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Emission of CO_2 and CH_4 to the atmosphere by sediments and open waters in two Tanzanian mangrove forests

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ABSTRACT: Carbon gas balance was evaluated in an anthropogenically impacted (Mtoni) and a pristine (Ras Dege) mangrove forest in Tanzania. Exchange of carbon dioxide (CO_2) was measured for inundated and air-exposed sediments during day and night using *in situ* and laboratory incubations. *In situ* methane (CH_4) emissions were measured in the dark during air exposure only. Emission of CO_2 and CH_4 from open waters (e.g. creeks) was estimated from diurnal measurements of CO_2, partial pressure (pCO_2) and CH_4 concentrations. CO_2 emission from darkened sediments devoid of biogenic structures was comparable during inundation and air exposure (28 to 115 mmol m^{-2} d^{-1}) with no differences between mangrove forests. Benthic primary production was low with only occasional net uptake of CO_2 by the sediments. Emissions of CH_4 from air-exposed sediment were generally 3 orders of magnitude lower than for CO_2. Presence of pneumatophores and crab burrows increased low tide emissions several fold. Emissions from open waters were dependent on tidal level and wind speed. Lowest emission occurred during high tide (1 to 6 mmol CO_2 m^{-2} d^{-1}; 10 to 80 µmol CH_4 m^{-2} d^{-1}) and highest during low tide (30 to 80 mmol CO_2 m^{-2} d^{-1}; 100 to 350 µmol CH_4 m^{-2} d^{-1}) when supersaturated runoff from the forest floor and porewater seepage reached the creek water. Based on global average primary production and measured gas emissions, the carbon gas balance of the 2 mangrove forests was estimated. The densely vegetated Ras Dege forest appears to be an efficient sink of greenhouse carbon gases, while extensive clear-cutting at the Mtoni forest apparently has reduced its capacity to absorb CO_2, although it is seemingly still a net sink for atmospheric CO_2.

KEY WORDS: Mangrove · Pneumatophore · Burrow · Carbon dioxide · Methane · Emission

INTRODUCTION

Emissions of carbon dioxide (CO_2) and methane (CH_4) by mangrove sediments are potential sources of greenhouse gas to the atmosphere and as such may contribute to global climate change (Purvaja & Ramesh 2001, Borges et al. 2003, Biswas et al. 2004, Barnes et al. 2006). On the other hand, the high primary production by mangrove trees, accretion and permanent storage of organic carbon in sediments point to the fact that many mangrove environments are actually sinks of atmospheric CO_2 (Alongi 2007, Tateda et al. 2007,

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Bouillon et al. 2008). There are, however, large geographical differences in published attempts to estimate mangrove carbon gas balance caused by variations in factors such as geomorphology, freshwater input and degree of eutrophication (Sotomayor et al. 1994, Purvaja & Ramesh 2001, Alongi et al. 2005). Furthermore, it is important not only to consider the carbon balance in terms of CO_2 because CH_4 has about 20 times greater global warming potential than CO_2. CH_4 can be a major product of sediment carbon mineralization (Canfield et al. 2005) and as such a potential greenhouse gas emitted from mangrove ecosystems (Barnes et al. 2006, Upstill-Goddard et al. 2007).

Heterotrophic activity in mangrove sediments is usually determined as the uptake of O_2 or release of CO_2 under inundated or air-exposed conditions (e.g. Alongi et al. 2000, Kristensen et al. 2008). In many cases the rates obtained are not fully representative because biogenic irregularities, such as pneumatophores and burrows, have been deliberately avoided during measurements. Benthic fluxes obtained from heterogeneous mangrove environments are highly variable in time and space, and by including biogenic structures during incubations the results become even more variable and much less consistent (Kristensen 2007a). Nevertheless, the impact of biogenic structures on carbon gas exchange between mangrove sediments and the atmosphere appears to be so important that they must be included to obtain reliable carbon budgets (Kitaya et al. 2002, Purvaja et al. 2004). However, our knowledge on their quantitative importance is limited and warrants more studies.

Carbon gases produced in mangrove sediments are not entirely lost by upward diffusion through the sediment or via biogenic structures. A fraction is instead drained by density-driven tidal exchange of porewater through channels in the sediment and washed into tidal creeks during low tide (Borges et al. 2003, Bouillon et al. 2007a). From here the gases can be emitted directly to the atmosphere or transported by tidal action to adjacent waters. Recent studies have noticed such an excess CO_2 emission from waters in mangrove creeks and the surrounding coastal waters (Borges et al. 2003, Bouillon et al. 2003, 2007a,b,c, Koné & Borges 2007), but only few, if any, have measured the emission from mangrove sediments and creek waters simultaneously.

The objectives of the present study were to identify and quantify CO_2 and CH_4 emissions to the atmosphere in an anthropogenically impacted (Mtoni) and a pristine (Ras Dege) mangrove forest in Tanzania. The partitioning between sediment–air and water–air emissions was addressed with focus on the role of biogenic structures (pneumatophores and crab burrows) and tidal action. Finally, we provide rough net budgets of carbon gas emission for the entire Mtoni and Ras Dege mangrove systems based on the estimated emissions from vegetated and fauna-inhabited sediments, clear-cut areas and creek tidal waters.

MATERIALS AND METHODS

Study area. The study was conducted in 2 mangrove locations, Mtoni and Ras Dege, near the city of Dar es Salaam, Tanzania (Fig. 1) during several sampling campaigns in September 2005, April 2006 and February 2007. The climate in the Dar es Salaam area is humid tropical with average day and night temperatures of 28 to 31°C and 19 to 25°C, respectively, warmest from October to February. The annual precipitation is ca. 1100 mm with 2 rainy seasons from March to May and October to November.

The Mtoni mangrove forest covers an area of ca. 3 km^2 and is drained by a 6 km long tidal creek, which comprises a side branch of Mzinga Creek that forms Dar es Salaam harbor. The creek receives freshwater particularly during wet seasons from streams entering at the head. There is also considerable diffuse groundwater seepage from the surrounding hills. The mangrove forest is impacted indirectly by sewage dis-

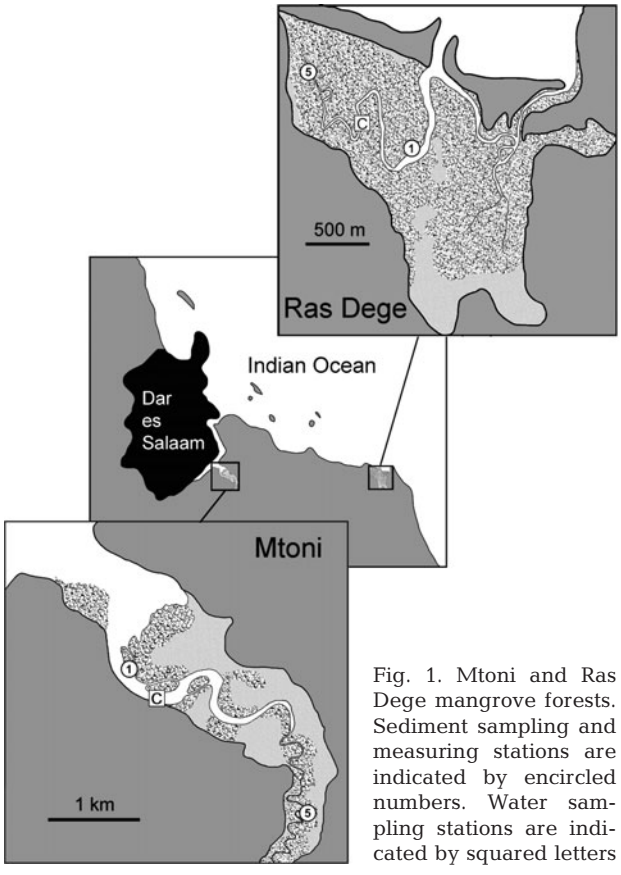

Fig. 1. Mtoni and Ras Dege mangrove forests. Sediment sampling and measuring stations are indicated by encircled numbers. Water sampling stations are indicated by squared letters

charges in the harbor area and suffers from extensive cutting of trees for charcoal production. The vegetation is mixed with dominance of *Sonneratia alba*, *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata.* The shallow area outside the mangrove forest is covered by extensive growth of drifting macroalgae during dry seasons.

