kristensen (1988) measured an oxic zone of about 0.5 mm around *A. marina* pneumatophores and roots. Holmer et al. (2002) similarly estimated a minimum root-mediated subsurface flux of O_2 into *Spartina anglica* sediment of about $4\text{ mmol m}^{-2}\text{ d}^{-1}$. Most, if not all, of this rhizosphere O_2 is utilized for microbial and chemical oxidation of reduced iron and sulfide rather than for aerobic degradation (Roden and Wetzel 1996; Weiss et al. 2003). The flux of O_2 estimated by Holmer et al. (2002) can therefore potentially generate $2\text{ mmol SO}_4^{2-}\text{ m}^{-2}\text{ d}^{-1}$ or $16\text{ mmol Fe(III)}\text{ m}^{-2}\text{ d}^{-1}$, which can potentially be used as electron acceptors in anaerobic microbial respiration. The presence of $10\text{--}20\text{ }\mu\text{mol Fe(III)}\text{ cm}^{-3}$ below 8-cm depth in the vegetated mangrove mesocosms compared with the low Fe(III) in unvegetated systems (Fig. 4A,B) emphasize that *A. marina* roots have the capacity to oxidize Fe(II) and therefore may provide the basis for iron reduction (King and Garey 1999). Assuming a steady concentration of Fe(III) in the rhizosphere, the roots must transfer at least $9\text{ mmol O}_2\text{ m}^{-2}\text{ d}^{-1}$ for Fe(II) oxidation in the 8–16-cm depth horizon to maintain the observed averaged FeR of $450\text{ nmol cm}^{-3}\text{ d}^{-1}$ (Fig. 10A,B). This is comparable to the estimate of Holmer et al. (2002) when all uncertainties in the estimates, the role of irrigating infauna, and the different growth forms of the involved plants are considered (Sorrell and Armstrong 1994; Kostka et al. 2002; Nielsen et al. 2003).

A substantial fraction of the translocated O_2 and associated subsurface Fe(III) regeneration is probably mediated by activities of chironomid larvae and deep-burrowing polychaetes. The presence of burrows down to at least 12-cm depth in all treatments, combined with a high turnover of Fe(III) adjacent to these irrigated and more or

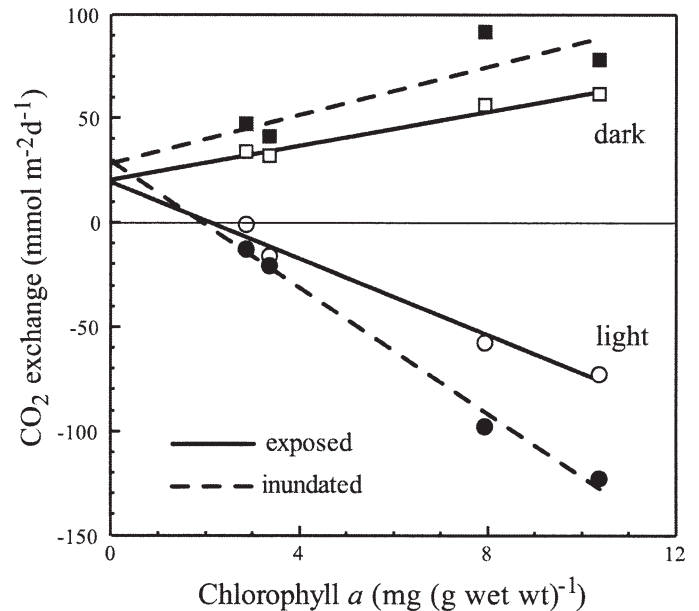


Fig. 11. Relationships between Chl *a* content in the upper 0–1 cm of the sediment from the four mesocosms and CO_2 exchange across the sediment–water and sediment–air interface in light and darkness. Lines are drawn according to least squares linear regression: L-inundated, $y = -15.1x + 28.9$, $r^2 = 0.99$; L-exposed, $y = -9.2x + 19.4$, $r^2 = 0.98$; D-inundated, $y = 5.7x + 28.7$, $r^2 = 0.75$; D-exposed, $y = 4.1x + 20.5$, $r^2 = 0.97$.

less temporary structures, may maintain FeR at a similar level in all treatments despite the oxidation capacity of roots in the vegetated sediment (Fig. 11A,B). MPN counts actually showed that FeRB in subsurface sediment are two to ten times more abundant in unvegetated than vegetated mesocosm (Kostka unpubl. data).