The Ras Dege mangrove area covers ca. 2 km^2 and is dominated by *Avicennia marina*, *Rhizophora mucronata*, *Sonneratia alba* and *Ceriops tagal*. The system is drained by 2 tidal creeks which open directly into the Indian Ocean. There are no major freshwater inputs except for surface drainage during the wet seasons. Ras Dege does not experience any anthropogenic influence and there is only limited cutting. The mouth of the creeks and the zone adjacent to the mouth are covered by seagrass beds.

Sampling sites. For sediment sampling and flux measurements, 2 stations were selected along the main creek at Mtoni and 2 stations along the western creek at Ras Dege (Fig. 1). The low intertidal M1 (06° 52.760′ S, 39° 17.961′ E) at Mtoni was located near the outer boundary and the high intertidal M5 (06° 53.513′ S, 39° 18.959′ E) near the upper reaches of the main creek. M1 was dominated by *Sonneratia alba* growing in sandy-mud sediment, while the muddy-sand at M5 had mixed vegetation dominated by *Ceriops tagal*. The low intertidal R1 (06° 52.667′ S, 39° 27.596′ E) at Ras Dege was located near the outer boundary and the mid to high intertidal R5 (06° 52.347′ S, 39° 27.169′ E) in the upper reaches of the forest. The sediment at R1 consisted of fine sand and the vegetation was dominated by *Avicennia marina*, whereas the muddy R5 had a vegetation of primarily *Rhizophora mucronata* mixed with few *C. tagal.* All 4 stations were populated by ocypodid and grapsid crabs that dug numerous burrows in the sediment.

For open water tidal samplings, 1 station (MC) was selected in the main creek at Mtoni (ca. 0.5 km inside M1) and 1 station (RC) in the western creek at Ras Dege (midway between R1 and R5) (Fig. 1).

Pneumatophore and burrow abundance. The abundance of pneumatophores and crab burrows at each sediment station was enumerated from digital photos taken in September 2005. Four photos each covering 0.2 m^2 (0.4 × 0.5 m) were taken perpendicular to the sediment surface at each station. All visible pneumatophores and burrow openings (irrespective of size) were counted from the photos without differentiating among species of trees and crabs. This poses no problem for pneumatophores because only 1 tree species forming these structures was present at each station. Burrows could not be identified to crab family, and the results represent the combined abundance of ocypodid and grapsid burrows. It is likely that not all crab burrows were inhabited. Based on the results of Skov et al. (2002) from Kenya, we assume that ~81% of the burrows in Mtoni and Ras Dege were inhabited.

Sediment characteristics. Triplicate sediment cores (5 cm i.d.) from each station were analyzed for organic content (loss on ignition, LOI) and chlorophyll *a* (chl *a*) concentration in September 2005. Cores were sliced into the following depth intervals: 0–1, 1–2, 2–3, 3–4, 4–6, 6–8, 10–12 and 14–16 cm. Organic content was determined as weight loss of dried sediment after combustion in a muffle furnace for 6 h at 520°C. Chl *a* content was analyzed by the standard spectrophotometric method (Parsons et al. 1984) on the 0 to 1 cm slice only. Subsamples of sediment were extracted overnight in 5 ml of 90% ethanol in darkness at 5°C. The extract was centrifuged at 1200 × *g*, and absorbance of the supernatant was measured at 665 nm and 750 nm before and after acidification.

Sediment–water CO_2 exchange. Exchange of CO_2 across the sediment–water interface in light and darkness was determined by the core-incubation technique in September 2005 and April 2006. Triplicate sediment cores (8 cm i.d. and 20 cm long) without any visible biogenic structures (pneumatophores and burrow openings) were carefully collected at the sampling stations during low tide. The air-exposed cores were immediately transported to the laboratory and submerged into tanks containing creek water from the sampling sites, such that the water surface was at least 2 cm above the upper edge of the core liners. The water column inside the core tubes was ca. 10 cm. The cores were maintained in the dark overnight under continuous aeration before initiating flux measurements. Water temperature was kept constant at 27 to 29°C, and salinity varied from 2 to 45 depending on season and station.

The cores were sealed gas tight with a transparent lid during flux incubations, and a magnetic stirrer driven by an external rotating magnet maintained a continuous water circulation at a rate below the resuspension limit. Incubations of 3 to 5 h were first performed in darkness. Water samples for total carbon dioxide (TCO_2) were taken from the water phase inside each core at the start (before inserting lids) and end (after removing lids). Subsequently, a greenhouse lamp was placed 50 cm above the sediment (light intensity at the sediment surface: ~300 µmol m^{-2} s^{-1}), and the incubation as mentioned above was repeated. Light measurements were only conducted in April 2006.

Samples for TCO_2 analysis were preserved with $HgCl_2$ and analyzed as soon as possible on a flow injection/diffusion cell analyzer (Hall & Aller 1992).

Sediment–air CO_2 and CH_4 emissions. In September 2005, primary production and respiration by air-exposed sediments were determined on sediment cores in the laboratory by measuring CO_2 exchange by

a flow-through technique using a Li-Cor LI-820 infrared CO_2 analyzer. In April 2006 and February 2007, CO_2 exchange measurements were conducted *in situ* using a Li-Cor LI-6400 Portable Photosynthesis System equipped with a custom-made CO_2 flux chamber.

For the September 2005 laboratory measurements, triplicate sediment cores without any visible biogenic structures were taken during low tide with 8 cm i.d. core liners at the 4 stations. After return to the laboratory, the depth of sediment cores was adjusted to allow 2 to 3 cm of air space above the sediment surface (100 to 150 ml headspace). The core tubes were then wrapped in aluminum foil below the sediment surface to protect the deeper sediment from light. CO_2 exchange was measured using a flow-through system. The cores were sealed with a lid containing 2 ports and serially connected to a peristaltic pump and the LI-820 infrared gas analyzer via gas-tight nylon tubing. The pump pulled ambient air into the headspace of the cores at a rate of 44 ml min^{-1} (equivalent to a turnover time of 1 to 3 min) and out through the gas analyzer. CO_2 exchange was calculated as the steady state concentration difference between excurrent gas and atmospheric air after maintaining the flow system for 1 to 2 h. Measurements were first done in the dark with cores covered completely with aluminum foil and subsequently under continuous daylight (at least 300 µmol m^{-2} s^{-1}).

For *in situ* CO_2 exchange measurements, the sensorhead of the LI-6400 was mounted on a transparent Plexiglas chamber (8 cm i.d. and 18 cm long). The chamber was open at the bottom and sealed permanently at the top by a transparent plexiglas lid through which a 0.5 cm equilibration hole was drilled. The equilibration hole was sealed with a rubber stopper during measurements. The chamber was deployed by carefully pushing the open end ca. 5 cm into the sediment while the equilibration hole was open. The measurement started immediately after the equilibration hole was sealed. The LI-6400 was set for closed-chamber measurement, while the circulation pump in the sensorhead assured a homogeneous gas phase in the chamber. Chamber CO_2 was allowed to change linearly for 5 to 10 min according to the net outcome of production and consumption processes within the sediment. At regular intervals, chamber CO_2 was scrubbed down below the ambient air concentration by soda lime or raised above this level using a CO_2 cartridge before a new measurement was initiated. Typically 2 or 3 of such repeated measurements were done in light (incident light was typically >500 µmol m^{-2} s^{-1}) and darkness (chamber wrapped in aluminum foil) during each deployment. The exchange of CO_2 was calculated from the slope of CO_2 concentration change and related to the volume and area of the chamber. Several deployments were conducted on sediment without biogenic structures at each station in the 2 mangrove forests followed by deployments on sediment with crab burrows at M1 and R5 and sediment with pneumatophores of *Sonneratia alba* at M1 and *Avicennia marina* at R1.

Sediment–air methane emission was determined simultaneously with the *in situ* CO_2 exchange measurements by inserting 8 cm i.d. and 12 cm long core tubes into the sediment. After 10 min equilibration, the core tubes were sealed gas tight with rubber stoppers equipped with sampling ports, leaving a 6 to 8 cm headspace. Three 4 ml air samples for CH_4 were taken at 30 min intervals using 5 ml syringes. The CH_4 samples were injected into 5 ml evacuated Exetainer glass vials and stored cool until analysis on a gas chromatograph within 1 mo.

The height and diameter of pneumatophores entrapped inside the LI-6400 chamber and methane chambers were measured to the nearest mm.

CO_2 exchange of crabs. The respiratory CO_2 exchange of fiddler crabs *Uca* spp. was determined from laboratory incubations at *in situ* temperature using the LI-6400 equipment. A group of 34 live fiddler crabs of different sex and size (0.4 to 8 g wet weight, wet wt) were caught randomly at M1 and R1 and immediately brought to the laboratory. The Plexiglas chamber connected to the sensor-head of the LI-6400 was fitted gas tight with a removable bottom. Individuals were placed in the bottom part, which was mounted to the chamber while the equilibration hole was open. The measurement started immediately after the equilibration hole was sealed as described in 'Sediment–air CO_2 and CH_4 emissions' section above. Respiratory CO_2 release by individual crabs was repeated 3 times in the dark with the chamber covered with aluminum foil.

Creek water CO_2 and CH_4 emissions. Tidal variation of carbon gas concentrations (partial pressure, pCO_2, and CH_4) and associated parameters in creek water from the Mtoni and Ras Dege mangrove forests (Fig. 1) were determined from hourly water samplings over a 24 h cycle at MC (9 to 10 September 2005) and RC (16 to 17 September 2005; Bouillon et al. 2007a). Tidal range was similar at ~2.5 m during both sampling occasions.

Surface water for field measurements of pH, temperature and salinity were taken with a 1.7 l Niskin bottle ~0.5 m below the surface. Water pH was measured using a Ross type combination electrode (Orion) calibrated on the NBS (US National Bureau of Standards) scale, as described by Frankignoulle & Borges (2001). Samples for determination of total alkalinity (TA) were obtained by filtering 100 ml of water through precombusted Whatman GF/F filters, followed by filtration through 0.2 µm Acrodisc syringe filters, and stored in high density polyethylene (HDPE) bottles until analysis by automated electro-titration on 50 ml samples with 0.1 M HCl as titrant. TCO_2 and pCO_2 concentra-

tions were computed from pH and TA measurements with the thermodynamic constants described in Frankignoulle & Borges (2001). Water samples for the determination of CH_4 concentrations were taken directly from the Niskin bottle into 40 ml headspace vials, preserved with $HgCl_2$ and capped with a butyl rubber plug. CH_4 concentrations were determined by gas chromatography, after creating a headspace with N_2, as described in Abril & Iversen (2002). Dissolved CH_4 concentration was calculated using the solubility coefficient of Yamamoto et al. (1976). Wind speed was measured during each sampling with a handheld anemometer.

The exchange of CO_2 and CH_4 (F) across the water–air interface was calculated according to

$$F = k \alpha \Delta C \quad (1)$$

where k is the gas transfer velocity, α the solubility coefficient for CO_2 and CH_4 and ΔC represents the difference in pCO_2 and CH_4 between water and air. Values of k in coastal environments are to a large extent determined by wind stress and other site-specific factors such as water currents and fetch-limitation (Borges et al. 2004). We used the k-wind parameterization proposed by Raymond & Cole (2001) for estuarine environments.

Statistical analysis. Differences in organic content were tested using repeated measures ANOVA, while chl *a*, gas fluxes and faunal abundance were tested using 2-way ANOVA. When relevant, the ANOVAs were followed by a Bonferroni adjusted Fishers' Least Significant Difference test to resolve which stations differed. A significance level of $\alpha = 0.05$ was used in all ANOVA tests, unless otherwise stated. Data were analyzed using SAS (version 9.1).

System-integrated gas emissions were determined as the sum of involved components upscaled by the appropriate abundances and areas. Standard errors of the system-integrated emissions were derived by the approach of Bevington (1969) as described by Stutes et al. (2007). The df of each standard error was calculated using the procedure of Welch (1947), and the 95% confidence intervals for determination of significant differences at $\alpha = 0.05$ was calculated according to Sokal & Rohlf (1981).

RESULTS

Vegetation mapping and tidal coverage

The exact area cover of Mtoni and Ras Dege was determined from GIS mapping using high resolution satellite images (European Space Imaging). The Mtoni mangrove forest system covers an area of 3.05 km^2 (Fig. 1). Only 0.74 km^2 (25%) was contiguous patches of mature mangrove tree vegetation in 2006, particularly along the main creek. The creek itself covers 0.44 km^2 (15%), while the remaining 60% in 2006 stood as deforested intertidal sediment scattered with mangrove tree stubs after years of extensive cutting. Only occasional young trees and saplings were present in the denuded area. The Mtoni area is completely covered by water during spring high tides, and only the creek contains water during low tides. Although the Ras Dege mangrove area (1.90 km^2) is smaller than Mtoni, as much as 1.51 km^2 (79%) consisted of contiguous and pristine mature forest in 2006 (Fig. 1). Only ca. 12% of the entire area was affected by cutting, mostly in the inland part. The creeks are relatively small and cover only 0.17 km^2 (9%), which is equivalent to the low tide open water area. The entire forested area is inundated during spring high tides.

Sediment and water characteristics

Organic content did not vary significantly with depth in the upper 15 cm of the sediment at any station (Fig. 2). Values were significantly lower at M1 (2.1 to 3.3%) than at R5 (9.3 to 17.0%) ($p < 0.001$), while the levels were intermediate ($p < 0.001$) and similar to each other at M5 (4.1 to 6.6%) and R1 (5.2 to 6.7%). Chl *a* content in the upper cm was similar at M1 (2.9 ± 1.3 µg g^{-1}), M5 (2.5 ± 0.4 µg g^{-1}) and R1 (3.3 ± 0.9 µg g^{-1}), while R5 was significantly lower (0.4 ± 0.2 µg g^{-1}).

Water temperature ranged from 24°C in the early morning to 31°C in the afternoon at both locations during the September 2005 sampling. At the same time, salinity near M1 in Mtoni was 35 and 28 during high and low tide, respectively. A freshwater source at the upper reaches reduced salinity near M5 to 25 and 13 during high and low tide, respectively. Near the mouth at Ras Dege (R1), the salinity was 34 and 37 during high and low tide, respectively, while evaporation increased salinity at R5 to 36 and 39, respectively.

Pneumatophore and burrow abundance

M1 and R1 had high and continuous abundance of pneumatophores, while these structures were only of scattered occurrence at M5 and R5. The abundance of *Sonneratia alba* pneumatophores at M1 and *Avicennia marina* pneumatophores at R1 were similar at ca. 140 m^{-2} (Table 1). Ocypodid and grapsid crab burrows were ca. 9 times more abundant at M1 than at M5 ($p < 0.001$). The abundance of crab burrows at the 2 Ras Dege stations was similar at a level of one-third to half of that observed at M1 ($p < 0.001$).

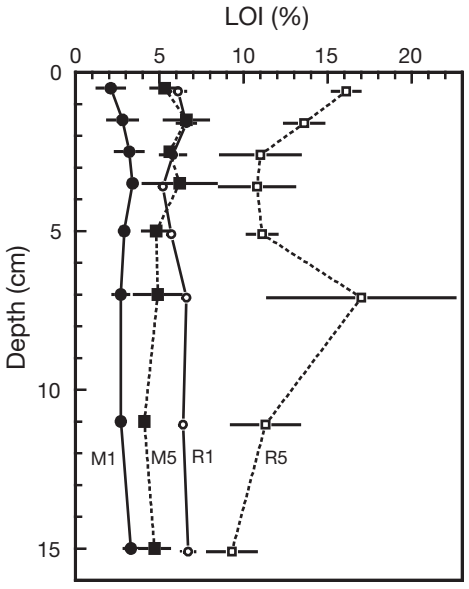

Fig. 2. Vertical profiles of organic matter (loss on ignition, LOI) at Stns M1 and M5 in Mtoni and Stns R1 and R5 in Ras Dege. Values are given as mean ± SE (n = 3)

CO_2 exchange across the sediment–water interface

The dark CO_2 efflux (respiration: RSP) by inundated sediment without biogenic structures in Mtoni and Ras Dege ranged from 28 to 115 mmol m^{-2} d^{-1} with no overall difference between the 2 mangrove forests (Fig. 3). RSP at M1 was 1.9 to 2.0 times higher ($p < 0.01$) than at M5 and 2.0 to 2.2 times higher ($p < 0.01$) for both stations in the wet than the dry season. R1 had 1.5 times higher RSP in the wet than the dry season ($p < 0.01$), while R5 behaved opposite with 2.2 times higher rates in the dry than the wet season ($p < 0.01$). As a consequence, the 2 Ras Dege stations showed similar RSP in the dry season, while R1 exceeded R5 by a factor of 2.9 in the wet season ($p < 0.01$).