The effect of *A. marina* on sediment biogeochemistry, however, appears counteractive; release of O_2 from the roots maintains high redox conditions in the rhizosphere, while exudation of labile DOC from the roots stimulates heterotrophic CO_2 generation in bulk sediment and pushes the averaged redox boundary upward. If steady state is assumed, the pore-water profiles of DOC and CO_2 suggest a 50–60% higher generation of these solutes in vegetated than unvegetated sediment (Fig. 6). This estimate is probably too high because of augmented solute transport and, thus, lowered pore-water concentration in the unvegetated sediments by the higher abundance of irrigating infauna and by excessive DOC loss from live roots cut during coring (Hines et al. 1994; Gribsholt and Kristensen 2002b). Nevertheless, DOC exudation from roots below 4-cm depth enhances SRR up to 80% (–C) and 190% (+C) (Fig. 10C,D) while the bacterial abundance is increased by up to 90% (Fig. 3C,D). A similar enhancement of sediment metabolism by DOC exudation from roots has been reported for other vegetated sediments (Holmer et al. 2001; Devereux 2005). DOC released from roots apparently diffuses across the Fe(III)-containing rhizosphere and into the adjacent reduced zone, where SRR is enhanced. Thus, MPN counts revealed one to two orders of magnitude higher abundance of SRB in vegetated than unvegetated

subsurface sediment (Kostka unpubl. data). Significant correlations between SRR and live below-ground root biomass similarly led Alongi et al. (2001) to suggest that exudates from live mangrove roots fuel SRB in the surrounding sediment. In contrast to the short-term SRR assay, the long-term anoxic incubations did not capture the effect of DOC leaching from roots as indicated by similar subsurface carbon oxidation in sediment from mesocosms with and without plants (Fig. 9A,B). Plant-derived labile DOC will be rapidly exhausted (few hours) when anoxic sediment is incubated in isolation for weeks, leaving fermentative-derived DOC as the sole carbon source for sulfate reducers and iron reducers. This is substantiated by the low net change in DOC during the anoxic incubations (Fig. 9C,D).

The apparent DOC exudation from roots in subsurface sediment seems to have a cascading effect on the iron biogeochemistry near the sediment surface (1–5-cm depth). All Fe(III) in excess of the rapidly regenerated pool directly associated with roots, burrows, and surface activity by crabs is efficiently reduced and converted into the solid Fe(II) pool (Fig. 4). Most of the FeR in this zone is probably fueled by DOC diffusing toward the surface and only a minor fraction by free sulfide. Thus, tests showed that FeR in the mesocosm sediment is unaffected when SRR is inhibited with molybdate (data not shown). All sulfide generated by SRB is instantly precipitated as iron sulfides (Canfield 1989) by the ample (up to 2 mmol L⁻¹ below 2–3 cm) supplies of dissolved Fe²⁺ in the pore water. The absence of Fe²⁺ in the upper few cm of the sediment must be caused by rapid reoxidation and precipitation as amorphous FeOOH (Thamdrup 2000; Canfield et al. 2005).

Storage of sulfide in the form of AVS rarely exceeded 1% of the CRS pool in any sediment treatment. Thus, these mangrove sediments are sufficiently reduced to support sulfate reduction, but the relatively high redox conditions caused by roots and burrows enable rapid precipitation and high stability of pyrite in preference of AVS (Rickard and Morse 2005). A similar trend where sulfide generated by SRR is converted rapidly to pyrite has been observed frequently for mangrove sediments (Kristensen et al. 1991; Alongi et al. 2000). It is interesting to note that the 0.5 mol L⁻¹ HCl extracted Fe(II) pool is about 100 times larger than the AVS pool. Since CRS is not extracted by this procedure, most of the extracted Fe(II) must be non-sulfur-bound (Thamdrup 2000). The speciation of this non-S-Fe(II) is generally not known, but potential candidates include Fe(II) containing sheet silicates, mixed Fe(II)/Fe(III) hydroxides, adsorbed Fe(II), and phosphate or mixed carbonate Fe(II) precipitates (Aller et al. 1986; Boughriet et al. 1997; Haese et al. 1997).