Benthic net primary production (NPP) during inundation was low in the wet season and net uptake of CO_2 was never detected (Fig. 3). Unfortunately, no light measurements were conducted in the dry season. Gross primary production (GPP = RSP – NPP) was similar at the Mtoni stations in the wet season showing rates of 56 to 63 mmol m^{-2} d^{-1}. These were almost twice ($p < 0.01$) the rates found in Ras Dege (29 to 36 mmol m^{-2} d^{-1}).

Table 1. Estimated abundance of pneumatophores and burrow openings at Stns M1 and M5 in Mtoni and R1 and R5 in Ras Dege (m^{-2}). Pneumatophores originate from *Sonneratia alba* at M1 and from *Avicennia marina* at R1. Burrow openings belong to both Ocypodid and Grapsid crabs. Results are given as mean ± SE (n = 4)

	M1	M5	R1	R5
Pneumatophores	143 ± 14	~0	138 ± 15	~0
Burrow openings	626 ± 65	68 ± 17	313 ± 20	237 ± 53

CO_2 and CH_4 exchange across the sediment–air interface

CO_2 emission from exposed and darkened sediment to the atmosphere (RSP) showed no specific pattern among stations and mangrove forests, except for slightly higher release at M1 than M5 ($p < 0.05$ only for the dry season; Fig. 3). RSP was consistently higher ($p < 0.01$) in the dry (47 to 88 mmol m^{-2} d^{-1}) than the wet season (38 to 46 mmol m^{-2} d^{-1}). In general, RSP of air-exposed sediment was similar to or lower ($p < 0.01$ for R1 and R5 in the dry season and M1 and R1 in the wet season) than that of inundated sediment.

NPP varied among stations and net CO_2 uptake was only registered at R1 in the dry season and M5 in the wet

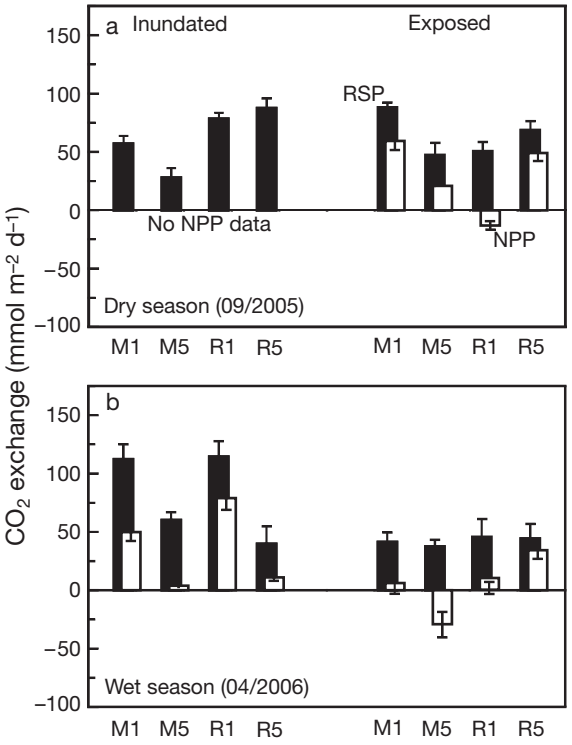

Fig. 3. Exchange of CO_2 across the surface of sediment without biogenic structures at Stns M1 and M5 in Mtoni and R1 and R5 in Ras Dege. Measurements were made under inundated (left) and air-exposed (right) conditions during the (a) dry and (b) wet seasons. Filled bars: dark measurements (= benthic respiration, RSP); open bars: light measurements (= benthic net primary production, NPP). No measurements were made in the light under inundated conditions during the dry season. Values are given as mean ± SE (n = 3, except for exposed wet season where n = 6)

season (Fig. 3). Despite the inter-station variability in RSP and NPP, GPP at the 2 exposed Mtoni stations and R1 in Ras Dege was similar in the dry (26 to 64 mmol m^{-2} d^{-1}) and wet (35 to 67 mmol m^{-2} d^{-1}) seasons, at the same level as found during inundation in the wet season. The low GPP of exposed sediment at R5 in Ras Dege (10 to 20 mmol m^{-2} d^{-1}) was also consistent with the low rate observed at this station during inundation.

The emission of CH_4 at low tide from sediments without biogenic structures varied both within and among stations (Fig. 4). In general, the emission of CH_4 was 3 orders of magnitude lower than CO_2 emissions. The highest ($p < 0.01$) release of CH_4 occurred at M5 (87.6 ± 21.1 µmol m^{-2} d^{-1}). Emissions at the other 3 stations did not differ significantly and ranged from 0 to 25 µmol m^{-2} d^{-1}.

CO_2 and CH_4 emissions by pneumatophores, burrows and crabs

Emission of CO_2 was enhanced considerably by the presence of pneumatophores and burrows. The measured rates of CO_2 release from chamber deployments with *Sonneratia alba* pneumatophores at M1 and *Avicennia marina* pneumatophores at R1 were 4.3 to 5.1 and 3 to 3.9 times higher, respectively, than across the sediment surface ($p < 0.001$; Fig. 4). The enhancement of CO_2 emission in deployments with burrows was of the same magnitude, i.e. a factor of 4.7 at M1 and 1.9 to 2.7 at R5 ($p < 0.001$). It is important to note here that the number of pneumatophores and burrows trapped inside the measuring chamber (1 to 2 or equivalent to 200 to 400 m^{-2}) was not identical to the natural abundance of these biogenic structures (see Table 1). Furthermore, the size of pneumatophores was probably in the low range of the natural size distribution because they were selected to fit inside the chamber (max. length of 13 cm).

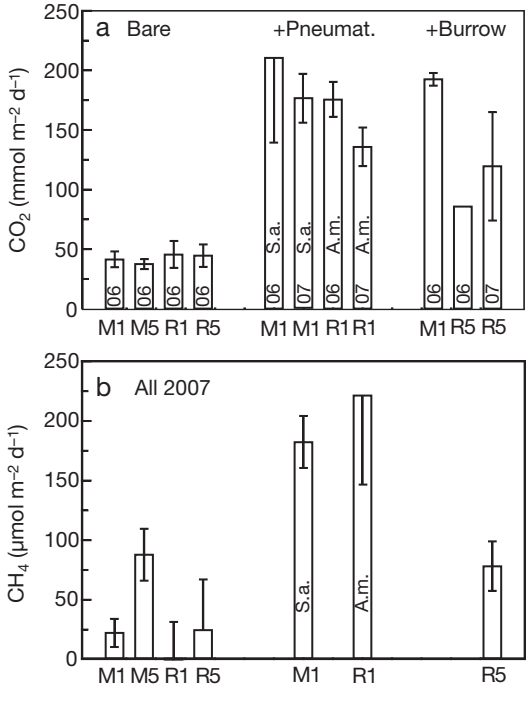

Fig. 4. (a) Emission of CO_2 and (b) CH_4 from air-exposed sediment in the dark at Stns M1 and M5 in Mtoni and R1 and R5 in Ras Dege. Rates are shown for sediment without biogenic structures (Bare), for sediment with 200 *Sonneratia alba* and 400 *Avicennia marina* pneumatphores m^{-2} (+Pneumat.) and for sediment with 200 crab burrows m^{-2} (+Burrow). CO_2 fluxes obtained in April 2006 and February 2007 are indicated with 06 and 07, respectively. All CH_4 fluxes were obtained in February 2007. Values are given as mean ± SE (n = 6)

The estimated emission of CO_2 from individual *Sonneratia alba* pneumatophores after subtraction of the sediment contribution was 58% higher than that of *Avicennia marina* pneumatophores (Table 2), which corresponds well to the overall difference in pneumatophore size of the 2 tree species. Thus, based on the height and diameter it was calculated that the examined *S. alba* and *A. marina* pneumatophores had an average individual surface area of 38.2 ± 6.0 and 16.7 ± 7.9 cm^2, respectively.

The average CO_2 emission from individual crab burrows was lower than the emission from pneumatophores ($p < 0.01$; Table 2). Most burrows contained one crab, but this could not be documented since crabs rapidly retreated to their burrows when disturbed. No attempts were made to recover the inhabitants, but in many cases, they were visible in the burrow opening. We therefore must rely on the estimate of Skov et al, (2002) that 81% of all burrows are inhabited. Part of the CO_2 emission from burrows must therefore originate from their inhabitants. The measured weight-specific respiration of *Uca* sp. decreased with increasing body weight according to a power function with a slope of –0.461 (Fig. 5). Thus, an average sized *Uca* individual of 3.2 g wet wt from M1 respired 161 ± 38 µmol CO_2 d^{-1}.

CH_4 emission was also strongly enhanced by the presence of pneumatophores and burrows. *Sonneratia alba* pneumatophores at M1 increased the measured total CH_4 emission 8.2 times ($p < 0.001$), while for *Avicennia marina* pneumatophores at R1 the effect was greater showing an increase from 0 for the sediment alone to 221 µmol m^{-2} d^{-1} (Fig. 4). CH_4 emission from burrows was only measured at R5 where these structures increased the release 3.2 times. The concern about unrealistic abundance of pneumatophores and burrows are also valid for CH_4 measurements because the chambers used were of identical diameter to the LI-6400 chamber. In addition, only relatively small and similar-sized pneumatophores of both species could be

Table 2. Calculated CO_2 and CH_4 emissions from individual pneumatophores of *Sonneratia alba* and *Avicennia marina* and opening of crab burrows during air exposure at low tide. Values were obtained as the difference between directly measured fluxes from sediment with and without pneumatophores/burrows. Values are given as mean µmol $pneu^{-1}$ d^{-1} or µmol $burrow^{-1}$ d^{-1} ± SE (n = 6). na: not applicable; nd: no data

Stn (yr)	*S. alba*		*A. marina*		Burrow	
	CO_2	CH_4	CO_2	CH_4	CO_2	CH_{43}
M1 (2006)	650 ± 154	na	na	nd	445 ± 8	na
M1 (2007)	678 ± 54	0.800 ± 0.066	na	nd	na	nd
R1 (2006)	na	nd	390 ± 22	na	na	nd
R1 (2007)	na	nd	451 ± 36	1.107 ± 0.105	na	nd
R5 (2006)	na	nd	nd	nd	207 ± na	na
R5 (2007)	na	nd	nd	nd	281 ± 74	0.268 ± 0.049

trapped inside the 4 to 6 cm air space of the chambers. The CH_4 emission by these young pneumatophores was probably lower than that of 2 to 3 times taller mature structures. The impact of pneumatophores on CH_4 emission as shown here must therefore be considered a minimum estimate.

The calculated emission of CH_4 from individual *Avicennia marina* pneumatophores after subtraction of the sediment contribution was 38% higher than that from *Sonneratia alba* pneumatophores (Table 2). The release of CH_4 from an individual crab burrow from R5 was lower and only accounted for 24% of that released from a single *A. marina* pneumatophore ($p < 0.01$).

CO_2 and CH_4 emissions from open water in creeks

The tidal behavior of pCO_2 and CH_4 concentrations in creek water varied between the 2 mangrove environments in September 2005 (Figs. 6 & 7). Tides caused pCO_2 to increase from ca. 500 ppm at high tide to 1700 ppm at low tide in MC, while CH_4 concentrations remained constantly high (ca. 150 nM) with no clear tidal pattern. The carbon gas concentrations in RC were also lowest during high tide when creeks received oceanic water in near-equilibrium with the atmosphere and were ca. 10 times higher (pCO_2 ~5000 ppm, CH_4 ~100 nM) when drainage water enriched with CO_2 and CH_4 from the mangrove forest dominated during low tide.

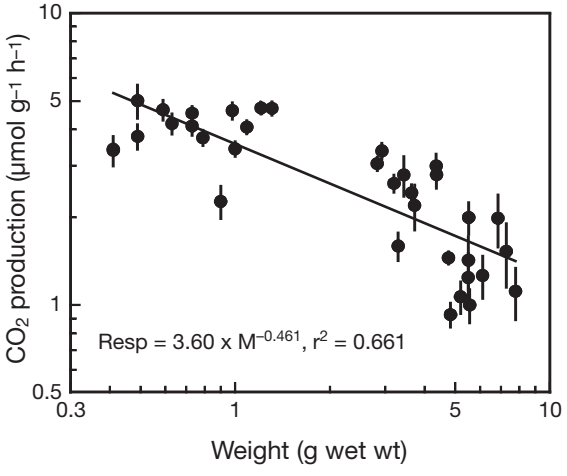

Fig. 5. Respiratory CO_2 production by fiddler crabs (*Uca* spp.) as a function of live body weight (M). The data include both males and females. Values are given as mean ± SE (n = 100 sequential 10 s measuring intervals). The regression equation is given

Emissions of CO_2 and CH_4 from open waters were obviously dependent on the tidal level, but wind speed exerted a strong secondary control. CO_2 emission from the Mtoni creek water to the atmosphere showed a minimum at high tide of 3 to 9 mmol m^{-2} d^{-1}, while only 1 to 2 mmol m^{-2} d^{-1} was released during high tide in Ras Dege, which corresponds well to the difference in pCO_2 at this time. At low tide, the creek water CO_2 emissions were very dependent on the wind and varied between 20 and 40 mmol m^{-2} d^{-1} in Mtoni and 50 and 80 mmol m^{-2} d^{-1} in Ras Dege. CH_4 emissions showed a tidal pattern similar to that of CO_2. The apparent tidal pattern of CH_4 emissions in the Mtoni creek was caused by changes in wind, resulting in 2 to 8 times higher rates than in the more tidally controlled Ras Dege creek. Lowest high tide CH_4 rates were estimated to be 70 to 90 µmol m^{-2} d^{-1} and 10 to 15 µmol m^{-2} d^{-1} in Mtoni and Ras Dege, respectively, while the highest rates at low tide were 150 to 350 µmol m^{-2} d^{-1} and 50 to 70 µmol m^{-2} d^{-1}, respectively.

DISCUSSION

Sediment–water/air exchange

Exchange of CO_2 across mangrove sediment surfaces devoid of biogenic structures (pneumatophores and burrows) represents the net outcome of near surface microheterotrophic carbon mineralization (e.g. aerobic respiration, iron reduction and sulfate reduction) and carbon fixation by microphytobenthic primary production (Kristensen & Alongi 2006). However, the heterotrophic activity within these sediments is not only dependent on the microphytobenthic production,

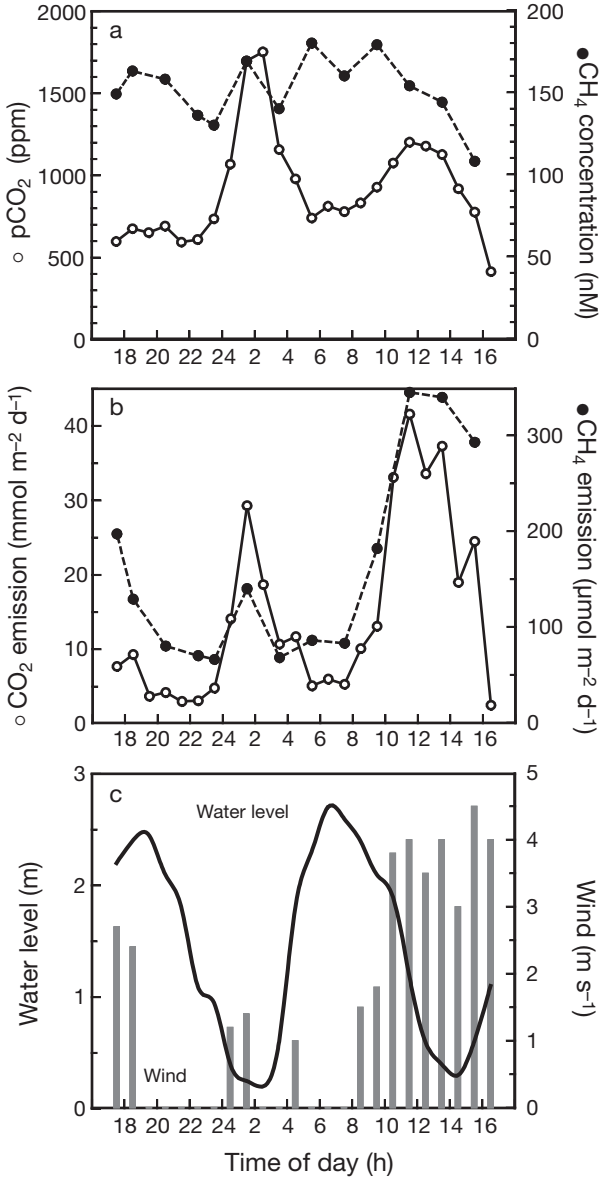

Fig. 6. (a) pCO_2 and CH_4 concentrations in creek water, (b) emission of CO_2 and CH_4 from creek water and (c) water level and wind speed at Stn MC in Mtoni. Measurements were conducted at hourly intervals for 24 h and covers 2 tidal periods, 1 in the dark and 1 in the light

but also on the delivery and burial of reactive organic carbon from other sources (litterfall, root production and tidal import) (Kristensen et al. 2008).