Benthic metabolism and partitioning of electron acceptors—Carbon fixation in sediments is among other factors controlled by the biomass of phototrophs and grazing by herbivores, whereas carbon oxidation primarily is influenced by the availability of labile organic matter and electron acceptors (Canfield et al. 2005). The dramatic response of benthic primary production and sediment respiration in mesocosms to the presence of grazing fiddler

crabs (Fig. 8) is obviously caused by the efficient removal of benthic microalgae and thus labile organic matter. A similar pattern was observed in a removal experiment with soldier crabs (*Mictyris longicarpus*) by Webb and Eyre (2004). As a consequence, Chl *a* in the upper 1 cm of the sediment is highly correlated ($r^2 = 0.75\text{--}0.99$) with the exchange of CO₂ in both light and dark (Fig. 11) at rates that are comparable to those found for other mangrove sediments (e.g., Holmer et al. 1999; Alongi et al. 2001). Thus, the gross primary production provides specific productivity ($\mu\text{mol C } [\mu\text{g Chl}]^{-1} \text{ d}^{-1}$) of the microalgae ranging from 0.8–1.0 during air exposure to 1.3–1.6 when inundated. These values are similar to those found at intertidal flats in temperate regions (Colijn and de Jonge 1984; Wolfstein et al. 2000). It is remarkable that the CO₂ exchange in both light and dark becomes identical when extrapolated to zero Chl *a* content (Fig. 11), although with 45% higher values during inundation (28.8 mmol m⁻² d⁻¹) than air-exposed (19.9 mmol m⁻² d⁻¹). These rates must represent the basic sediment metabolism not influenced by microalgae. On a daily basis (12 h light : 12 h dark and 1.25 h inundation : 10.75 h exposure cycles), only the treatments without crabs are net autotrophic (1–8 mmol m⁻² d⁻¹), while the treatments grazed by crabs are net heterotrophic (8–18 mmol m⁻² d⁻¹), indicating an accumulation in the former and exhaustion in the latter of reactive organic matter.

It appears that CO₂ fluxes measured during air exposure are problematic and may not represent a true integrated measure of sediment metabolism. In dark, the CRQ values of 2–3 for inundation sediments are similar to those found in other mangrove environments (Kristensen et al. 1992; Nedwell et al. 1994; Holmer et al. 1999), while the low CRQ values of 0.6–0.7 for air-exposed sediment seem biased. The few studies that have measured sediment–air and sediment–water fluxes simultaneously in intertidal areas during night reveal a similar trend for hampered CO₂ release and enhanced O₂ uptake during air exposure (Alongi et al. 1998; Holmer et al. 1999; Gribsholt and Kristensen 2002a). Also the 25–50% lower specific productivity of the microalgae during air-exposure than inundation indicates a hampered exchange of CO₂ from air to sediment. Exchange of CO₂ across the sediment–air interface is probably weakened by a less steep pCO₂ gradient across the interface under stagnant conditions and at a sedimentary pH >7; particularly in the light (Vanderborght et al. 2002; Borges et al. 2004). This may create a transient storage or depletion of pore-water TCO₂ during air exposure, followed by an excessive initial exchange just after flooding (Smart and Peñuelas 2005). Any such rapid pulse of TCO₂ to or from the overlying water will not be captured when sediment–water flux incubations, as here, are initiated 3 h after sediment flooding. Accordingly, the estimated daily time-integrated release of CO₂ from mesocosm sediment in the dark only accounts for 40–85% of the daily 0–16-cm depth-integrated anaerobic (jar) CO₂ production (Table 2). O₂ uptake measured simultaneously in the dark, on the other hand, is almost identical to the depth-integrated CO₂ production and may therefore provide a more reliable time-integrated measure of benthic respiration, given that all

reduced end products of anaerobic processes are reoxidized by O₂ (i.e., an overall CRQ of one).

The enhanced subsurface heterotrophic activity in vegetated mesocosms caused by DOC exudation from roots is not clearly evident from the measured benthic respiration. In the mesocosms without crabs, this contribution is probably masked by the dynamic near-surface microbial communities degrading the microalgal mat. Thus, the upper 2 cm of the sediments without crabs account for 36–51% of the 0–16-cm depth-integrated anaerobic CO₂ production (Table 2). A similar situation has been observed for other mangrove sediments with high benthic primary production and low abundances of fiddler crabs (Holmer et al. 2001; Kristensen et al. 2000). This explanation is, however, not valid for the mesocosms with crabs, where the upper 2 cm only is responsible for only 7–11% of the depth-integrated anaerobic CO₂ production. No plausible explanation for the missing response of total metabolism to DOC exudation from roots is available at present, except for uncertainties in the measured fluxes because of methodological flaws.

Fe(III) appears to be the most important electron acceptor for total carbon oxidation in mesocosms without crabs, with FeR (assuming an Fe : C conversion factor of 4) accounting for 63–70% of the total, while SRR (assuming a S : C conversion factor of 0.5) is responsible for only 18–23% (Table 2). FeR is less important in mesocosms with crabs, accounting for 37–62% compared to 36–44% for SRR. The presence of plants and thus DOC exudation by roots seems in all cases to favor subsurface SRR. The partitioning observed here with dominance of FeR is comparable to results obtained for other iron-rich mangrove sediments (Kristensen et al. 2000) and salt-marshes (Kostka et al. 2002; Gribsholt et al. 2003), substantiating the potential importance of Fe(III) as electron acceptor in vegetated and bioturbated sediments. Mn(IV) reduction is probably unimportant in the present mesocosm sediments as the concentration of Mn(IV) generally is <10 μmol cm⁻³ (data not shown). Accordingly, Thamdrup (2000) found that Mn(IV) reduction, in general, does not contribute significantly to carbon oxidation when the concentration of Mn(IV) is <20 μmol cm⁻³. Redox cycling involving Mn(IV)/Mn(II) may, however, be intense and shuttle electrons to O₂ through the reoxidation of reduced iron and sulfur species (Canfield et al. 2005). As in other pristine mangrove environments (Kristensen et al. 1998; Alongi et al. 1999), denitrification is assumed modest in the mesocosms because pore-water NO₃⁻ was generally <5 μmol L⁻¹ near the surface (data not shown) and therefore insignificant for carbon oxidation.

FeR and SRR do not add up to the total anaerobic carbon oxidation in any case. Because the anaerobic jar incubations include surface sediment otherwise exposed to O₂, the contribution of O₂ as electron acceptor must at least be responsible for the missing 14% (-C+P), 12% (-C-P), 19% (+C+P), and 2% (+C-P) of carbon oxidation that (falsely) has been generated by sulfate reduction in the anoxic jars. A similar aerobic contribution around 10% has previously been reported for mangrove sediments (Kris-

tensen et al. 1994, 2000). An unknown fraction of carbon oxidation via FeR, as measured in the upper 0–2 cm of anaerobic jars, should probably also be diverted to O₂ respiration because Fe(III) under undisturbed conditions is replaced by O₂ as electron acceptor in the upper oxic 2–3 mm of the sediment (Kristensen et al. 1994). If, for example, 20% of the 0–2-cm FeR is converted to aerobic respiration, then only an additional 4% (-C+P), 10% (-C-P), 0.3% (+C+P), and 0.3% (+C-P) of the total depth integrated respiration should be devoted to O₂ as electron acceptor.

Ecological and biogeochemical implications—From an ecological viewpoint, the association between mangrove saplings, such as *A. marina*, and burrowing deposit-feeders, such as *U. vocans*, seems mutually beneficial because of their separated, but complementary biogeochemical effects. Crabs prefer to construct burrows and forage near solid surfaces, such as tree stems and pneumatophores, while the growth performance of trees (or at least saplings) is stimulated by the activities of crabs. It may be speculated that oxidized [Fe(III)-rich] conditions maintained by crabs in the near-surface part of the sediment alleviate potential damage from sulfide and augment growth of newly established roots. Rhizospheres of mature roots, on the other hand, are rich in Fe(III) that acts as an efficient sulfide buffer despite their simultaneous stimulation of bulk sulfate reduction. Trees may also have easier access to nutrients in the presence of crabs as competition with nutrient scavenging microalgae is reduced considerably by grazing. Conversely, crabs may benefit from access to food in the form of increased microbial biomass fuelled by DOC leaching from roots and deposited litter on the sediment surface. Particularly, crabs inhabiting burrows near stems and roots will have easier access to the rich microbial communities associated with these structures.

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