The consistently higher near-surface microheterotrophic activity observed at M1 than M5, as indicated by higher CO_2 release in the dark during both inundation and air exposure (Fig. 3), is probably caused by import of reactive detritus at the outer reaches in Mtoni. Floating macroalgae from the shallow eutrophic area outside the mangrove forest are transported into the forest via tides, trapped by pneumatophores and low branches and buried into the sediment by crabs (Kristensen 2007b). As these processes primarily occur in the outer part of the forest (M1), more reactive detritus is available here for microheterotrophs. The rapid degradation of reactive detritus deposited at M1 causes the sediment organic content to be low compared with M5 where mangrove detritus of low reactivity accumulates (Fig. 2). A similar inconsistency between heterotrophic activity and bulk sediment organic content has been observed previously in other mangrove environ-

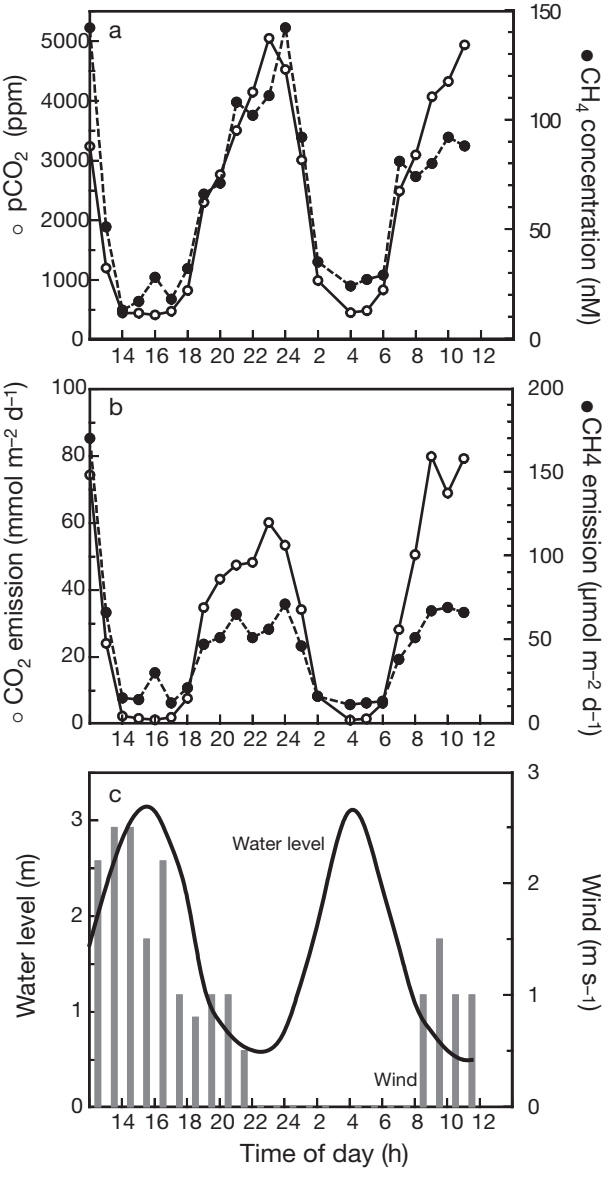

Fig. 7. (a) pCO_2 and CH_4 concentrations in creek water, (b) emission of CO_2 and CH_4 from creek water and (c) water level and wind speed at Stn RC in Ras Dege. Measurements were conducted at hourly intervals for 24 h and covers 2 tidal periods, 1 in the dark and 1 in the light

ments (Holmer et al. 1999, Alongi et al. 2000), and it is also clearly evident at Ras Dege. Here the 3 times higher organic content at R5 than R1 is not reflected in the heterotrophic activity. Dark CO_2 release is similar at the 2 stations, except during inundation in the wet season where R1 actually exhibited 3 times higher rates. R5 deep in the Ras Dege mangrove forest seems to be a deposition area for refractory mangrove detritus due to slow currents, while the strong currents at the outer R1 resuspend mangrove detritus. Since the oligotrophic waters entering Ras Dege with tides do not carry large amounts of algal detritus, microheterotrophic activity in R1 sediments must be supported primarily by autochthonously derived microphytobenthic production. In fact, benthic primary production is several times higher at R1 than at R5.

Several studies have shown that CO_2 exchange across the sediment–water/air interface measured selectively at sites devoid of biogenic structures may seriously underestimate the true rates (Holmer et al. 1999, Kitaya et al. 2002). The results from Mtoni and Ras Dege indeed show that pneumatophores and burrows increase sediment–air release of CO_2 in the dark several fold (Table 3), particularly at M1 and R1 where these structures are abundant (Table 1). The impact is most pronounced during air exposure because gas exchange is prohibited when lenticels of pneumatophores are closed and burrows are plugged by their inhabitants during inundation (De la Iglesia et al. 1994, Skelton & Allaway 1996, Allaway et al. 2001). Transport of gases is then largely limited to diffusion across the horizontal sediment–water interface. Open lenticels during air exposure allow for rapid diffusion of CO_2 from the air-filled aerenchyma tissue of roots to the atmosphere (Purnobasuki & Suzuki 2004, 2005). The CO_2 is generated by root respiration (Kitaya et al. 2002, Lovelock et al. 2006) or derived from microheterotrophic production in the surrounding deep sediments via transport across the root epidermis (Scholander et al. 1955). Also crab burrows, which are opened by their inhabitants at low tide, will augment the gas exchange by providing a much larger surface area available for diffusive transport of CO_2 to the atmosphere (Table 3). In this case the emitted CO_2 will originate from respiration of the crab inhabitant (if present) and from microheterotrophic production in the deep sediments (Pinder & Smits 1993, Datta 2005).

The estimated emission of CO_2 from examined pneumatophores of *Sonneratia alba* (0.65 to 0.68 mmol d^{-1}) and *Avicennia marina* (0.39 to 0.45 mmol d^{-1}) in Mtoni and Ras Dege (Table 2) is similar to the rates found by Kitaya et al. (2002) in Japan for 30 to 50% taller pneumatophores of the same 2 species (0.66 and 0.26 mmol d^{-1}, respectively). The CO_2 budget in the dark at M1 and R1 (Table 3) indicates that pneumatophores of the size examined are responsible for 29% of the total emission from air-exposed sediment. This is probably an underestimate of the true emission from larger pneumatophores that did not fit into the measuring chamber. It is uncertain, however, how the emission is partitioned into root respiration and microheterotrophic sediment respiration. Emission of CO_2 from mangrove sediments is usually considered an integrated measure of heterotrophic activity by the decomposer food chain (Canfield et al. 2005) and as such represents degradation of the forest net production and imported organic sources. The fraction of pneumatophore CO_2 emission that is derived from root respiration, on the other hand, should be considered a part of tree GPP and in reality can not be included in the decomposer contribution. We cannot differentiate between the 2 sources here because no knowledge is available on the origin of CO_2 emitted from pneumatophores.

The contribution of crab burrows to the total CO_2 emission from sediments is significant, but varies considerably depending on burrow abundance. At M1, R1 and R2, where crabs were abundant, 49 to 62% of the total emission occurs through burrow openings, while the contribution is only 36% at the less-populated M5 (Table 3). Most of the total burrow emission is due to CO_2 diffusing from the surrounding sediment (58%), while the remainder is due to crab respiration when the ~0.81 crabs present per burrow are fiddler crabs or species that respire similarly. In contrast to root respiration, the contribution of crabs must be considered an integrated part of the decomposer food chain as they consume and metabolize microphytobenthic and bacterial net production (Kristensen & Alongi 2006).

Table 3. CO_2 emission budget in the dark during low tide for Stns M1, M5, R1 and R5. Rates are shown for sediment supplemented with the contribution of pneumatophores, burrows and crabs. Rates for sediment are from Fig. 4. Individual rates of the biogenic structures are given in Table 2 and in the text, while the abundance of pneumatophores as well as the abundance of burrows at each station is given in Table 1. It is assumed that 0.81 crabs were present inside each burrow. Rates are given as mean ± SE (mmol m^{-2} d^{-1}). Numbers in parenthesis are the % contribution of each compartment. na: not applicable

	M1	M5	R1	R5
Sediment	41 ± 6 (12)	38 ± 4 (64)	46 ± 11 (23)	45 ± 9 (38)
Pneumatophores	95 ± 25 (29)	na	58 ± 9 (29)	na
Burrows	113 ± 52 (34)	12 ± 6 (20)	58 ± 26 (23)	43 ± 22 (30)
Crabs	81 ± 21 (25)	9 ± 3 (16)	41 ± 10 (25)	31 ± 10 (32)
Total	330 ± 63	59 ± 8	203 ± 31	119 ± 26

Methanogenesis is usually considered a minor pathway for diagenetic organic carbon degradation in marine sediments, and it occurs only where all electron acceptors (O_2, NO_3^-, Fe(III) and SO_4^{2-}) are depleted. Efflux from sediments rarely occurs because CH_4 is oxidized by methanotrophs before reaching the sediment surface (Canfield et al. 2005). The low diffusive emission of CH_4 across the sediment–air interface in Mtoni and Ras Dege agrees well with previous reports of undetectable or low CH_4 emissions from a variety of pristine mangrove sediments (Alongi et al. 2000, Kreuzwieser et al. 2003, Barnes et al. 2006, Allen et al. 2007). In fact, the emission of 31 to 48 µmol CH_4 m^{-2} d^{-1} found by Lyimo et al. (2002) from sediments adjacent to *Sonneratia alba* vegetation in Mtoni compares very well with the rate of 22 µmol CH_4 m^{-2} d^{-1} obtained here from M1 (Fig. 4). Low emissions do not reflect the rates of methanogenesis within mangrove sediments, which can be orders of magnitude higher (Sotomayor et al. 1994, Giani et al. 1996, Lyimo et al. 2002). High CH_4 emissions from mangrove sediments are primarily found in eutrophic areas where large inputs of labile organic matter increase sediment metabolism and cause depletion of sulfate near the surface (Sotomayor et al. 1994, Purvaja & Ramesh 2001). High rates of methanogenesis and CH_4 emissions can also occur in mangrove environments influenced by freshwater (e.g. rivers and precipitation) because SO_4^{2-} is diluted and competitive sulfate reduction is diminished (Lu et al. 1999). These mechanisms are probably driving the generally higher diffusive CH_4 emission in Mtoni than Ras Dege and, in particular, the 4 times higher rates at the low saline M5 compared with the much more saline M1, R1 and R5 (Fig. 4).

Pneumatophores and burrows serve as conduits for not only CO_2 but also for CH_4 emission. They act as channels through which CH_4 from deep sediment layers can escape oxidation and rapidly diffuse to the atmosphere. The emission of CH_4 from the sediment is extensive when pneumatophores and burrows are abundant, such as M1 and R1 where these structures are responsible for 93 to 100% of the total emission (Table 4). In areas devoid of pneumatophores and less densely populated by crabs, like M5, the total system emission diminishes significantly to only 30 to 40% of that in populated areas (M1 and R1). A similar large impact of pneumatophores on CH_4 emissions have been reported previously (Sotomayor et al. 1994, Kreuzwieser et al. 2003, Bauza 2007), while there are to our knowledge no such reports on the role of burrow structures. The individual rates found here for relatively small pneumatophores (Table 2) agree well with values ca. 1 µmol CH_4 $pneu^{-1}$ d^{-1} found by Sotomayor et al. (1994), but are low compared with rates from eutrophic mangrove environments (Purvaja et al. 2004). It must be emphasized that CH_4 emitted from pneumatophores and burrows originate solely from methanogenesis in the surrounding sediment because plant roots and crabs residing inside burrows do not generate CH_4.

Table 4. CH_4 emission budget in the dark during low tide for Stns M1, M5, R1 and R5. Rates are shown for sediment supplemented with the contribution of pneumatophores and burrows. Individual rates of the biogenic structures are given in Table 2, while the abundance of pneumatophores as well as the abundance of burrows at each station is given in Table 1. Rates are given as mean ± SE (µmol m^{-2} d^{-1}). Numbers in parenthesis are the % contribution of each compartment. na: not applicable

	M1	M5	R1	R5
Sediment	22 ± 11 (7)	88 ± 21 (83)	0 ± 31 (0)	25 ± 42 (28)
Pneumatophores	114 ± 15 (38)	na	153 ± 22 (64)	na
Burrows	168 ± 35 (55)	18 ± 6 (17)	85 ± 17 (36)	64 ± 19 (72)
Total	304 ± 40	106 ± 22	238 ± 42	89 ± 46

Water–air exchange

The emission of CO_2 and CH_4 from open water in the creeks of Mtoni and Ras Dege mangrove forests is very dynamic and depends on both tidal level and wind (Figs. 6 & 7). The tidal influence is evident as a strong inverse relationship between creek water concentrations of CO_2 and CH_4 and water level (Borges et al. 2003, Bouillon et al. 2007a). Tides therefore seem to be the primary controlling factor, but variable winds superimpose an unpredictable and at times important secondary control (Mukhopadhyay et al. 2002). The range of emissions observed in the present mangrove environment agrees well with those for CO_2, reported by Borges et al. (2003) and Ramesh et al. (2007), and for CH_4, reported by Barnes et al. (2006) and Upstill-Goddard et al. (2007). In accordance with observations of Barnes et al. (2006), creek water emissions of both CO_2 and CH_4 in Mtoni and Ras Dege are within the same order of magnitude as emissions from air-exposed sediments.

Emitted CO_2 and CH_4 from creek water have several possible sources. While subtidal creek sediments contribute continuously, the rapidly increasing emission of both gases after high tide slack coincides with the arrival in the creek of runoff from the forest. During inundation of the forest floor at high tide, the water column receives CO_2 and CH_4 via diffusive flux from the sediment in sufficient amounts to supersaturate creek water during receding tides (Bouillon et al. 2007a). The

subsequent emission peak occurring at low tide slack indicates that porewater seepage from creek banks provides an additional source of dissolved CO_2 and CH_4 to the shallow creeks (Kristensen & Suraswadi 2002, Bouillon et al. 2007a). Thus, crab burrows and large pores remaining after decay of dead roots increase the hydraulic conductivity along creek banks at ebb tides and function as conduits for rapid porewater seepage (Ridd 1996, McKee 2001, Susilo et al. 2005). CO_2 is also produced within the creeks by heterotrophic microbial oxidation of dissolved organic carbon (DOC) that is delivered by surface runoff, porewater seepage and excretion by creek water phytoplankton (Kristensen & Suraswadi 2002, Bouillon et al. 2003, 2007a). No such internal creek water source is active for CH_4 because anaerobic methanogenesis cannot occur in oxic creek water (Reeburgh 2007).

Carbon gas balance in Mtoni and Ras Dege mangrove areas

The carbon gas balance of any ecosystem is the outcome of net CO_2 fixation by primary producers and release of CO_2 and CH_4 by heterotrophic processes. The major primary producers in mangrove environments are the trees, while algae usually accounts for less than 20% of total primary production (Kristensen et al. 2008). Unfortunately, there are no data available on primary production in Mtoni and Ras Dege. Reported rates of net tree primary production in a variety of mangrove forests vary considerably with values ranging from 50 to 1300 mmol C m^{-2} d^{-1} (Clough et al. 1997, Clough 1998, Alongi 2002, Okimoto et al. 2007), but most estimates are close to the global average of ~311 ± 103 mmol C m^{-2} d^{-1} (mean ± SE) (Bouillon et al. 2008). A rough estimate of total emissions of the carbon gases, CO_2 and CH_4, by the Mtoni and Ras Dege mangrove systems can be provided by upscaling the presently measured contribution by the various mangrove compartments to the geomorphology and vegetation distribution (Table 5). Since the exact water cover is defined best at low and high tides, we have chosen only to provide estimates during these extremes. Still a number of assumptions are required for the calculations to be valid: (1) the open water cover is confined to creeks during low tide and covers the entire mangrove area at high tide; (2) the emission from open water throughout the systems is similar to the rate measured at low and high tide in the creeks; (3) the area vegetated by trees has a median of 70 pneumatophores m^{-2} and 300 inhabited crab burrows m^{-2}; (4) the measured emissions from a limited number of pneumatophores and burrows are representative for all these structures in both areas; (5) the denuded areas are devoid of pneumatophores and crabs; and (6) microphytobenthic primary production is included in net benthic respiration by averaging sediment–air exchange of CO_2 during day and night. We are aware that some of these assumptions may not be entirely fulfilled, but at present it is the best approach available.

Table 5. Calculation overview of daily (24 h) total system carbon gas emission budgets. The table is separated into measured input parameters and calculated budget components. The latter contains upscaling procedures to obtain results given in Table 6. Basic assumptions: (a) 1 d has 12 h light and 12 h dark periods; (b) sediment is covered by water (high tide) during half of each 12 h period; (c) high tides cover the entire mangrove area with water, while only creeks contain water at low tide; (d) abundance of pneumatophores (pneu) and crab burrows is equal to a crude median of all examined stations: 70 and 300 m^{-2}, respectively; (e) burrows contain on average 0.81 crab inhabitants (Skov et al. 2002); (f) the area of denuded flats, vegetated forest and creeks are specific for each mangrove environment. Input parameter: time = time of day; budget component: time = timing per day

	Acronym	Calculation/ upscaling	Unit	Time	Tidal level	Data location
Input parameter						
Sediment emission	Se	Measured	mmol m^{-2} h^{-1}	Light/dark	Low	Fig. 4, Tables 3 & 4
Sediment emission + *x* pneu	PSe	Measured	mmol m^{-2} h^{-1}	Light/dark	Low	Fig. 4
Sediment emission + 1 burrow	BSe	Measured	mmol m^{-2} h^{-1}	Light/dark	Low	Fig. 4
Pneumatophore emission	Pe	(PSe–Se) x^{-1}	mmol ind.$^{-1}$	Dark	Low	Table 2
Total burrow emission	TBe	BSe–Se	mmol bur.$^{-1}$	Dark	Low	Table 2
Crab emission	Ce	Measured	mmol ind.$^{-1}$	Dark	Low	Text
Burrow emission	Be	TBe–0.81Ce	mmol bur.$^{-1}$	Dark	Low	Text
Open water	We	Measured	mmol m^{-2} h^{-1}	Light/dark	Low/high	Figs. 6 & 7
Budget component						
Denuded sediment emission	DSe	Se × m^2 denuded area	mmol (12 h)$^{-1}$	6 h light + 6 h dark	Low tide	
Vegetated sediment emission	VSe	(Se + 70Pe + 300TBe) × m^2 vegetated area	mmol (12 h)$^{-1}$	6 h light + 6 h dark	Low tide	
Open water low tide emission	LWe	We × m^2 creek area	mmol (12 h)$^{-1}$	6 h light + 6 h dark	Low tide	
Open water high tide emission	HWe	We × m^2 total area	mmol (12 h)$^{-1}$	6 h light + 6 h dark	High tide	

The calculations show that emission of CO_2 and CH_4 is significantly larger during low tide than high tide primarily due to the facilitated emission via pneumatophores and burrows in air-exposed sediment (Table 6). The total CO_2 emission (TCE) at low tide is 10 (Mtoni) to 80 (Ras Dege) times higher than at high tide. The large vegetated area in Ras Dege emits 2 times more CO_2 than the sparse vegetation in Mtoni during low tide (Table 6). At this time, the open water is only responsible for 4 to 5% of the TCE. An opposite pattern with 6 times higher total and 4 times higher area-specific TCE in Mtoni than Ras Dege is evident during high tide, when open water is responsible for all CO_2 emissions (Table 6). The difference in area-specific TCE is probably a consequence of Mtoni exchanging water with Mzinga Creek, while Ras Dege is connected directly to the Indian Ocean. The former shallow and eutrophic semi-enclosed water body is continuously supersaturated in CO_2 and the latter is oceanic water much closer to equilibrium with the atmosphere.

Based on the global average estimate of net tree primary production and the cover of vegetated area, total net primary production (TNPP) in Mtoni and Ras Dege should be 115 ± 38 and $235 \pm 78 \times 10^3$ mol 12 h^{-1} (mean ± SE). While autotrophic and heterotrophic processes seem balanced in Mtoni during an avg. 12 h day:night low tide period (TNPP:TCE ~1), Ras Dege appears to be slightly, but not significantly, autotrophic (TNPP:TCE ~2). Conversely, both areas are highly autotrophic during an avg. 12 h day:night high tide period (TNPP:TCE ~10 at Mtoni and 150 at Ras Dege) indicating a net sequestration of carbon (Table 6). It must be emphasized here that CO_2 emissions from pneumatophores during low tide is included solely as a heterotrophic process, ignoring the fact that much of this contribution is derived from GPP. Furthermore, the small size of pneumatophores allowed by the chamber enclosures probably underestimates emissions from these structures. However, the TNPP:TCE ratios will not change dramatically if pneumatophores are ignored due to the large burrow contribution.

The estimated low emissions of CH_4 do not contribute significantly to the carbon gas balance. Thus, carbon emitted as CH_4 accounts for only 0.1 to 0.2% and 0.8 to 1.2% of the CO_2 contribution during low and high tide, respectively (Table 6). Alongi (2007) came to the same conclusion based on estimates from a variety of mangrove environments. The emission of CH_4 in Mtoni and Ras Dege showed the same overall temporal and spatial pattern as that for CO_2. However, the emissions were only 2 (Mtoni) and 10 (Ras Dege) times stronger at low than high tide. Besides an unrepresentative size of pneumatophores examined here, another possible source of error in the present CH_4 emission estimate is the missing contribution from ebullition flux of CH_4 (Barnes et al. 2006).

In conclusion, the densely vegetated and pristine Ras Dege mangrove forest appears to be an efficient sink of greenhouse carbon gases, while the extensive clear-cutting at Mtoni has apparently reduced its capacity to absorb atmospheric CO_2. Only strongly eutrophic mangrove environments tend to be sources of greenhouse gases primarily due to excessive CH_4 release (Sotomayor et al. 1994, Purvaja & Ramesh 2001). While eutrophication in Mtoni seemingly increases CH_4 emission from sediment and open water several fold (Table 6), the impact is apparently too weak to reverse the greenhouse carbon gas balance. If the harvest of trees for charcoal production continues, this environment may eventually turn into an unvegetated tidal flat and become a significant source of atmospheric carbon gases.

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Table 6. Total emission of CO_2 and CH_4 to the atmosphere in the Mtoni (3.05 km^2) and Ras Dege (1.90 km^2) mangrove areas during spring low tide and high tide. CO_2 values represent day and night means. The emissions are partitioned between denuded sediment areas (DSe, assumed devoid of pneumatophores and burrows), vegetated sediment areas with pneumatophores and burrows (VSe, assumed 70 pneu. m^{-2} and 300 bur. m^{-2}) and open water area (creeks at low tide, LWe, and the entire mangrove area during high tide, HWe). See Table 5 for further explanation. The rates were calculated for 12 h low tides and 12 h high tides d^{-1}. Error values are SE. na: not applicable

	Mtoni		Ras Dege	
	Low	High	Low	High
CO_2 (10^3 mol 12 h^{-1})				
Denuded	26.0 ± 9.7	na	3.9 ± 0.8	na
Vegetated	62.0 ± 11.1	na	119.4 ± 20.4	na
Open water	5.1 ± 2.1	9.8 ± 5.0	5.0 ± 1.2	1.6 ± 0.5
Total	93.1 ± 14.9	9.8 ± 5.0	128.3 ± 20.5	1.6 ± 0.5
Total (km^{-2})	30.5 ± 4.9	3.2 ± 1.6	67.5 ± 10.8	0.8 ± 0.3
CH_4 (mol 12 h^{-1})				
Denuded	51.3 ± 16.9	na	1.3 ± 2.6	na
Vegetated	70.7 ± 8.8	na	128.4 ± 21.9	na
Open water	61.5 ± 21.1	115.1 ± 13.0	6.7 ± 0.7	12.2 ± 1.4
Total	183.5 ± 28.4	115.1 ± 13.0	136.4 ± 22.1	12.2 ± 1.4
Total (km^{-2})	60.2 ± 9.3	37.7 ± 4.3	71.8 ± 11.6	6.4 ± 0.7

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